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BROOD PARASITISM BY BROWN-HEADED COWBIRDS ON BROWN THRASHERS: FREQUENCY AND RATES OF REJECTION[1]

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Abstract. Rates of brood parasitism by Brown-headed Cowbirds *Molothrus ater* on nests of Brown Thrashers *Toxostoma rufum* in south-central North Dakota ranged from 3% to 18% from 1984–1986. The average observed rate of parasitism, 12%, was higher than typically reported for Brown Thrashers. We conducted an experiment to determine if these high observed rates of parasitism were a result of unusually high rates of parasitism by cowbirds or unusually low rates of rejection by thrashers. Brown Thrashers removed 58% of experimentally-placed cowbird eggs. This rate of rejection is significantly lower than that previously reported for Brown Thrashers and for other rejector species. We conclude that thrashers in this area are parasitized at a high rate, but that low rates of rejection are at least partially responsible for the high observed rate of parasitism. These results suggest that the classification of Brown Thrashers as a rejector species should be reevaluated and that further study of geographic variation in cowbird host behavior and the role of learning in egg recognition is warranted.

Key words: brood parasite, egg recognition, egg rejection, host behavior, Molothrus ater, Toxostoma rufum.

INTRODUCTION

Brown-headed Cowbirds (*Molothrus ater*) parasitize a wide range of North American birds, sometimes so heavily that they have been implicated in population declines. As cowbirds expanded their range into eastern North America following extensive land clearing for agriculture and introduction of domestic livestock (Mayfield 1965), they began parasitizing species with which they previously had probably not come into contact. Several authors (Mayfield 1965, Robinson et al. 1993) have suggested that the lack of historical contact with a brood parasite makes eastern species of North American songbirds particularly vulnerable to parasitism. Common potential hosts that occurred within the historic range of cowbirds, such as Red-winged Blackbird (*Agelaius phoeniceus*), Common Grackle (*Quiscalus quiscula*), Yellow Warbler (*Dendroica petechia*), and American Robin (*Turdus migratorius*), respond to cowbirds by attacking adults, burying eggs in nest lining, and removing eggs (Friedmann 1963, Peer and Bollinger 1997). Because an evolutionary history of co-occurence with cowbirds could allow potential hosts to develop defenses, some authors have expected Great Plains populations of widespread species to have at least equal if not higher rates of defensive behavior as do their eastern counterparts (Mayfield 1965, Briskie et al. 1992).

From 1984–1986 we conducted an observational study of nesting Brown Thrashers (*Toxostoma rufum*) in Sioux County, North Dakota. During the course of this study, we observed Brown-headed Cowbird eggs or young in thrasher nests more frequently than we would have expected based upon published reports of experiments indicating that Brown Thrashers reject cowbird eggs at nearly 100% of nests (Rothstein 1975a) and on the relatively low levels of observed parasitism reported in published accounts (Friedmann 1963, Friedmann et al. 1977).

One explanation for a high observed rate of parasitism is that thrashers on our study area do not reject cowbird eggs. We tested the hypothesis that thrashers on this study area remove cowbird eggs at a lower rate than thrashers studied previously by conducting experiments to determine rate of rejection of cowbird eggs. This information allowed us to calculate a more ac-

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curate estimate of actual rates of parasitism on the study area as well as gave important insight into regional variation in behavior of cowbird hosts. We report the observed rates of cowbird parasitism on Brown Thrashers in our study area from 1984–1986 as well as data on the success of cowbirds with this host and the apparent effect of cowbird parasitism on thrasher reproductive success.

METHODS

The study area was located in Sioux County, between Cannonball and Solen, southwest of the confluence of the Cannonball and Missouri Rivers, in south-central North Dakota. This area is within the historic range of Brown-headed Cowbirds (Mayfield 1965). The native vegetation of this area is western mixed-grass prairie (Johnsgard 1979), which contains isolated patches of trees and shrubs along rivers, temporary creeks, and in other sites where the topography and soils allow woody vegetation to grow. In the last century, trees and shrubs have been planted as shelterbelts around farmsteads and fields. These artificial woody habitats support bird communities similar to those in native woody habitats (Haas 1997), although the behavior of birds in both of these patchy habitats may be different from that in more extensive riparian woodlands that occur in the area (Titus and Haas 1990). We conducted this work in over 50 shelterbelts and several woody draws. Cowbirds occurred and bred throughout the study area (Haas 1997).

In 1984–1986, we located 136 nests of Brown Thrashers by searching every tree and shrub. We returned to check the status of nests approximately once each week, more frequently when we could not estimate a hatching date, less frequently if the nest was at a remote site and the parents were not banded. We recorded nest contents and monitored the outcome of nests until they failed or the young fledged. We calculated observed rates of parasitism by dividing the number of nests containing cowbird eggs or young by the total number of nests found.

In 1986 we regularly monitored the status of 48 nests of banded Brown Thrashers. In this subset of nests, we banded all young that reached the age of 7 days (thrashers usually fledge at 9–11 days, Harrison 1978), and revisited the nest within a week to determine whether young had fledged from the nest or not. We report the number of young fledged as the number of young banded in nests known to have fledged subsequently.

From 1990–1996, we placed cowbird eggs in 64 thrasher nests and monitored these nests to see if eggs would be accepted or removed. In 1990 and 1991 we considered a pair to have accepted an egg if it remained in the nest for 3 days (Burhans and Freeman 1997). Although almost all egg rejection did occur within 3 days (see Results), from 1992–1996 we used a more restrictive criterion of acceptance, retention for 5 days, in order to compare our results to studies with more conservative standards suggested by Rothstein (1975a; pers. comm.).

We attempted to place cowbird eggs into the nests of laying thrashers, but often we found nests after the clutch was complete. We placed cowbird eggs into nests in both stages, but present the results for laying and incubating thrashers separately, because most natural cowbird parasitism occurs during the laying stage (Friedmann 1929). We placed cowbird eggs in more than 64 thrasher nests, but because many of these nests failed or had hatchlings before the 5-day period was over we could not include them unless rejection occurred prior to nest failure. To consider an egg accepted it had to remain in the nest for 5 days, but to consider an egg rejected it could disappear any time within 5 days. Therefore, our estimate of rejection rate could be biased in favor of rejection (Rothstein 1982). To eliminate this bias, we also present results only for those nests that survived for at least 5 days after the cowbird egg was introduced, even if rejection occurred in the first day.

We used chi-square tests to compare the fledging success of parasitized and nonparasitized nests and the rates of rejection from nests experimentally parasitized at different stages. We used a significance level of $P < 0.05$. Values reported are means $\pm$ SD. We compared the number of young fledging from parasitized and unparasitized nests using a two-tailed Mann-Whitney U-test.

RESULTS

The observed rate of parasitism between 1984–1986 averaged 12%, but varied greatly among years (Table 1). Observed rates of parasitism will be lower than actual rates of parasitism if parasitic eggs are removed before the nest is checked. Because the mean number of days that elapsed between each nest check decreased

TABLE 1. Observed rate of Brown-headed Cowbird parasitism on Brown Thrashers, rate at which cowbird eggs disappeared from nests, and the number of cowbird fledglings produced per parasitized nest and per cowbird egg, 1984–1986, in Sioux County, North Dakota.

Year	Parasitism rate % (*n*)	Disappearance of BHCO eggs[a]	BHCO young fledged nest^{-1}	BHCO young fledged egg^{-1}
1984	3 (32)	0/1 (0/1)	0/1	0/1
1985	10 (50)	2/5 (2/5)	2/5	2/5
1986	18 (54)	3/10 (4/11)	1/10	2/13
Total	12 (136)	5/16 (6/17)	3/16	4/19

[a] Top line shows number of nests from which cowbird eggs disappeared, over total number of nests found containing cowbird eggs. Second line (in parentheses) shows number of cowbird eggs that disappeared, over the total number of cowbird eggs found.

across years, it is not clear whether the variation we observed in rates of parasitism reflects natural levels of variability or whether it is partially an artifact of increasing sampling effort. The mean number of days between nest checks (including nests in other parts of the study area) was 6.7 ± 3.1 (n = 44) in 1984, 5.0 ± 2.9 (n = 81) in 1985, and 5.8 ± 3.2 (n = 67) in 1986. Although there was variation among years ($F_{2,190}$ = 4.49, P = 0.012), there was no significant difference in number of days between nest checks between 1984 and 1986 (t = 1.54, P = 0.13), the years when the biggest difference in levels of observed parasitism occurred.

Cowbird eggs disappeared from 5 of the 16 (33%) nests parasitized between 1984–1986 (Table 1). Cowbird young fledged from 3 of 16 (19%) parasitized nests and from 4 of 19 (21%) cowbird eggs found (Table 1). Parasitized nests failed to produce cowbird young when they were depredated (n = 3), when they were deserted (n = 4), when cowbird eggs disappeared (n = 5), or when cowbird eggs failed to hatch (n = 1).

To determine whether cowbird parasitism affected the probability of a thrasher nest producing any young that survived to fledging, we compared the proportion of parasitized and nonparasitized nests producing young. Seventy-four of 120 (62%) nonparasitized nests produced at least one fledgling, whereas 7 of 16 (44%) parasitized nests produced at least one fledgling. These proportions were not significantly different (χ^2_1 = 1.9, $P > 0.10$). In 1986, a similar number of thrasher young fledged per nest from unparasitized (2.2 ± 1.7, n = 40) and from parasitized (1.5 ± 1.7, n = 8) nests (Mann-Whitney U = 1,021.5, $P > 0.25$).

In experimentally-parasitized nests, thrashers removed 37 of 64 (58%) cowbird eggs (Table 2). Restricting the results only to those nests experimentally parasitized during the laying period and surviving 5 days and to those cowbird eggs being retained in the nest for 5 days (i.e., accepted), thrashers removed 10 of 15 (67%) cowbird eggs (Table 2). There was no significant difference in rates of rejection between nests experimentally parasitized during the laying and incubation stages (χ^2_1 = 0.9, $P > 0.25$ for all 1992–1996 nests; χ^2_1 = 1.0, $P > 0.25$ for 1992–

TABLE 2. Rate of rejection by Brown Thrashers of Brown-headed Cowbird eggs placed experimentally in nests in Sioux County, North Dakota, 1990–1996. Nests were experimentally parasitized during the laying or incubation stage. Percentages indicate frequency of removal of experimentally-placed eggs within 5 days (1992–1996) or within 3–5 days (1990–1996). The top row shows data from only those nests that survived 5 days after experimental parasitism (see text for explanation). The number of Brown Thrasher nests in which Brown-headed Cowbird eggs were experimentally placed is shown in parentheses.

Data set	Laying % (*n*)	Incubating % (*n*)	Combined % (*n*)
1992–1996 nests, surviving 5 days	67 (15)	50 (22)	57 (37)
All 1992–1996 nests	71 (17)	56 (25)	62 (42)
All 1990–1996 nests	62 (24)	55 (40)	58 (64)

TABLE 3. Published rates of cowbird parasitism and rates of rejection of experimentally-placed cowbird eggs in nests of Brown Thrashers and other mimids.

Species	% nest parasitized (range)	Average % nests parasitized (*n*)	Citations[b]	Average % eggs rejected (*n*)	Citations[b]
Brown Thrasher *Toxostoma rufum*	0–37.5	2.9 (2,177)	1–6	96.3 (26)	13
Long-billed Thrasher *T. longirostre*[a]	0	0 (62)	5	—	
Bendire's Thrasher *T. bendirei*[a]	0	0 (88)	5	—	
Curve-billed Thrasher *T. curvirostre*[a]	0	0 (228)	5	—	
California Thrasher *T. redivivum*	0	0 (245)	5	0 (unknown)	8
LeConte's Thrasher *T. lecontei*	0	0 (140)	5	0 (unknown)	8
Crissal Thrasher *T. dorsale*	0	0 (98)	5, 7	100 (9)	7
Gray Catbird *Dumetella carolinensis*	0.3–44.0	2.5 (1,178)[c]	5, 8–10	94.3 (53)	13
Sage Thrasher *Oreoscoptes montanus*[a]	0	0 (21)	8	90.0 (10)	8
Northern Mockingbird *Mimus polyglottos*	0	0 (48)	12	45.8 (~24)	12, 13

[a] Friedmann et al. (1977) report single records of cowbird parasitism of these species.
[b] References cited: (1) Elliott 1978, (2) Partin 1977, (3) Graber et al. 1970, (4) Hill 1976, (5) Friedmann et al. 1977, (6) Cavitt 1998, (7) Finch 1982, (8) Rich and Rothstein 1985, (9) Scott 1977, (10) Darley, pers. comm. in Scott 1977, (11) Nickell 1958, (12) Mason, pers. comm. in Friedmann and Kiff 1985, (13) Rothstein 1975a.
[c] Did not include Nickell's (1958) figures (few out of 3,000 nests) in calculation of average, but did include his figure of 0.3% as lowest in range. Next lowest figure was 1.1% from Cornell Nest Record Card Program reported in Friedmann et al. 1977.

1996 nests surviving 5 days). Most eggs were removed within 3 days of being placed in the nest. At 20 nests that were checked within 3 days and again at 5 days after egg introduction, 15 of 19 cowbird eggs were rejected in 1 or 2 days and 19 of 20 within 3 days. There was no significant difference in rates of rejection as measured in 1990–1991 (3-day retention criterion) and 1992–1996 (5-day retention criterion) (11/22 versus 26/42, $\chi^2_1 = 0.8$, $P > 0.25$).

DISCUSSION

Observed rates of cowbird parasitism and fledging success in Brown Thrasher nests were higher in this study than rates typically reported elsewhere (Table 3) and in the range of what Mayfield (1965) considered a moderate (10–30%) frequency of parasitism. Given that we did not find all nests during laying, did not check them daily, and did not check in early morning, our 12% mean observed rate of parasitism seems unusually high. Rates of cowbird parasitism are known to increase in areas of high density of cowbirds (McGeen 1972). North Dakota rangelands have higher densities of cowbirds during the breeding season than any other region in the U.S. (Sauer et al. 1997).

Although the number of days between nest checks did differ among years of the study, it seems unlikely that this could have caused most of the annual variation in observed rates of parasitism. This variation also might have been a result of factors such as annual variation in the density of cowbirds or availability of alternate hosts. Although we do not report data on rates of parasitism in the years during which the experiment was conducted, we saw no major trend over this period of time (unpubl. data).

If thrashers rejected 67% of all cowbird eggs placed in their nests, then the observed rates of parasitism obtained by looking infrequently in the nests of thrashers would be substantially lower than actual rates of parasitism. If the nests found containing cowbird eggs represented only 33% of all nests that were parasitized, the actual rate of parasitism would be 36%. These calculations assume that all the cowbird eggs we found in nests had been accepted by thrashers. We know that some of the cowbird eggs we detected were subsequently missing, possibly removed by the thrashers. It is not clear how many of the other eggs might have been removed by thrashers had the nests survived. The true rate of parasitism probably falls somewhere between these estimates, averaging between 12–36% of nests on the study area.

This relatively high level of parasitism did not have a major effect on reproductive success of thrashers. Parasitized nests successfully produced young. Parasitized nests fledged a mean of 0.7 and a median of 2 fewer nestlings per nest than unparasitized nests, but the number of young fledged per nest was not significantly lower in parasitized nests. Our power to detect differences was probably quite low, given the small sample sizes and large variance. However, as reported by Elliott (1978) for the Eastern Meadowlark (*Sturnella magna*) and by Ortega

and Cruz (1988) for Red-winged (*Agelaius phoeniceus*) and Yellow-headed (*Xanthocephalus xanthocephalus*) Blackbirds, the cost for a large-bodied host in terms of mean number of host fledglings produced per nest is probably not greater than one.

The only other study reporting the response of Brown Thrashers to experimentally-introduced Brown-headed Cowbird eggs combined the results of experiments conducted in four locations, Connecticut, Nebraska, Michigan, and Manitoba (Rothstein 1975a, 1975b). In those studies, cowbird eggs were rejected at 25 of 26 (96%) nests, a rate significantly ($\chi^2_1 = 6.6$, $P < 0.03$) higher than our 67% rate in North Dakota. The exact locations of these experiments (and number of nests tested at each location) were not reported. Connecticut and Michigan are outside the historic range of cowbirds, but all of Nebraska and some of Manitoba are within it (Mayfield 1965). Published reports of rejection behavior in other mimids are summarized in Table 3.

Rothstein (1975a) classified all potential hosts into acceptor and rejector species. In his study, acceptor species ejected or built nests over less than 42% of cowbird eggs, whereas rejector species ejected or built over more than 88% of cowbird eggs placed in their nests. The 67% rate of rejection on our study site puts this population of thrashers between acceptor and rejector status.

This work provides an additional example that host response to cowbird parasitism varies significantly among populations of host species. Thrashers in this Great Plains population were more likely to accept cowbird eggs than were thrashers from other sites, including a population in the east. Rothstein (1974) also found a slightly lower rate of rejection by Gray Catbirds (*Dumetella carolinensis*) in western North America (rejected at 22/25 nests in Manitoba and Nebraska) than in eastern North America (rejected at 30/30 nests in Connecticut, Maryland, and Michigan).

Cowbird eggs in this region may resemble thrasher eggs more closely than they do in other areas. Both species have somewhat similarly-sized eggs with brown speckles on light backgrounds (Friedmann et al. 1977). Mean length and width measurements of 15 thrasher eggs (from 7 nests) and 8 cowbird eggs (from 5 nests, none of which were Brown Thrashers') in this study were 25.8 x 19.9 mm for thrashers and 22.4 x 16.8 mm for cowbirds. There was some overlap in length, which ranged from 23.5–27.8 mm for thrashers and 21.4–24.0 mm for cowbirds, but not in width, which ranged from 18.5–21.1 for thrashers and 16.3–17.6 mm for cowbirds. Some thrashers that could distinguish cowbird eggs apparently could not distinguish thrasher eggs experimentally introduced from other thrasher nests. Thrashers accepted 9/9 conspecific eggs (6 tests lasted 3 days, 3 tests lasted 5 days) we placed in nests during the incubation stage, even when the introduced egg easily could be recognized by human observers (e.g., an egg with a distinctly green background color introduced into a nest containing eggs with tan background color). At seven of these same nests, cowbird eggs were rejected (no cowbird eggs were placed in the other two nests).

Another possible explanation for the lower rates of rejection is individual learning of natural egg variation. Females of host species may learn to recognize their own eggs by examining their first clutch (Rothstein 1974, Lotem et al. 1995). In regions where rates of cowbird parasitism are extremely high, the percentage of host individuals whose first clutch receives a cowbird egg also would be high. These individuals then would learn to recognize a cowbird egg as their own, and subsequently accept cowbird eggs. In this study, the age and identity of acceptor and rejector individuals were unknown, so it is not possible to differentiate between these two explanations.

These results suggest that a strict categorization of potential cowbird hosts as acceptor or rejector species may need to be re-evaluated. Like hosts of the Common Cuckoo (*Cuculus canorus*) (Rothstein 1990), Brown Thrashers appear to show an intermediate response to parasitism. This may be true of Northern Mockingbirds (*Mimus polyglottos*) as well (Table 3). More attention needs to be paid to geographic (Cruz and Wiley 1989, Briskie et al. 1992) and even local (Knapton 1979) variation in host behavior. We currently are attempting to document individual consistency in rejection behavior, but such work might be more effectively carried out in an aviary or on a host in which only females attend the nest during laying and incubation and in which multiple-brooding within a season is more frequent.

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