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Brian D. Peer, *Eastern Illinois University*

Eric K. Bollinger, *Eastern Illinois University*



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EXPLANATIONS FOR THE INFREQUENT COWBIRD PARASITISM ON COMMON GRACKLES¹

BRIAN D. PEER² AND ERIC K. BOLLINGER

Department of Zoology, Eastern Illinois University, Charleston, IL 61920

Abstract. We determined the factors responsible for the lack of parasitism on Common Grackles (*Quiscalus quiscula*) by Brown-headed Cowbirds (*Molothrus ater*). We found no evidence of parasitism on the 401 grackle nests we monitored in east-central Illinois. By the time cowbirds began laying eggs, 88.5% of all grackle nests were beyond the point of successful parasitism. Grackles rejected cowbird eggs more frequently during the prelaying stage of the nesting cycle (38.2%) compared to later stages (12.3%). Thirty-three cowbird eggs and nestlings were cross-fostered into grackle nests. Data were collected on 15 cowbird nestlings, of which three fledged. The cross-fostered cowbird eggs that did not hatch appeared to have been incubated ineffectively. These eggs were in clutches that contained four to six eggs, whereas the cowbird eggs that hatched were in clutches of three eggs or less. Grackles also responded more aggressively toward female cowbird models than to Fox Sparrow (*Passerella iliaca*) models in five of seven response categories. Cowbirds avoid parasitizing grackles even though the opportunity existed. Nest abandonment and infestation of grackle nests with ectoparasitic mites may decrease the suitability of grackles as hosts; however the primary reason for the infrequent cowbird parasitism on grackles appears to be past rejection behavior. Grackles likely rejected cowbird eggs at a higher frequency in the past and as a consequence grackles were avoided by cowbirds. Rejection apparently decreased in the absence of parasitism due to the high degree of intraclutch egg variability exhibited by grackles which would increase the chances of them mistakenly rejecting their own discordant eggs.

Key words: brood parasitism, Brown-headed Cowbird, Common Grackle, egg rejection, host selection, *Molothrus ater*, *Quiscalus quiscula*.

INTRODUCTION

Avian brood parasitism is an uncommon reproductive strategy in which females lay their eggs in the nests of other birds thereby relinquishing further parental care to the host species. To maximize their reproductive effort, brood parasites must locate compatible hosts with life history traits similar to their own. Thus, the breeding seasons of parasite and host must overlap (Briskie et al. 1990, Ortega and Cruz 1991) and hosts should not possess any significant anti-parasite adaptations such as rejection of the parasitic egg (Rothstein 1975a).

Once a parasite's egg is in a host's nest it must be incubated effectively to ensure hatching (Friedmann 1929, Hofslund 1957, Rothstein 1975a). If the host's eggs are considerably larger than the parasite's or if the clutch size is excessively large, then the chances of the para-

site's egg hatching will decrease (Wiley 1985, Peer and Bollinger, in press a). After the parasitic egg hatches, the nestling requires an adequate diet (Friedmann 1929, Middleton 1991) and parental care (Friedmann 1929, Mills 1988). Finally, host nestlings must have growth rates similar to the parasite's because if they grow too quickly the parasitic nestling will be at a disadvantage (Friedmann 1963, Fraga 1985).

The Brown-headed Cowbird (*Molothrus ater*) is the only obligate brood parasite that is widespread in North America. It has parasitized at least 220 species of birds, 144 of which have successfully reared cowbirds (Friedmann and Kiff 1985). The Common Grackle (*Quiscalus quiscula*) is an infrequent host of the cowbird, with only 20 documented cases of parasitism (Peer and Bollinger, in press b), and Common Grackles have never been known to fledge cowbirds (Friedmann and Kiff 1985). This is unusual because the Common Grackle is widespread and abundant, and ostensibly both grackles and cowbirds have had overlapping ranges and habitat requirements throughout their evo-

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² Present address: Department of Zoology, University of Manitoba, Winnipeg, MB R3T 2N2, Canada.

lutionary histories (Mayfield 1965, Fretwell 1973). Furthermore, Common Grackles build large, conspicuous nests and usually accept cowbird eggs (Rothstein 1975a, Peer 1993). Friedmann et al. (1977:39) made the following statement regarding this enigmatic relationship:

"The reason for the lack of parasitism [on grackles] is not clearly known. The cowbird may avoid parasitizing species as large as the grackle, but the American Robin and the Brown Thrasher are nearly as large and have been found to be parasitized many more times than the grackle, even though they are rejecter species. Perhaps the grackle's colonial nesting may be a factor. It may be difficult for cowbirds to escape detection when entering grackle colonies. But many grackles do not nest in colonies, in which case other factors may be responsible for the low incidence of parasitism."

In this study we attempted to determine the factors responsible for the lack of cowbird parasitism on Common Grackles by (1) determining the synchrony of grackle and cowbird breeding seasons, (2) placing artificial cowbird eggs into grackle nests to determine whether there has been a change in the grackles' egg-rejection frequency since Rothstein's (1975a) original study, (3) cross-fostering cowbird eggs and nestlings into grackle nests to determine if cowbirds could fledge from grackle nests, (4) testing if coloniality is an effective deterrent against brood parasitism by comparing the responses of colonial- and noncolonial-nesting grackles to models of female cowbirds, and (5) observing if noncolonial grackles are parasitized more frequently than colonial grackles.

MATERIALS AND METHODS

STUDY SITE

We monitored grackle nests at 10 sites throughout Coles County, Illinois during the 1992 and 1993 breeding seasons. We collected most of our data at four sites, including two cemeteries and two Christmas tree farms. The cemeteries contained scattered rows of northern white cedar (*Thuja occidentalis*), 2–3 m in height. The Christmas tree farms had evenly distributed rows of scotch pine (*Pinus sylvestris*), 2–2.5 m in height. The remaining sites consisted of several roadside thickets, a small nature preserve,

a lake edge, and a residential park. Each site was bordered on at least one side by agricultural fields.

BREEDING SEASON

We recorded the dates of initiation of grackle clutches and egg-laying dates of cowbird eggs found in 1992 and 1993. Only eggs whose laying dates could be determined by direct observation were used in this study.

ARTIFICIAL PARASITISM

Artificial cowbird eggs were made of wood, painted with waterbased acrylic paints, and coated with a clear acrylic sealer. Their dimensions were 23.91 × 16.67 mm and they weighed 2.5 g. Real cowbird eggs average 21.45 × 16.42 mm (Bent 1958) and weigh 3.17 g (Ankney and Johnson 1985). Thus, we feel that our eggs were an effective mimic of real cowbird eggs.

In 1992, we attempted to simulate natural cowbird parasitism by replacing a single grackle egg with an artificial cowbird egg, or genuine cowbird eggs when available. Although there is variation in the frequency of host-egg removal by cowbirds (Sealy 1992), we followed the same protocol used by Rothstein (1975a). We also artificially parasitized grackle nests with real grackle eggs collected from nonexperimental grackle nests during the 1993 season. These manipulations were performed to determine whether rejection behavior was in response to intra- rather than interspecific parasitism.

We categorized each nest into one of three stages of the nesting cycle: (1) Prelaying, nest construction appeared to be complete but no eggs had been laid, (2) Laying, eggs were being laid, and (3) Incubation, the clutch was complete and being incubated. Grackles often begin incubation prior to clutch completion (Maxwell and Putnam 1972), however we did not classify nests as in the incubation stage until laying was completed. We categorized nests as colonial or noncolonial based on the distance between nearby grackle nests. Colonies consisted of at least three nests within 10 m of each other. Colonial-nesting grackles at our sites formed very cohesive groups and responded to the alarm calls of conspecifics from distances of at least 10 m (pers. observ.).

We added one artificial cowbird egg to each nest between 06:00 and 12:00 CDT because cowbirds typically confine egg-laying and host-

searching activities to the morning hours (Rothstein et al. 1984, Neudorf and Sealy 1994). Nests were inspected every 1–2 days to record host response, and nests were parasitized during the entirety of the breeding season. Responses were considered “rejections” if the artificial egg was ejected from the nest, pecked, buried under nest lining, or if the nest was deserted. We considered a nest deserted if it was abandoned within five days of egg replacement (Rothstein 1975a).

CROSS-FOSTERING COWBIRD EGGS AND NESTLINGS

Cowbird eggs and nestlings were collected from other species' nests in and near our study sites. We replaced single grackle eggs with one and in some cases two cowbird eggs. All transferred cowbird eggs had been laid within 1–2 days of the time the grackle eggs had been laid. In some cases we cross-fostered cowbird nestlings into nests with grackle nestlings. In all but one of these cases the nestlings were the same age, the only exception being a cowbird nestling that was a day younger than its two grackle nestmates.

Nestlings were weighed every 1–2 days to the nearest gram using 50-g and 100-g Pesola scales. We measured gape (width of bill at loreal feathering), exposed culmen, and tarsometatarsus length to the nearest 0.01 mm with calipers according to Baldwin et al. (1931). Grackle and cowbird egg lengths and widths were measured to the nearest 0.01 mm.

RESPONSE TO COWBIRD MODELS

The aggressive response of grackles to cowbirds was tested in 1992 using taxidermically prepared models of female Brown-headed Cowbirds. Mounts of Fox Sparrows (*Passerella iliaca*) were used as controls. Although Fox Sparrows do not breed in Coles County, they are a common spring migrant throughout the study area during the early portion of the grackle breeding season. Mounts were prepared in the same way and mounted in upright positions.

Models were placed approximately 0.5 m from a grackle nest and at the same level as the nest. The Fox Sparrow model was presented first in one half of the trials, and the cowbird model was presented first in the other half of the trials. Each model was presented for 5 min with a 10 min interval before the presentation

of the second model. Following the presentation of each cowbird model a grackle egg was replaced with an artificial cowbird egg. No nests were tested with the models more than once.

Behavioral responses were recorded by the same individual (BDP) in all trials and included the following: alarm calls, fly-by investigation, nest attentive (bird situated between the model and the nest), hovering near the model, individual attack, mob by ≥ 2 individuals, and physically striking the model. Once a model was physically struck the trial ended to preserve the model.

STATISTICAL ANALYSES

We used chi-square tests to analyze the egg rejection data. Growth rates of grackles and cowbirds were compared from days 2 through 8. Growth was linear during this period, therefore linear regression was used to determine the slope for each individual bird. To compare measurements of grackles and cowbirds, we used an approximate *t*-test that did not assume equal variances. In this test, the degrees of freedom are determined by approximation and are conservative (i.e., fewer dfs) relative to *t*-tests that assume the variances are equal (Ryan et al. 1976). Both standard deviations for linear measurements and standard errors for means were used as measures of variance. We used $P < 0.05$ as our level of accepted significance.

RESULTS

BREEDING SEASON PHENOLOGY

The first grackle eggs were laid on 23 March 1992 and 1 April 1993. Clutch initiation for the two years combined peaked from 12 to 25 April, when 215 of 401 (53.6%) clutches were initiated (Fig. 1). The first cowbird eggs were found on 16 May 1992 and 17 May 1993 in the nests of other hosts. Cowbird egg laying peaked from 24 May to 6 June, encompassing 28 of 45 (62.2%) eggs found (Fig. 1). By the time the first cowbird egg was laid on our study area in both years, 355 of 401 (88.5%) grackle nests were in the incubation stage or later and thus beyond the point of being successfully parasitized.

FREQUENCY OF COWBIRD PARASITISM

None of the 401 grackle nests that we monitored was naturally parasitized (Table 1). Northern Cardinals (*Cardinalis cardinalis*), Song Spar-

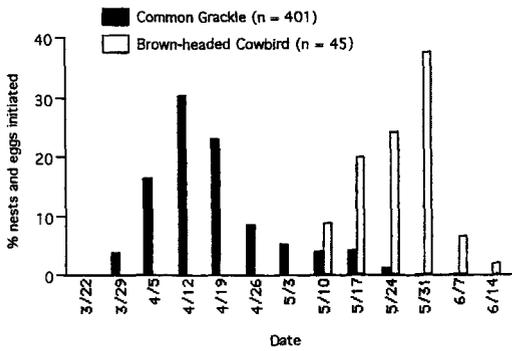


FIGURE 1. Percentages of Common Grackle nests initiated and Brown-headed Cowbird eggs laid in Coles County, Illinois during the 1992–1993 breeding seasons.

rows (*Melospiza melodia*), and House Finches (*Carpodacus mexicanus*) were the most commonly parasitized hosts (Table 1), with 85.7% of cardinal nests parasitized, 60.0% of Song Sparrow nests, and 58.3% of House Finch nests.

EGG REJECTION

Cowbird eggs were rejected at 32 of 188 (17.0%) experimentally parasitized nests. Rothstein (1975a) recorded eight rejections from 70 nests (11.4%). However, as Rothstein performed no egg additions during the prelaying stage, a direct comparison of our data without prelaying trials yields a similar rejection frequency of 12.3% (19 of 154 nests; $\chi^2_1 = 0.02$, $P > 0.75$). Most rejections ($n = 32$) in our study were by egg ejection (59.4%), followed by de-

sertion (21.9%), pecking the cowbird egg (12.5%), and burial (6.2%).

Rejections occurred significantly more often during the prelaying stage (13 of 34 nests, 38.2%) than later in the nesting cycle (19 of 154, 12.3%; $\chi^2_1 = 13.9$, $P < 0.001$). There were no significant differences in egg rejection frequencies between nests presented with cowbird models compared to those without models during the prelaying ($\chi^2_1 = 3.1$, $P > 0.05$) or later stages ($\chi^2_1 = 0.09$, $P > 0.75$). Real cowbird eggs were rejected at similar frequencies to artificial cowbird eggs (21.0%, 3 of 14 nests, $\chi^2_1 = 0.18$, $P > 0.50$), and all 10 grackle eggs introduced into grackle nests were accepted.

CROSS-FOSTERING EXPERIMENTS

Thirty-three cowbird eggs and nestlings were cross-fostered into grackle nests. Data were collected on 15 nestlings, of which 10 hatched from transferred eggs and five were nestling transfers. In no instance did two cowbird eggs hatch in a single nest. Three cowbirds fledged. One of the cowbirds had no competitors, and the other two cowbirds hatched two and four days before any of the grackles. In three cases, cowbird nestlings died 2–3 days after hatching despite being the sole occupant of the nest. The other nine cowbird nestlings died in the presence of grackle nestmates an average of 2.1 days after hatching.

Grackle hatchlings weighed more than twice as much as cowbird hatchlings (t -test, $P < 0.001$; Table 2). The differences between

TABLE 1. Frequency of Brown-headed Cowbird parasitism on hosts in Coles County, IL from 1992–1993.

Species	Number of cowbird eggs per nest				
	0	1	2	3	≥4
Mourning Dove (<i>Zenaida macroura</i>)	102	—	—	—	—
Blue Jay (<i>Cyanocitta cristata</i>)	1	—	—	—	—
Brown Thrasher (<i>Toxostoma rufum</i>)	4	—	—	—	—
Gray Catbird (<i>Dumetella carolinensis</i>)	8	—	—	—	—
American Robin (<i>Turdus migratorius</i>)	14	—	—	—	—
Wood Thrush (<i>Hylocichla mustelina</i>)	2	—	—	—	—
Red-eyed Vireo (<i>Vireo olivaceus</i>)	—	1	—	—	—
Yellow Warbler (<i>Dendroica petechia</i>)	1	—	—	—	—
Common Yellowthroat (<i>Geothlypis trichas</i>)	1	—	—	—	—
Red-winged Blackbird (<i>Agelaius phoeniceus</i>)	339	5	—	—	—
Common Grackle (<i>Quiscalus quiscula</i>)	401	—	—	—	—
Baltimore Oriole (<i>Icterus galbula</i>)	1	—	—	—	—
Northern Cardinal (<i>Cardinalis cardinalis</i>)	2	6	4	2	—
House Finch (<i>Carpodacus mexicanus</i>)	5	5	2	—	—
Chipping Sparrow (<i>Spizella passerina</i>)	2	1	—	—	—
Song Sparrow (<i>Melospiza melodia</i>)	2	—	—	1	2

TABLE 2. Hatching values (mean \pm SD) for mass, gape, culmen, and tarsometatarsus for Common Grackles ($n = 42$) and Brown-headed Cowbirds ($n = 8$) during the 1992–1993 breeding seasons.^a

Measurement	Grackle	Cowbird	t^b	P	df
Mass (g)	5.57 \pm 0.86	2.53 \pm 0.65	11.5	<0.001	12
Gape (mm)	11.33 \pm 1.00	8.1 \pm 0.92	9.1	<0.001	10
Culmen (mm)	6.38 \pm 0.73	4.56 \pm 0.53	8.3	<0.001	12
Tarsometatarsus (mm)	8.02 \pm 0.85	5.23 \pm 1.04	4.4	<0.05	2

^a Tarsometatarsus lengths were recorded only in 1993. For grackles $n = 20$ and for cowbirds $n = 3$.
^b Two-tailed t -test.

grackle and cowbird gape width, culmen length, and tarsometatarsus length also were significantly different at hatching (Table 2). Among individuals that fledged, growth rates of grackles also were significantly greater than those of the cowbirds (t -test, $t_3 = 4.21$, $P < 0.025$). Cowbirds required 2.5 days to reach the hatching values of grackles for weight, gape, and tarsometatarsus, and 3.5 days for the culmen (Fig. 2).

EGG SIZE

The average size of grackle eggs was $28.76 \pm 1.4 \times 21.36 \pm 0.8$ mm ($n = 131$), and cowbird eggs averaged $20.38 \pm 1.2 \times 16.05 \pm 0.6$ mm ($n = 19$). Of the eight cowbird eggs that did not hatch, four appeared to be ineffectively incubated (the remaining cowbird eggs that did not hatch were depredated, rejected, or infertile). These eggs were in clutches containing four to six eggs, whereas

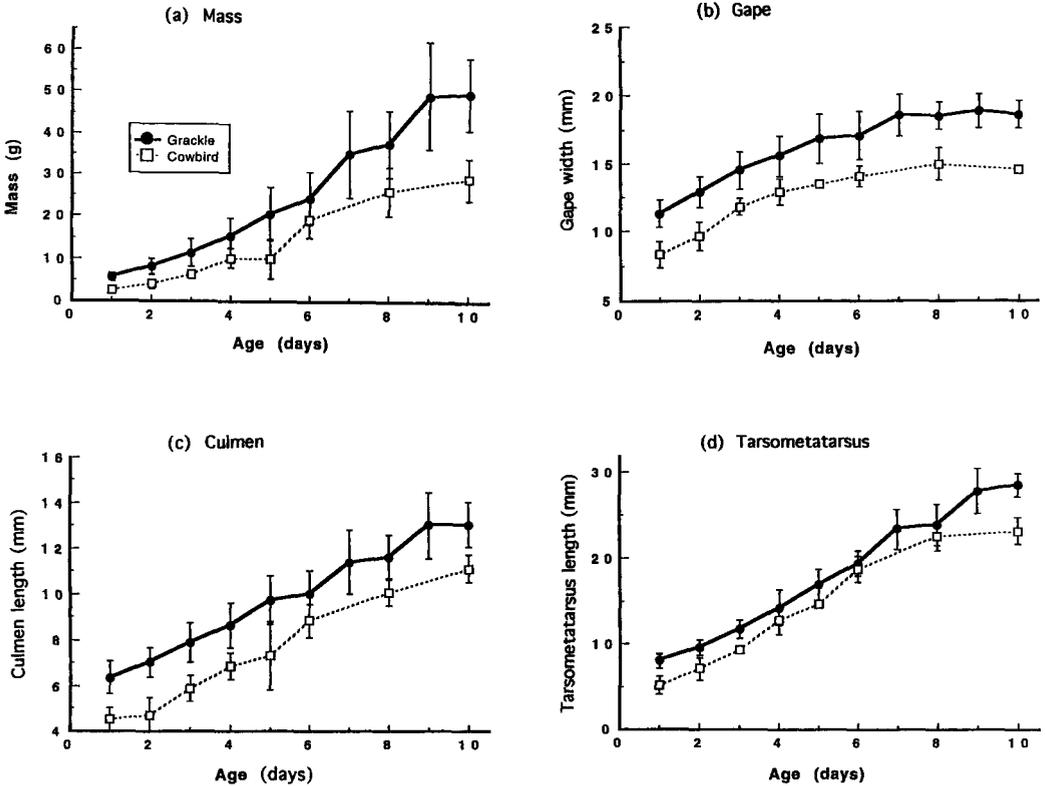


FIGURE 2. Relationship between age and (a) mass (g), (b) gape width (mm), (c) culmen length (mm), and (d) tarsometatarsus length (mm) for nestling Common Grackles and Brown-headed Cowbirds for the first 10 days after hatching (mean \pm SD).

TABLE 3. Responses of Common Grackles to model female Brown-headed Cowbirds and Fox Sparrows presented near the nest ($n = 105$ nests). Values indicated are the mean number of seconds (\pm SE) given per 5 min trial.

Response	Cowbird	Sparrow	P^a
Alarm calls	10.5 \pm 0.84	4.8 \pm 0.74	0.047
Fly-by investigation	23.1 \pm 1.73	5.3 \pm 0.62	0.001
Nest-attentive	58.1 \pm 3.78	26.3 \pm 2.11	0.001
Hover	25.2 \pm 2.13	14.4 \pm 3.29	0.007
Individual attack	1.9 \pm 0.23	2.9 \pm 0.72	ns
Mob by ≥ 2 individuals	18.0 \pm 1.54	11.9 \pm 1.64	ns
Physical contact	29.4 \pm 1.91	7.5 \pm 1.48	0.005

^a Results of Wilcoxon signed-ranks test between models.

the eggs that did hatch were contained in clutches of three eggs or less.

RESPONSE TO COWBIRD MODELS

Grackles responded more aggressively toward the cowbird models than to the Fox Sparrow models in five of the seven behavioral categories ($n = 105$ nests; Table 3). There were no significant differences in aggressive response to cowbird models between colonial- and noncolonial-nesting grackles.

DISCUSSION

BREEDING SEASON PHENOLOGY

The early initiation of the grackle breeding season may contribute to the lack of parasitism, as only 11.5% ($n = 46$) of all grackle nests were available for parasitism once cowbirds began laying. This is similar to other species where the absence or low level of parasitism has been linked to mismatched breeding seasons with cowbirds (Briskie et al. 1990, Ortega and Cruz 1991). Yet, there were more grackle nests available for parasitism compared to any of the other hosts at our study sites, with the exception of the Red-winged Blackbird (*Agelaius phoeniceus*; see Table 1). Instead of parasitizing grackles, cowbirds parasitized individual nests of other hosts repeatedly (such as Song Sparrows; Table 1). This, in conjunction with the relatively few cases of parasitism on grackles that have been recorded (Peer and Bollinger, in press b), clearly indicates that cowbirds avoid parasitizing grackles.

Another factor that may contribute to the avoidance of grackles is that they sometimes abandoned nests later in the breeding season. In May of 1992, grackles abandoned their nests at three of our study sites. This behavior occurs frequently in grackles (Peer and Bollinger, in

press b) and other icterines (Orlans 1961, Ortega and Cruz 1991), which presumably makes them less reliable hosts.

EGG REJECTION

Rothstein (1975b) classified the grackle as an accepter species that is rarely parasitized. Relatively few grackle nests were available for parasitism over the course of our study and those that were available were not parasitized, indicating that there is no current selection pressure on grackles to reject parasitic eggs. This is supported by the fact that there has been no change in the rejection frequency of grackles since Rothstein's (1975a) study.

Thus, the following question arises: why does the rejecter genotype exist at a low level within grackle populations? Species that have not been subjected to brood parasitism, whether it be intra- or interspecific, generally do not exhibit egg rejection behavior as it has no adaptive value in the absence of parasitism (Rothstein 1982b, 1990). The only apparent exceptions are ground-nesting seabirds that breed in dense colonies and risk confusing their eggs with others (Tschanz 1959, Birkhead 1978).

There are four potential explanations for the existence of this behavior in grackles. First, it may be in response to intraspecific nest parasitism. Grackles nest semi-colonially and there exists ample opportunity for conspecific nest parasitism. However, recent studies have shown that despite the coloniality of many icterine species there is little evidence of intraspecific parasitism (Harms et al. 1991, Lyon et al. 1992, Rothstein 1993). We recorded only one incident of intraspecific parasitism in 401 nests (0.2%), and only two other cases have been documented in Common Grackles (Peer and Bollinger, in press b). Furthermore, grackles did not reject

any of the conspecific eggs that were added to their nests. Therefore, it seems unlikely that egg rejection has resulted from intraspecific nest parasitism.

Second, egg rejection may result from an adaptation that is entirely unrelated to brood parasitism. Rothstein (1975a) speculated that egg-robbing species such as the Blue Jay (*Cyanocitta cristata*) may be ejecters because of the egg-robbing habit, rather than it having anything to do with cowbird parasitism. The mechanics used in egg predation are similar to those required in egg ejection. Rothstein discounted the egg predation hypothesis and suggested that rejection should be more variable than the 100% recorded for Blue Jays. The grackle is an egg predator (Peer and Bollinger, in press b) and its rejection behavior is variable. In addition to grackles, Gray Catbirds (*Dumetella carolinensis*), Baltimore Orioles (*Icterus galbula*), Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*), and Black-billed Cuckoos (*Coccyzus erythrophthalmus*) are all egg predators and also demonstrate some level of egg rejection (Rothstein 1975a, Dufty 1994, Sealy 1994). Rejecters of Shiny Cowbird (*M. bonariensis*) eggs also tend to be egg predators (Wiley 1982).

However, not all egg predators exhibit rejection behavior. Corvids (*Corvus*, *Pyrrhocorax* spp.) in Europe accept foreign eggs (Yom-Tov 1976, Soler and Møller 1990). Eastern (*Sturnella magna*) and Western (*S. neglecta*) Meadowlarks, also egg predators (Schaeff and Picman 1988, Picman 1992), are frequently parasitized by Brown-headed Cowbirds but apparently do not reject cowbird eggs (Rothstein 1975a, Friedmann et al. 1977, Friedmann and Kiff 1985). As rejection has no apparent adaptive value until a species is parasitized, it seems unlikely that the egg predation habit alone results in rejection behavior. Egg predation may enhance some hosts' ability to evolve rejection once they are parasitized because of the similarity in mechanics between the two behaviors. This would explain the large number of egg-predators that also are rejecter species.

The third possible explanation is that the grackle was parasitized by cowbirds more frequently in the past and as a consequence evolved egg rejection. Fretwell (1973) suggested that grackles were probably one of the

cowbird's initial hosts during the development of the parasitic habit. He also stated that grackles are rejecters of cowbird eggs, but did not present any supporting evidence. Larger species in general were likely parasitized more often in the past as all but four rejecters of Brown-headed Cowbird eggs, the Cedar Waxwing (*Bombycilla cedrorum*), Bullock's Oriole (*I. bullockii*), Baltimore Oriole (Rothstein 1975a, 1977), and Warbling Vireo (*Vireo gilvus*; Sealy 1996), are larger than the cowbird. Cowbirds subsequently may have been forced to parasitize smaller hosts once the frequently parasitized larger species began rejecting cowbird eggs (Rothstein 1975a, Mason 1980, Peer and Bollinger, in press a).

It is unlikely that egg rejection has evolved recently in grackles considering that they are not currently parasitized and have not been parasitized in recent history. If grackles were rejecter species, it would have been advantageous for cowbirds to avoid parasitizing them because their eggs would be rejected (Sealy and Bazin 1995). As cowbirds began avoiding grackles, the rejection frequency likely decreased from near 100% to its current level due to the costs of maintaining rejection behavior in the absence of parasitism (see Cruz and Wiley 1989). The most obvious cost would be ejection of one's own eggs (Marchetti 1992). Grackles exhibit an extremely high level of intraclutch egg variation (Møller and Petrie 1991, Peer and Bollinger, in press b, S. I. Rothstein, pers. comm.) and these odd eggs would be rejected if grackles displayed the same level of discrimination that is demonstrated by typical rejecter species (Rothstein 1982a). Egg rejection would then be selected against in the absence of parasitism.

Indeed, grackles appear to be more similar to rejecter species than accepters, because they exhibit all of the traits of a rejecter. The first of these traits is the method of egg rejection. The most frequent means of rejection displayed by grackles in our study was ejection or pecking the cowbird eggs (72%). On the rare occasions that accepter species reject parasitic eggs it is usually accomplished by nest desertion or burial of the parasitic egg (Rothstein 1975a). Birds desert nests for a variety of reasons (Hill and Sealy 1994) and egg burial may simply be a continuation of the nest building process (but see Sealy 1995). In contrast, ejection and pecking of a parasitic egg are in direct response to

that egg, and as a result are considered to be clear evidence of true rejection behavior (Rothstein 1975a). Grackles also rejected a high percentage of cowbird eggs during the prelaying stage (38%) unlike acceptor species such as the Eastern Phoebe (*Sayornis phoebe*) and Red-winged Blackbird which accept cowbird eggs regardless of when the egg is introduced (Rothstein 1975a, Rothstein 1986, Ortega and Cruz 1988). Other traits grackles share with rejecters include eggs that contrast with those of cowbirds, a long history of sympatry with the cowbird, large population size, the removal of fecal sacs, a large beak that allows for easy removal of the parasitic egg, and large, easily located nests (Rothstein 1975a).

The fourth possible explanation for the existence of rejection behavior is that it is an ancestral trait. Rejection is common to all grackle species (*Quiscalus*) that have been tested, including Great-tailed Grackles (*Q. mexicanus*; Carter 1986), Greater Antillean Grackles (*Q. niger*; Wiley 1982, Post et al. 1990), and Carib Grackles (*Q. lugubris*; Post et al. 1990). This indicates that egg rejection is an easily evolved trait in this genus, or perhaps, it evolved once and is lost so slowly that evidence of it can be found in all grackles. If the latter is true, then it is possible that the Common Grackle was never parasitized that often and simply inherited this low level of rejection from an ancestor. However, we do not favor this interpretation. The generalist nature of the Brown-headed Cowbird, the large population size of the grackle, the long history of sympatry with cowbirds, and the suitability of the grackle as a host (see below) are all compelling evidence that Common Grackles should have been parasitized more often in the past. In addition, the Common Grackle is unique in that it is the only species in North America that displays a low level of true rejection behavior throughout its range (Rothstein 1975a). There also is an obvious source of selection against the retention of rejection behavior in the grackle, namely the high level of intraclutch egg variation. Further experiments on the rejection behavior of the other grackle species will be beneficial in understanding the evolution of rejection behavior in this genus.

EGG SIZE, INCUBATION, AND NESTLING SURVIVAL

Our data suggest that the size and number of grackle eggs were correlated with the effective-

ness of incubation of the smaller cowbird eggs. In a subsequent study (Peer and Bollinger, in press a), we demonstrated that it is necessary for a female cowbird to remove at least one grackle egg to ensure adequate incubation of her own egg. Cowbird eggs required shorter incubation periods, hatched earlier than grackle eggs more often, and exhibited the largest hatching differential in smaller clutches. The frequency of unhatched eggs that were considered fertile also was greater in larger clutches.

Egg removal appears to be essential if cowbirds are to fledge successfully from grackle nests. The average cowbird incubation period is 11–12 days (Rothstein 1975a), whereas the grackle's is 13.5 days (Peer and Bollinger, in press a). We found that cowbirds required 2.5–3.5 days to attain the size of a newly hatched grackle. If cowbirds hatch at the same time or later than the grackles it is unlikely that they will survive because grackles have faster growth rates (this study) and grackles typically reduce their broods by starving their smallest nestlings (Howe 1976). No grackle hatchlings under 4.5 g fledged, whereas the largest cowbird hatchling was only 3.5 g. Each of the three cowbirds that fledged weighed at least 3.0 g at hatching.

The mortality of cowbird nestlings that had no grackle nestmates cannot be linked to competition with the larger grackle nestlings. It also is unlikely that the type of food delivered to cowbird nestlings is a constraint because grackles, just like other passerines, feed their young mostly insects (reviewed in Peer and Bollinger, in press b). Instead, the problem may be the size of the food. Howe (1979) noted that insects delivered to older grackle nestlings were too large for younger nestlings. Adult grackles deliver food that is suitable for their own nestlings, yet it may be too large for cowbird nestlings of the same age. Only cowbird nestlings that weigh at least 3.0 g may be physically capable of handling the larger food items.

Nestling survival also may be affected by ectoparasitic mites. Our hands and arms were covered by mites (Dermanyssidae) after handling nestlings. Although our observations are anecdotal, it appeared that the mites contributed to the mortality of nestlings because infested nests rarely produced fledglings. The abundance of ectoparasitic mites is likely the result of grackle nesting ecology. Grackles often constructed their nests on top of old nests and members of

this family of mites are known to overwinter in old nests (Phillis 1972). The incidence of ectoparasitic infestation also may decrease the suitability of grackles as cowbird hosts (see Ortega and Cruz 1991).

However, the low survivability of cowbirds in host nests does not necessarily preclude parasitism. Fraga (1985) found that 78.1% of Chalk-browed Mockingbird (*Mimus saturninus*) nests were parasitized by Shiny Cowbirds despite the fact that only 6.2% of cowbirds fledged from the nests of this larger host. Therefore, the lack of parasitism on grackles does not appear to be solely a result of the low survivability of cowbirds in grackle nests.

NEST DEFENSE

Grackles responded more aggressively toward the cowbird models than to the Fox Sparrow models in five of the seven categories, which suggests that they may recognize cowbirds as a unique threat. Yet, it is unclear why there were no differences in the frequency of individual attacks and mobbing behavior directed toward the two models. Grackles may respond aggressively toward any species that comes near their nests which in effect deters parasitism. Grackles kill and eat other passerines (Davidson 1994), so the risk of injury to the cowbird is great.

Nevertheless, aggressive nest defense alone cannot explain the absence of parasitism. Neither colonial- nor noncolonial-nesting grackles were parasitized, and there were no differences in the responses between colonial and noncolonial nesters to the cowbird models. Wiley (1982) found that Greater Antillean Grackles nesting in isolation and on the periphery of colonies were parasitized by Shiny Cowbirds more frequently than those in the middle of the colonies. This indicates that nesting in colonies decreases the frequency of parasitism but does not eliminate it. Therefore, we would expect parasitism on at least the solitary nesting grackles. Neudorf and Sealy (1994) also found that Common Grackles only were present at their nests for approximately half of the 30-minute time period during which cowbirds were most likely to parasitize them. Thus grackle nests are vulnerable to parasitism.

CONCLUSIONS

Despite the early initiation of the grackle's nesting season, there were more grackle nests available for parasitism compared to all other hosts

except for one, and yet no grackles were parasitized. Colonial-nesting and aggressive nest defense do not appear to be responsible for the infrequent parasitism, because there was no parasitism on either colonial or solitary nesters. Grackles are suitable hosts, although they appear to be at the uppermost size limit for successful parasitism. Cowbirds are capable of fledging from grackle nests when the following conditions occur: clutch size has been reduced to ensure efficient incubation of the smaller cowbird egg (see also Peer and Bollinger, in press a), the cowbird hatches at least two days earlier than the grackle nestlings, and the cowbird hatchling weighs at least 3 g. Nest abandonment and infestation of grackle nests with ectoparasitic mites may decrease their suitability as hosts, however the primary reason for the infrequent parasitism on grackles appears to be past rejection behavior. The grackle likely was parasitized more often in the past and as a consequence evolved rejection behavior. Parasitism of grackles would then be selected against to avoid wasting eggs on a rejecter species. Rejection by grackles apparently decreased in the absence of parasitism due to the high degree of intraclutch egg variability exhibited by grackles which would increase the chances of them mistakenly rejecting their own discordant eggs.

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