

**AN EXPERIMENTAL INVESTIGATION OF EGG REJECTION
BEHAVIOR IN THE GRACKLES (*QUISCALUS*)**

BY

BRIAN D. PEER

A thesis presented to the University of Manitoba, Department of Zoology,
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy

Winnipeg, Manitoba

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A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University

of Manitoba in partial fulfillment of the requirements of the degree

of

DOCTOR OF PHILOSOPHY

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ABSTRACT

This study was an experimental investigation of the responses of grackles (*Quiscalus*) to foreign eggs in their nests. No evidence of conspecific brood parasitism was recorded at 797 Great-tailed Grackle (*Q. mexicanus*) nests, and I failed to induce this behavior by experimentally removing nests. Great-tailed Grackles are not indeterminate layers, an attribute often associated with conspecific brood parasites. Great-tailed Grackles rejected 8.1% of experimentally introduced conspecific eggs. Neither Bronzed Cowbird (*Molothrus aeneus*) nor Brown-headed Cowbird (*M. ater*) parasitism was recorded on Great-tailed Grackle nests. Cross-fostered Bronzed Cowbird nestlings, but not Brown-headed Cowbird nestlings, fledged from grackle nests, indicating that Great-tailed Grackles are unsuitable hosts for the Brown-headed Cowbird. Great-tailed Grackles rejected eggs via true egg recognition and populations sympatric and allopatric with Bronzed Cowbirds rejected 100% of model cowbird eggs. An allopatric population of the Boat-tailed Grackle (*Q. major*), a sibling species of the Great-tailed Grackle, rejected 100% of model eggs. Rejection in these grackles apparently evolved in response to Giant Cowbird (*Scaphidura oryzivora*) parasitism, and has been maintained by the Boat-tailed Grackle in the absence of parasitism for at least 10,000 years since it split from the Great-tailed Grackle. The Common Grackle (*Q. quiscula*), which lays the most variable eggs among the grackles, is the only grackle that has lost most of its rejection behavior. With extreme intraclutch egg variation, Common Grackles may be more likely to reject their own aberrant eggs, which would select against rejection behavior in the absence of parasitism. These results have significant implications for host-parasite cycles. Finally, a review of the correlates of egg rejection in Brown-headed Cowbird hosts revealed that historic contact, body size, taxonomic affiliation,

and bill size are correlated with egg rejection. These results support evolutionary lag as an explanation for the acceptance of cowbird parasitism by most species, although hosts with eggs that resemble cowbird eggs may be in an evolutionary equilibrium with cowbirds.

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GENERAL INTRODUCTION

Avian brood parasitism is a breeding strategy in which birds lay their eggs in the nests of other birds, and rely on these hosts to raise their young. There are two forms of brood parasitism. Conspecific brood parasitism (CBP) is a facultative strategy in which birds may lay eggs in the nests of conspecifics in addition to tending their own clutches. Interspecific brood parasitism (IBP) is either a facultative, or an obligate strategy, with obligate interspecific brood parasites relying exclusively on their hosts to raise their young. IBP is typically more costly in terms of host fitness than CBP because interspecific brood parasites are frequently larger than their hosts and they often possess specialized adaptations that allow them to outcompete host nestlings (Rothstein 1990, Payne 1997). As a consequence, antiparasite defenses are manifested more prominently in hosts of interspecific brood parasites (Rothstein 1990).

The most obvious and perhaps most effective host adaptation against brood parasitism, whether it be IBP or CBP, is ejection of the parasite's eggs from the nest. The earliest animal behaviorists tested the egg rejection abilities of Common Cuckoo (*Cuculus canorus*) hosts by adding foreign eggs to nests (Lottinger 1775, 1795 cited in Jourdain 1925; Baldamus 1892; Swynnerton 1918; Rensch 1924, 1925; Ali 1931). Rothstein (1975a) perfected this method in his monumental study of egg rejection behavior by hosts of the parasitic Brown-headed Cowbird (*Molothrus ater*). Rothstein (1975a) was the first to use model eggs to test the egg rejection behavior of host species. In the present study, I use an experimental approach, much of it based on the procedure pioneered by Rothstein, to investigate egg rejection behavior in the grackles (*Quiscalus spp.*). This genus of birds is rarely parasitized by cowbirds or conspecifics, and yet all species that had been tested prior to this study

exhibited some level of egg rejection (Rothstein 1975a; Cruz et al. 1985; Carter 1986; Rohwer and Freeman 1989; Post et al. 1990; Peer and Bollinger 1997a, b). I also use comparative analyses to determine what host characteristics are important in the evolution of egg rejection behavior in hosts of the Brown-headed Cowbird.

Great-tailed Grackles are colonial, which may predispose them to CBP (MacWhirter 1989, Rohwer and Freeman 1989). Therefore, I tested the hypothesis that egg rejection in Great-tailed Grackles has evolved in response to CBP (Chapter 1). I monitored grackle nests for evidence of CBP and attempted to induce this form of parasitism by removing nests during the laying period. Indeterminate laying, where a bird continues to lay eggs in response to egg removal, is often characteristic of conspecific parasites (Kendra et al. 1988, McRae 1988), so I tested whether Great-tailed Grackles are indeterminate layers. Lanier (1982) tested a small number of Great-tailed Grackles for conspecific egg recognition and concluded that this species does not reject conspecific eggs, although some eggs disappeared from nests he experimentally parasitized. I tested whether Great-tailed Grackles do indeed reject conspecific eggs by switching eggs between nests and by adding them to other grackle nests.

I also examined the evolution of egg rejection behavior in the grackles in terms of IBP, and its implications for host-parasite cycles (Chapter 2). First, I tested the hypothesis that egg rejection in Great-tailed Grackles evolved in response to Bronzed Cowbird (*M. aeneus*) parasitism. Great-tailed Grackle nests were monitored for parasitism and cowbird nestlings were cross-fostered into Great-tailed Grackle nests to determine whether this large bird is a suitable host. I tested the responses of a population of Great-tailed Grackles sympatric with Bronzed Cowbirds to experimental parasitism. I also tested a

Great-tailed Grackle population allopatric with Bronzed Cowbirds for egg rejection with the prediction that these individuals would demonstrate a lower level of rejection than the sympatric population, similar to previous studies (Järvinen 1984, Davies and Brooke 1989a, b, Brown et al. 1990, Briskie et al. 1992). Second, the Boat-tailed Grackle (*Q. major*), a sibling species of the Great-tailed Grackle, was tested for egg rejection. This species is not sympatric with any large-bodied brood parasite, and it is not a conspecific brood parasite (Post et al. 1996), so I predicted this species would not display rejection behavior. Third, I quantified variation in the appearance of eggs within grackle clutches and compared this to the frequency of egg rejection for five of the six extant grackle species to determine whether this influences the retention of egg rejection behavior in the absence of parasitism. Species with high levels of intraclutch egg variation may be more likely to reject their own discordant eggs, and such behavior would be selected against in the absence of parasitism (Peer and Bollinger 1997a). Finally, I discuss the implications of retaining rejection versus the loss of rejection in the absence of parasitism and how this can influence host parasite cycles.

One of the most enigmatic issues in the study of brood parasitism is why some hosts have not evolved egg rejection behavior when parasitism is clearly harmful to them. Two competing hypotheses have been proposed to explain this acceptance. The evolutionary equilibrium hypothesis states that there are costs incurred in the ejection of parasitic eggs which make acceptance of parasitism more beneficial (e.g. Zahavi 1979, Rohwer and Spaw 1988, Lotem et al. 1992, 1995). In contrast, the evolutionary lag hypothesis states that there may be some time lag after parasitism begins and before rejection evolves, but rejection is almost always the optimal behavior rather than acceptance (e.g. Rothstein 1975a, 1990, 1996, Davies and Brooke 1989a, b,

1996, Sealy 1996). I tested these hypotheses using comparative analyses to examine whether there are any specific characteristics of hosts of the Brown-headed Cowbird that make them more likely to evolve egg rejection (Chapter 3). I used six characteristics proposed by Rothstein (1975a), including historical contact with cowbirds, well-developed nest sanitation, eggs that differ from cowbird eggs, large easily found nests, large bills, and large population sizes, plus two others, taxonomic affiliation and egg predation.

CHAPTER 1

CONSPECIFIC BROOD PARASITISM AND EGG REJECTION IN GREAT-TAILED GRACKLES

INTRODUCTION

Egg rejection by passerine birds has evolved most commonly in response to interspecific brood parasitism (IBP), and less frequently to conspecific brood parasitism (CBP) (Rothstein 1990, Chapter 2; see also Peer and Bollinger 1998). Recognition and rejection of conspecific eggs is more difficult because eggs laid by females of the same species are so similar. The relatively few bird species that reject conspecific eggs usually do so prior to clutch initiation (Emlen and Wrege 1986, Brown and Brown 1989, Stouffer et al. 1987; but see Jackson 1990). In this manner, they avoid mistakenly rejecting their own eggs. Therefore, a much finer level of discrimination is typically required to recognize conspecific eggs (Gifford 1993) compared to the eggs of interspecific brood parasites such as the Brown-headed Cowbird (*Molothrus ater*; Rothstein 1982b), whose eggs differ markedly from those of most of its hosts (Chapter 3).

Great-tailed Grackles (*Quiscalus mexicanus*) reject Bronzed Cowbird (*M. aeneus*) eggs and possibly conspecific eggs (Lanier 1982, Carter 1986), yet neither form of parasitism has been recorded in Great-tailed Grackles (Yom-Tov 1980, Friedmann and Kiff 1985, Carter 1986, MacWhirter 1989, Rohwer and Freeman 1989). Great-tailed Grackles nest in dense colonies (Fig. 1.1), which would facilitate the evolution of CBP because it provides a potential parasite with a large supply of nests to parasitize that are similar to its own (MacWhirter 1989, Rohwer and Freeman 1989).

Figure 1.1. Great-tailed Grackle nests constructed immediately adjacent to one another at the Welder Wildlife Refuge, Sinton, TX.



The objective of this study was to test the hypothesis that CBP has selected for egg rejection behavior in Great-tailed Grackles. First, I inspected grackle nests for evidence of CBP and attempted to induce CBP by removing grackle nests during laying. Most conspecific brood parasites lay their eggs in the nests of nearby conspecifics after their own nests have been experimentally disturbed or removed during laying (Haramis et al. 1983, Emlen and Wrege 1986, Feare 1991, Stouffer and Power 1991, McRae 1998; but see Jackson 1993); whereas at least one species in which CBP is rare, the Red-winged Blackbird (*Agelaius phoeniceus*), does not lay its eggs in the nests of conspecifics as a result of nest loss (Rothstein 1993). If Great-tailed Grackles are conspecific brood parasites, I predicted they would lay eggs parasitically in response to nest removal. Second, I determined whether grackles are indeterminate layers by recording their responses to experimental egg removal and egg addition. Indeterminate laying may also facilitate CBP by allowing a female to lay in a neighbor's nest and still lay a full complement of eggs in her own nest (e.g. Hamilton and Orians 1965, Kendra et al. 1988, McRae 1998). Third, I tested whether Great-tailed Grackles do indeed possess the ability to recognize and reject conspecific eggs by experimentally parasitizing nests with grackle eggs.

METHODS

STUDY AREA

This study was conducted at the Welder Wildlife Refuge in San Patricio County, Texas (28°0' N, 97°5' W), from 1994 to 1996. As many as 500 Great-tailed Grackles nested annually at the refuge (see also Tutor 1962), mainly on Big and Pollita lakes. Most nests were constructed over water in bulrush

(*Scirpus californicus*). Fewer grackles nested at cattle tanks scattered throughout the refuge.

NEST INSPECTIONS

Grackle nests were inspected daily from approximately 7:00 to 12:00 (CST) for evidence of CBP, that is, whether more than one grackle egg was laid on the same day, or an egg appeared three or more days after laying had stopped (MacWhirter 1989, Rothstein 1993). Birds lay only one egg per day (Sturkie 1976), and Great-tailed Grackles occasionally skip a day, but not more than one (pers. obs.). Grackle eggs were numbered daily, which allowed me to detect whether a parasitic female removed a host egg and replaced it with her own (Lombardo et al. 1989). This method would not allow detection of single parasitic eggs laid the day before the host began laying or the day after the host stopped laying. However, using laying sequence data is the most reliable method in the absence of DNA analyses (McRae 1997b, McRae and Burke 1996). Other researchers have used the appearance of an oddly colored egg as evidence of CBP (Freeman 1988, Jackson 1992a). This is not a reliable indicator of CBP in grackles because of intraclutch variability in this genus (Rothstein 1974a; Peer and Bollinger 1997a, b; Chapter 2).

NEST REMOVAL EXPERIMENTS

Nest removal experiments were conducted at Big Lake in 1995 and at Pollita Lake in 1996. Few grackles nested at Pollita Lake in 1995 and none nested at Big Lake in 1996 due to drought. I first determined the time at which Great-tailed Grackles laid their eggs. After locating nests, I visited them on the following day to confirm additional eggs had not been laid. Nests were then revisited 5 to 20 min later, depending on when the female departed. I

considered the midpoint of each of these periods as the laying time (Scott 1991). Sunrise data were obtained from the website of the United States Naval Observatory Astronomical Applications Department (<http://aa.usno.navy.mil/AA/>). I recorded seven laying events at six nests and found that Great-tailed Grackles laid their eggs $47.1 \text{ min} \pm 7.1 \text{ SE}$ after sunrise (range 25-69 min). Therefore, I removed grackle nests just after sunrise ($\bar{x} = 28 \text{ min}$, range 11-56 min) the morning before the second egg was to be laid, thus ensuring that this egg would not be resorbed (see Rothstein 1993). Removal at this time also ensured that additional eggs would be laid as the mean clutch size of the grackle is approximately three eggs (see below).

Most nests that were removed had at least one nest within 1 m in the same colony that was also in the laying stage. A colony was defined as all of the nests within a clump of bulrush, although these clumps were often within 1 m of one another. Later the same morning, and for at least two days following nest removal, I searched the bulrushes near the former nest sites for eggs. All nests were monitored daily for signs of parasitism.

LAYING DETERMINANCY EXPERIMENTS

Laying determinancy was ascertained in two ways. First, the second egg was removed from grackle clutches the morning it was laid. I compared the clutch size of these removal nests to unmanipulated control nests. If grackles are indeterminate layers they should have laid additional eggs (Davis 1955, Kennedy and Power 1990). The mean ($\pm \text{SE}$) clutch size of Great-tailed Grackles is $3.2 \text{ eggs} \pm 0.04$ ($n = 276$; Peer unpubl. data), so no more than one egg was removed to ensure that nests were not deserted. All eggs were numbered and nests were checked daily.

Second, I compared the clutch sizes of nests in which single grackle eggs were added with the clutch sizes of unmanipulated control nests. These data were from the conspecific egg recognition experiments. If Great-tailed Grackles are indeterminate layers they should have laid fewer eggs in this experiment (Davis 1955, Kennedy and Power 1990). Only nests in which the eggs were added after one host egg was present were included in this analysis. All eggs were numbered and nests were checked daily.

EXPERIMENTAL CBP

Initially, grackles were tested for conspecific egg rejection by adding grackle eggs to other grackle nests during the laying period. It was unclear from these experiments whether grackle eggs were being rejected or if they broke as a result of "wear and tear" in the enlarged clutches and were then removed by the adults, giving the appearance of being rejected (Lerkelund et al. 1993). A second set of experiments was conducted in which grackle eggs were switched between nests during the laying and incubation stages. Eggs were also added to nests during the prelaying stage, after the female had finished building her nest but had not started laying. In these experiments, the experimentally added eggs were ranked according to the amount of difference they exhibited relative to the host's eggs (the exception being the eggs added during the prelaying stage, because there were no host eggs present for comparison). If the experimental eggs were rejected, I predicted that the eggs that differed the most from the host's eggs would be rejected more often and those that varied little or not at all would be rejected infrequently. Experimental eggs were ranked as follows (see Moksnes 1992, Braa et al. 1992, Moksnes and Røskoft 1992): (1) the egg was indistinguishable from the host's eggs, (2) the egg was moderately different from the host's eggs, (3) the

egg was dramatically different from the host's eggs, and (0) host eggs differed from each other. It was impossible to rank the experimental egg relative to the host's eggs when the host's own eggs differed, so these clutches were given the rank of "0".

In both experiments, experimental eggs were added to nests with eggs that appeared to be similar in size and of equal age. Experimental and host eggs were numbered with indelible ink, and nests were visited daily for signs of rejection (i.e. the disappearance of the experimental egg). Experimental eggs were considered rejected if they disappeared from the nest, and accepted if they remained until at least one egg in the clutch hatched. It is difficult to ascertain whether nest desertion is a response to parasitism because birds desert their nests for a variety of reasons (Rothstein 1975a, Hill and Sealy 1994). Therefore, I compared the incidence of desertion in experimental nests to that in control nests to determine whether there was a difference. Control nests were treated in the same manner as experimental nests (i.e. checked daily and eggs numbered), but they were not parasitized.

STATISTICAL ANALYSES

Laying determinancy was evaluated using the Mann-Whitney *U*-test because clutch size does not have a normal distribution. Chi-square tests, and Fisher exact tests when expected frequencies were less than five, were used to analyze egg rejection behavior. The Kruskal-Wallis test was used to analyze the time required to reject conspecific eggs over the nesting cycle and the time required to reject based on the differences experimental eggs exhibited relative to the hosts' eggs. Standard error was used as a measure of variance, $P < 0.05$ was the accepted level of significance, and all tests were two-tailed unless otherwise indicated.

RESULTS

FREQUENCY OF CBP

There was no evidence of CBP on the 797 Great-tailed Grackle nests that were monitored. Four grackle eggs laid after the host had stopped laying appeared to be instances of CBP; however, alternative explanations can account for these observations. Nest 94-130: a three-egg clutch was completed on 29 May, and the nest contents remained the same until one egg disappeared on 4 June. On 8 June, a fourth grackle egg was laid. The eggs began hatching on 21 June, 26 days after the first egg was laid. Nest 95-170: a three-egg clutch was complete on 12 May and the contents remained the same until 3 June. I was unable to check this nest from 4 June to 7 June while I was conducting experiments in Kansas (see Chapter 2). There were six grackle eggs present at the next visit on 8 June. Nest 95-235: a two-egg clutch was completed on 17 May, and the contents remained the same until 21 May when a single egg was laid each of the next three days, bringing the clutch to five eggs. The first two eggs looked very different from the last three eggs. On 27 May, one of the first two eggs disappeared. The first egg hatched 3 June. On 8 June, a second egg had hatched and one of the original eggs was present. Nest 96-28: one egg was laid in this nest on 9 May. The contents remained the same until 14 May when one egg was laid each day over the next three days. The nest contents remained the same until the nest was depredated on 27 May.

RESPONSES TO EXPERIMENTAL NEST REMOVALS

No cases of CBP were recorded after I removed 13 nests (Table 1.1). There were, however, two unusual events. On 30 May 1995, nests 95-346 and 95-360 were removed from colony three. On 31 May, a freshly laid egg was found at nest 95-250 also in colony three, lodged between the nest rim and a

Table 1.1 Responses of Great-tailed Grackles to experimental nest removals.

Nest Removed	Date	<u>Nests available for parasitism^a</u>	
		Laying	Incubation
95-161	5/11	1 (59)	0 (116)
95-163	5/11	1 (59)	0 (116)
95-186	5/12	0 (53)	0 (135)
95-275	5/20	2 (23)	9 (157)
95-276	5/20	1 (24)	15 (151)
95-299a	5/24	2 (23)	2 (99)
95-343	5/28	6 (15)	18 (76)
95-348	5/28	10 (11)	36 (58)
95-346 ^b	5/30	4 (8)	36 (61)
95-360 ^b	5/30	4 (8)	36 (61)
96-42	5/12	3 (24)	1 (8)
96-59	5/12	26 (1)	8 (1)
96-116	5/22	49 (3)	3 (13)

^a Nests available for parasitism in which the host was laying or incubating on the day of nest removal at Big Lake in 1995, and Pollita Lake in 1996. The first number is the number of nests available in the same colony from which the nest that was removed, and the second number represents all nests available at the particular lake.

^b An egg was found on the rim of nest 95-250 on the day after these two nests were removed.

strand of bulrush (i.e. outside of the nest cup). This nest was within 2 m of the nests that were removed, so the egg could have been laid by either of these females. This parasitism was unusual not only because of the location of the egg, but also because the nest contained two nestlings. The second event occurred after I removed nest 96-116 on 22 May 1996. Approximately 1.5 hr later, an egg was found on the rim of nest 96-64, which was located less than 1 m from nest 96-116. This was egg four from nest 96-64 and it was not on the rim when I removed nest 96-116. It remained there after the eggs in the nest hatched.

In addition to these experimental nest removals, there were 40 nest failures ($n = 837$ nests) during the egg-laying stage from 1994-1996, but there were no observed cases of CBP. Nest failure during laying was highest in 1994 (9.5% of 380 nests) compared to 1995 (0.9% of 350) and 1996 (0.9% of 107).

LAYING DETERMINANCY

The mean clutch size of removal clutches (2.1 eggs ± 0.1 , $n = 29$) was significantly smaller than control clutches (3.2 eggs ± 0.1 , $n = 57$; Mann-Whitney U -test, $W = 666.5$, $P < 0.0001$). The mean clutch size of enlarged clutches (4.2 eggs ± 0.07 , $n = 80$) was significantly larger than control clutches (3.1 eggs ± 0.1 , $n = 54$; Mann-Whitney U -test, $W = 6958.5$, $P < 0.0001$).

RESPONSES TO EXPERIMENTAL CBP

Conspecific eggs were rejected from 8.1% of experimentally parasitized nests ($n = 246$; Table 1.2). At two of these nests, single host eggs were either damaged or missing following rejection. The parasitic egg and at least one host egg disappeared at two other nests, but these appeared to be depredated as all but one egg was damaged or missing from one nest and all eggs eventually

Table 1.2. Rejection of conspecific eggs by Great-tailed Grackles in relation to stage of parasitism and mean number of days (\pm SE) for rejection.

Stage	% Rejection (<i>n</i>)	Days
Prelying	11.1 (9)	1.0
Laying	8.0 (201)	6.4 \pm 0.61
Incubation	8.3 (36)	1.0 \pm 0.0

disappeared from the second. Four other nests at this colony were also depredated at the same time.

One ($n = 8$) or two ($n = 1$) host eggs also disappeared from 3.7% of experimentally parasitized nests in which the parasitic eggs remained. This rate of egg loss did not differ from the number of single eggs lost from control nests (4.4%, 10/229 nests; $\chi^2 = 0.155$, $df = 1$, $P > 0.50$), therefore these were not considered rejections. Three nests into which conspecific eggs were switched during laying were deserted. These were not considered rejections because this was not different than the rate of desertion of control nests (6 of 229; Fisher exact test, $P > 0.05$). Runt eggs laid in two nests were both rejected in two days; these data were not included in the analyses.

Experimental eggs were not rejected more often when added to nests than when they were switched between nests during the laying stage (9/90 vs. 7/111; $\chi^2 = 0.93$, $df = 1$, $P > 0.75$). There was a trend for these eggs to be rejected more often when added during incubation, but the difference was not significant (3/17 vs. 0/19; Fisher exact test, $P = 0.095$). Therefore, these data were pooled. There was also no relationship between rejection and the stage when parasitism occurred ($\chi^2 = 0.12$, $df = 2$, $P > 0.90$; Table 1.2). The time required to reject the parasitic eggs differed among the three nest stages. Rejection took longer when nests were parasitized during laying versus prelaying or incubation (Kruskal-Wallis one-way ANOVA, $H = 9.40$, $df = 2$, $P = 0.009$; Table 1.2). Divergent eggs tended to be rejected more frequently ($\chi^2 = 3.30$, $df = 3$, $P > 0.25$) and sooner for all stages of the nesting cycle combined (Kruskal-Wallis one-way ANOVA, $H = 5.35$, $df = 2$, $P = 0.069$; Table 1.3); however, the differences were not significant.

Table 1.3. Rejection of conspecific eggs by Great-tailed Grackles in relation to difference between parasitic egg and host eggs for all stages of the nesting cycle, and mean number of days (\pm SE) for rejection.

Difference	% Rejection (<i>n</i>)	Days
0	0.0 (10)	---
1	4.5 (66)	8.0 \pm 1.5
2	7.3 (41)	4.3 \pm 1.8
3	13.3 (30)	2.0 \pm 0.58

DISCUSSION

FREQUENCY OF NATURAL AND EXPERIMENTALLY INDUCED CBP

I did not detect natural CBP in Great-tailed Grackles and there are no previous records of such behavior in this species (Yom-Tov 1980, MacWhirter 1989, Rohwer and Freeman 1989). Four cases in which eggs were laid after the host had stopped laying may have been instances of CBP, but this seems unlikely. In each case the eggs remained in the nests much longer than the grackle's normal incubation period of 13-14 d (Peer unpubl. data). The original nest owners probably deserted these nests or died and the nests were taken over by new females that laid their own eggs in the nests. This accounts for the extended period of time that the eggs remained in the nests. It also appears that one of the new females rejected one of the original owner's eggs (see above). Similar nest-acquisition behavior has been reported for Boat-tailed Grackles (*Q. major*; Post 1987).

I found only one egg laid in response to the nest removal experiments and it was located on the rim of a nest containing nestlings. There were four nests in the laying stage in this colony and 36 nests in the incubation stage that would have been more suitable for parasitism (Table 1.1). The fate of the other 12 eggs is unknown. It seems highly unlikely, if not impossible, that the eggs were resorbed because the nests were removed within an hour of when eggs were to be laid (Sturkie 1976; see also Rothstein 1993). It is possible that some of the eggs were laid in conspecific nests and were rejected. However, this too seems improbable because only 8% of the population exhibited rejection behavior. Moreover, it usually required more than one day for these eggs to be rejected and I checked all nests daily. It is also unlikely that eggs were laid in other parts of the refuge or on other properties because parasitic eggs are typically laid in the nests of nearby neighbors (Brown and Brown

1989, Lyon 1993, McRae 1997a, 1998), and I searched the refuge thoroughly for grackle nests. Perhaps these eggs were laid and then eaten by the females (Lyon et al. 1991, Rothstein 1993). In this way, they could recoup the energy expended in producing the eggs.

Birds that lose their nests during laying can make the best-of-a-bad-situation by dumping physiologically committed eggs in the nests of nearby conspecifics (Hamilton and Orians 1965; see also Yom-Tov 1980). Wood Ducks (*Aix sponsa*), Common Moorhens (*Gallinula chloropus*), White-fronted Bee-eaters (*Merops bullockoides*), and European Starlings (*Sturnus vulgaris*), all conspecific brood parasites, parasitize other nests after their own nests have been experimentally disturbed or removed (Haramis et al. 1983, Emlen and Wrege 1986, Feare 1991, Stouffer and Power 1991, McRae 1998; but see Lank et al. 1989, Jackson 1993). Attempts to induce CBP in Red-winged Blackbirds, which rarely parasitize conspecifics were unsuccessful (Rothstein 1993; see also Harms et al. 1991, Lyon et al. 1992). Thus, it is possible that only species that are conspecific brood parasites can be induced to lay in the nests of others.

LAYING DETERMINANCY

Great-tailed Grackles did not vary clutch size in response to experimental egg removal or egg addition. Therefore, this species is not an indeterminate layer (Davis 1955, Kennedy and Power 1990) and this trait is often associated with CBP (Hamilton and Orians 1965, Kendra et al. 1988, Lyon 1993, McRae 1998; but see Victoria 1972, Kennedy and Power 1990, Ringsby et al. 1993).

WHY IS CBP ABSENT IN GREAT-TAILED GRACKLES?

Why don't female Great-tailed Grackles parasitize conspecifics, especially after they have lost their nests during laying? Laying physiologically committed eggs indiscriminately in the environment would be a waste of reproductive effort, unless the females ate the eggs. CBP should be a successful reproductive strategy in Great-tailed Grackles because only 8% of females in the population ejected conspecific eggs. It may be that nest loss during laying is too infrequent for selection to favor CBP in Great-tailed Grackles. Nest loss during laying approached 10% in 1994, but it occurred at less than 1% of nests in 1995 and 1996. Nevertheless, nest loss is higher in other colonial icterines, but they also do not regularly practice CBP (e.g. Red-winged Blackbirds, Yellow-headed Blackbirds [*Xanthocephalus xanthocephalus*], Brewer's Blackbirds [*Euphagus cyanocephalus*], Common Grackles [*Q. quiscula*], Boat-tailed Grackles; Harms et al. 1991, Lyon et al. 1992, Rothstein 1993, Post et al. 1996, Peer and Bollinger 1997b).

The two most plausible reasons for the absence of CBP appear to be that CBP may not exist in the "behavioral repertoire" of Great-tailed Grackles (see Harms et al. 1991, Lyon et al. 1992). Second, Great-tailed Grackles and Common Grackles (*Q. quiscula*) occasionally desert their colonies when many nests have been lost (Peer and Bollinger 1997a, b; see also Orians 1961, Ortega and Cruz 1991). This occurred in 1994 at Lake Pollita and in 1996 at a smaller colony. In both instances, a number of nests were progressively lost and essentially all birds deserted within a week. Apparently, some grackle species require the presence of other conspecifics when nesting (see Ortega and Cruz 1991). Therefore, if colonies are frequently deserted following extensive nest losses, female grackles would not benefit by laying eggs in conspecific nests. This, combined with the fact that CBP is relatively unsuccessful in

many species that practice it (Emlen and Wrege 1986, Lyon 1993, Sorenson 1993; but see Brown and Brown 1989, 1998, McRae 1998), indicates selection apparently does not favor the evolution of this alternative breeding strategy in the Great-tailed Grackle (see also Kempenaers et al. 1995).

CONSPECIFIC EGG REJECTION BEHAVIOR

Lanier (1982) switched eggs between 15 Great-tailed Grackle nests and recorded three rejections. He reasoned that two of these were likely artifacts of his experimental procedure and concluded that Great-tailed Grackles accept conspecific eggs. Initially, I believed that Great-tailed Grackles accepted conspecific eggs because they took an average of more than six days to reject eggs that were experimentally placed into their nests during the laying stage. In contrast, almost all experimentally added cowbird eggs were rejected within 24 h (Chapter 2). It appeared that the conspecific eggs broke from "wear and tear" in the enlarged clutches (Lerkeiund et al. 1993) and then were removed by grackles, leading to the impression that the eggs were rejected. However, the eggs still disappeared even when eggs were switched between nests, which refutes "wear and tear" as the explanation for the eggs' disappearance. Furthermore, when nests were parasitized during the prelaying and incubation stages the experimental eggs were rejected within 24 h.

In accord with my prediction, there was a trend for parasitic eggs that differed the most from the host's eggs to be rejected more frequently by those females that exhibited this behavior, and the more the eggs differed, the faster they were rejected (see also Victoria 1972, Braa et al. 1992, Lotem et al. 1995). Presumably, grackles recognize these eggs more easily. Grackles also tended to reject conspecific eggs that were added to nests more often compared to those that were switched between nests during incubation. Apparently the

increase in clutch volume alerted some females to the change in the nest contents, which increased the likelihood of rejection. Thus, contrary to Lanier's (1982) conclusions, some Great-tailed Grackles reject conspecific eggs.

One apparent constraint on conspecific egg rejection is intraclutch egg variation (Lotem et al. 1995, Soler and Møller 1996). No eggs were rejected from nests in which the host egg patterns varied. One host egg disappeared from a nest I parasitized in which the host's eggs varied and this may have been a recognition error (see also Davies and Brooke 1988, Marchetti 1992, Lotem et al. 1995, Sealy 1995). It may be difficult, if not impossible, for the female to distinguish between the experimental egg and her own eggs in these nests. Species that are parasitized by conspecifics often demonstrate minimal intraclutch egg variation and higher levels of interclutch egg variation which may facilitate the detection of parasite's eggs (Freeman 1988, Jackson 1992a). If intraspecific parasitism is a strong selective pressure on grackles, then I would expect that they, too, should exhibit minimal intraclutch egg variation. However, 34% of clutches demonstrated some variation (see Chapter 2), a trend that is evident in most if not all species of *Quiscalus* (Chapter 2).

There are two potential costs involved in rejecting parasitic eggs: rejection costs (i.e. damage caused to host eggs during ejection) and recognition errors (see above). Great-tailed Grackles incurred minimal costs when rejecting conspecific eggs. Only 0.1 grackle egg was lost per rejection attempt, and there was little evidence that grackles regularly reject the wrong egg, other than the one mentioned above. Host eggs disappeared from both control nests (4.4%) and from experimentally parasitized nests in which the parasitic eggs remained (3.7%). However, the number of eggs lost in these two treatments did not differ, so I did not classify the disappearances from parasitized nests as

recognition errors. I also did not consider the disappearances of host eggs from control nests as recognition errors. At least one egg was dramatically different in 9% of control grackle clutches that were ranked for intraclutch egg variation ($n = 167$; see Chapter 2), and I would expect these eggs to be rejected as grackles are apt to reject divergent eggs from their nests. However, none of these eggs was rejected.

These interpretations are contrary to Marchetti (1992) who found that eggs disappeared from both experimentally parasitized and unparasitized nests (10% and 4%, respectively) of the Yellow-browed Leaf Warbler (*Phylloscopus inornatus*). Marchetti (1992) concluded that these eggs were mistakenly rejected by the warblers. Similarly, Lotem et al. (1995) suggested that Great Reed Warblers (*Acrocephalus arundinaceus*) mistakenly reject up to 14% of their own eggs from unparasitized nests. However, as Rothstein and Robinson (in press) have pointed out, it is impossible to know whether these eggs were rejected or taken by predators that removed only single eggs (e.g. Sealy 1994, Hauber 1998), or whether they broke and were removed by the females (Kemal and Rothstein 1988). For example, one or two eggs have been recorded disappearing from 8.7% of the nests of the Eastern Phoebe (*Sayornis phoebe*) and 10.6% of the nests of Abert's Towhee (*Pipilo aberti*), both accepters of Brown-headed Cowbird eggs (Finch 1983, Rothstein 1986). It is unlikely that these eggs were rejected by these two hosts.

Why do some Great-tailed Grackles reject conspecific eggs? CBP has not selected for egg rejection in Great-tailed Grackles because this behavior rarely occurs, if at all, in this species. Even species that are parasitized by conspecifics rarely reject conspecific eggs and when they do, it is prior to clutch initiation when they do not have to choose between their own eggs and the parasite's egg (Emlen and Wrege 1986, Stouffer et al. 1987, Brown and Brown

1989; see also Vehrencamp 1977, Bertram 1979, Mumme et al. 1983). Species that have evolved rejection in response to cowbird parasitism generally only reject conspecific eggs that are added prior to clutch initiation (Briskie et al. 1992, Bischoff and Murphy 1993, Sealy and Bazin 1995; see also Sealy et al. 1989). One of the few passerine species that displays a greater ability to recognize conspecific eggs than the Great-tailed Grackle is the Northern Masked Weaver (*Ploceus taeniopterus*) (see also Moksnes and Røskaft 1992). CBP occurs at frequencies of 22.8% to 34.7% of nests in Northern Masked Weavers (Jackson 1990, 1992a), so it is evident why this species has evolved the ability to reject conspecific eggs. Some Great-tailed Grackles apparently possess the ability to reject conspecific eggs because ejection has evolved in response to Giant Cowbird (*Scaphidura oryzivora*) parasitism (Chapter 2). Giant Cowbird eggs resemble grackle eggs, hence, enhanced discriminatory ability is needed (Chapter 2).

CHAPTER 2

EVOLUTION OF EGG REJECTION BEHAVIOR IN GRACKLES: IMPLICATIONS FOR HOST-PARASITE CYCLES

INTRODUCTION

Avian brood parasites and their hosts coevolve through a series of intricate reciprocal adaptations (Rothstein 1990). The most obvious host adaptation against brood parasitism is rejection of a parasite's eggs. Once rejection behavior becomes fixed in a host population, it is to the advantage of the parasite to switch to a new host that will accept its eggs, or to evolve mimetic eggs to circumvent rejection (Dawkins and Krebs 1979, Davies and Brooke 1989b, Nakamura 1990, Nakamura et al. in press). If rejection declines in the initial host in the absence of parasitism, the parasite can re-exploit it or switch to another new host once the second host evolves a high frequency of rejection (Davies and Brooke 1989b). Rejection may be lost in the absence of parasitism if a host rejects its own aberrant eggs (Peer and Bollinger 1997a) or through genetic drift (see Rothstein 1990). If rejection is lost, the host-parasite association may persist indefinitely through a cyclical process of parasitism and avoidance (Thompson 1994; see also May and Robinson 1985). In this manner, the costs of rejection behavior are greater than the benefits and the parasites and their hosts can coexist in an evolutionary equilibrium (e.g. Zahavi 1979, Rohwer and Spaw 1988, Marchetti 1992, Lotem et al. 1992, 1995, Soler et al. 1995, Brooker and Brooker 1996).

In contrast to the evolutionary equilibrium hypothesis, the evolutionary lag hypothesis predicts that there may be some time "lag" before the appropriate random mutations and genetic recombinants arise for rejection to

evolve (e.g. Rothstein 1975a, b, 1990, Davies and Brooke 1989a, b, Davies et al. 1996, Sealy 1996), but once it evolves, it should be maintained for long periods of time (Rothstein 1976b, 1990, 1996). Egg rejection may become a neutral trait in the absence of parasitism (Rothstein 1976b, 1990) because brood parasitism is the only context in which birds are regularly subjected to foreign eggs in their nests (Rothstein 1974b, 1990, Peer and Bollinger 1997a, 1998). Accordingly, rejection behavior should be maintained at a high level in the absence of parasitism and hosts should become increasingly intolerant of parasitism, thereby forcing brood parasites to specialize on relatively few host species (Rothstein 1996, Rothstein and Robinson in press).

The grackles (*Quiscalus*) are an ideal group to determine the fate of rejection behavior in the absence of parasitism. They are largely unparasitized by cowbirds (*Molothrus*) and there were high frequencies of rejection in three of the four species tested prior to this study (Rothstein 1975a, Cruz et al. 1985, Carter 1986, Post et al. 1990, Cruz et al. 1995). The Common Grackle (*Q. quiscula*), apparently is an exception; it has seemingly lost rejection in the absence of parasitism (Peer and Bollinger 1997a).

This study consists of three parts to examine the evolution of egg rejection behavior in grackles and its implications for host-parasite cycles. First, I conducted a series of experiments to test the hypothesis that egg rejection in Great-tailed Grackles (*Q. mexicanus*) has evolved in response to Bronzed Cowbird (*M. aeneus*) parasitism. Great-tailed Grackles reject conspecific eggs at a low level (Chapter 1) and in a small-scale experiment Great-tailed Grackles also rejected Bronzed Cowbird eggs (Carter 1986). However, neither form of parasitism has been recorded in nature (Friedmann and Kiff 1985, Carter 1986, MacWhirter 1989, Rohwer and Freeman 1989,

Chapter 1), and conspecific brood parasitism (CBP) is apparently not the selective pressure responsible for rejection in this species (Chapter 1).

Great-tailed Grackle nests were monitored for evidence of cowbird parasitism. Cowbird nestlings were cross-fostered into grackle nests to determine whether they could fledge from nests of the large grackle species (see Peer and Bollinger 1997a); failure to survive, would be indicative of an inappropriate host and such hosts are usually avoided (Davies and Brooke 1989a, Moksnes et al. 1990; but see Rothstein 1976b, Kozlovic et al. 1996). This would indicate that Bronzed Cowbird parasitism has not selected for egg rejection in this species. One population of Great-tailed Grackles sympatric with Bronzed Cowbirds was tested for cowbird egg rejection. A second Great-tailed Grackle population allopatric with Bronzed Cowbirds was also tested for egg rejection with the prediction that these individuals would demonstrate a lower level of rejection than the sympatric population in accordance with previous studies (Järvinen 1984, Davies and Brooke 1989a, b, Briskie et al. 1992).

The Boat-tailed Grackle (*Q. major*), a sibling species of the Great-tailed Grackle (Avisé and Zink 1988), was tested for evidence of egg rejection behavior. It is one of two grackles whose response to experimental cowbird eggs has not been tested. The Boat-tailed Grackle is not sympatric with any large-bodied brood parasite, and it is not a conspecific brood parasite (MacWhirter 1989, Rohwer and Freeman 1989, Post et al. 1996), hence I predicted that Boat-tailed Grackles would accept cowbird eggs (see Brown et al. 1990).

I quantified variation in the appearance of eggs within grackle clutches and compared this to the level of egg rejection for five of the six extant grackle species to determine whether variation influences the retention of rejection

behavior. Species with high levels of intraclutch egg variation may be more likely to reject their own aberrant eggs, and such behavior would be selected against in the absence of parasitism (Peer and Bollinger 1997a). I predicted that high frequencies of rejection in the absence of parasitism would be correlated with relatively low levels of intraclutch egg variation.

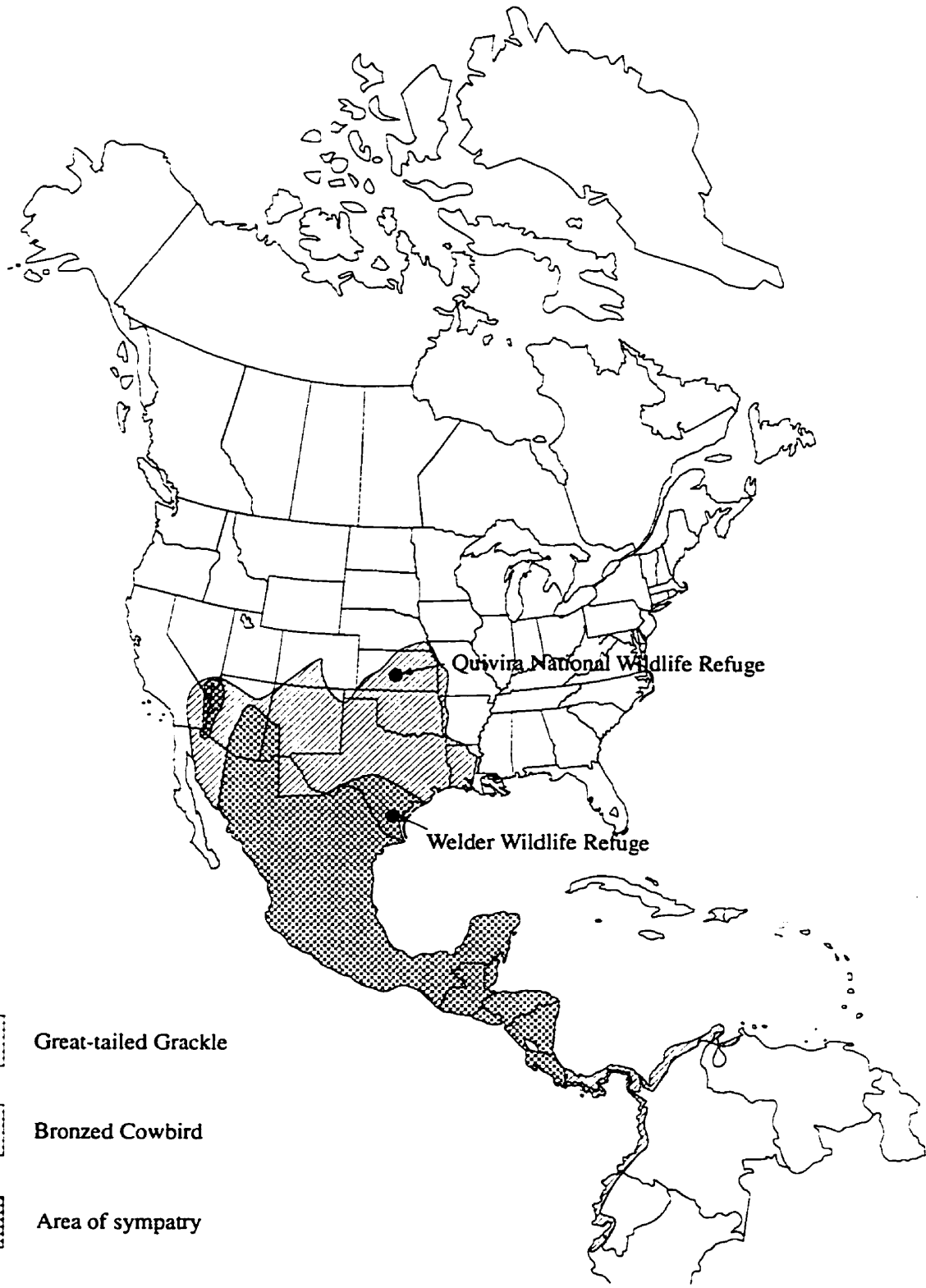
METHODS

STUDY AREA

Most of this study was conducted at the Welder Wildlife Refuge in San Patricio County, TX (28°0' N, 97°5' W), from 1994 to 1996, where Great-tailed Grackles breed in sympatry with both Bronzed and Brown-headed (*M. ater*) cowbirds (Fig. 2.1; see also Lowther 1993). The refuge is in a somewhat unique geographic location in that there are equal numbers of Bronzed and Brown-headed cowbirds present during the breeding season (pers. obs.). To the south, there are mainly Bronzed Cowbirds with very few Brown-headed Cowbirds, and to the north, there are mainly Brown-headed Cowbirds with very few Bronzed Cowbirds (Carter 1986, Price et al. 1995, pers. obs.). The emphasis of this portion of the study was on the interactions between Bronzed Cowbirds and Great-tailed Grackles. Although Brown-headed Cowbirds also occur in this area of south Texas, they are not likely to parasitize this grackle because of the difference in size of the two species (see below). Nevertheless, experiments were conducted with Brown-headed Cowbirds to examine the possibility that they have influenced rejection behavior in the Great-tailed Grackle.

Great-tailed Grackles nested in abundance at the refuge (up to 500 nests annually; see also Tutor 1962), mostly at two lakes, Big Lake and Pollita Lake. Fewer grackles nested at cattle tanks and smaller bodies of water throughout the refuge. The lakes were relatively shallow, not more than 1.5 m

Figure 2.1. Breeding ranges of the Great-tailed Grackle and Bronzed Cowbird and locations of the Welder Wildlife Refuge and Quivira National Wildlife Refuge (after National Geographic Society 1987, Ridgely and Tudor 1989, Lowther 1995).



deep in any location. Grackles nested mainly in bulrush (*Scirpus californicus*) growing in the lakes. Their nesting assemblages were very conspicuous due to their location, large numbers, and the highly vocal courting males.

NEST INSPECTIONS

Brown-headed Cowbirds lay their eggs just prior to sunrise (Scott 1991, Neudorf and Sealy 1994), but when my study began the time of day Bronzed Cowbirds lay was unknown. I determined this by witnessing five parasitism events at Northern Cardinal (scientific names listed in Table 2.2) nests. I directly observed three events, including one in which two females parasitized a single nest the same morning, and two laying events were estimated. The estimates were calculated by taking the midpoint of repeated visits to each nest, 8 min and 4 min apart, respectively (Scott 1991). Sunrise data were obtained from the website of the United States Naval Observatory Astronomical Applications Department (<http://aa.usno.navy.mil/AA/>).

Bronzed Cowbirds lay their eggs $18.2 \text{ min} \pm 1.7$ before sunrise (range 14-24 min before sunrise). Therefore, to detect cowbird eggs before they were ejected (Scott 1977) I monitored grackle nests daily, typically beginning 30 min prior to sunrise (05:00-05:15 CST). A number of hosts reject cowbird eggs immediately (Rothstein 1977, Sealy and Bazin 1995, Sealy and Neudorf 1995, Sealy 1996, see below), hence, the early watches allowed an accurate determination of the parasitism frequency. The nests of other species on the refuge were monitored less regularly, to determine which species were parasitized.

CROSS-FOSTERING EXPERIMENTS

Bronzed and Brown-headed cowbird eggs were collected and incubated, and nestlings were then cross-fostered as soon as they hatched into Great-tailed Grackle nests. I placed cowbird nestlings into grackle nests the same day the grackle nestlings hatched, and up to three days prior to any grackles hatching to approximate the "head-start" cowbirds would gain in naturally parasitized nests (McMaster and Sealy 1998, Peer and Bollinger in press). Great-tailed Grackles have an incubation period of 13-14 d (Peer unpubl. data) and that for the two cowbird species is approximately 11-12 d (Carter 1986, Lowther 1993). Nestling measurements were taken every 1-2 d. Mass was recorded to the nearest 0.01 g using a portable electronic scale. Gape width, culmen length from the nostril to tip of the bill, and tarsometatarsus length were recorded to the nearest 0.01 mm using calipers according to Baldwin et al. (1931). Egg dimensions of Great-tailed Grackles, Bronzed Cowbirds and Brown-headed Cowbirds were also measured with calipers.

EXPERIMENTAL COWBIRD PARASITISM

Texas Great-tailed Grackle population

Great-tailed Grackle nests were experimentally parasitized with real and artificial Bronzed and Brown-headed cowbird eggs (Table 2.1). Artificial cowbird eggs were made of wood and painted with waterbased acrylic paints and coated with an acrylic sealer to mimic genuine cowbird eggs (see Peer and Bollinger 1997a, 1998). Bronzed Cowbird eggs are pale blue and immaculate; Brown-headed Cowbird eggs are white and densely spotted with brown and gray. Only a single egg type was added to each nest, and most nests were experimentally parasitized during laying when 1-2 host eggs were present. The remaining nests were parasitized during early incubation. Most cowbird eggs

Table 2.1. Attributes of real and artificial cowbird and grackle eggs mentioned in this study.

Egg Type	Length x Breadth (mm) ^a	<i>n</i>	Mass (g) ^a	<i>n</i>	Volume (ml) ^b	Ref. ^c
Artificial Cowbird	22.7 (0.1) x 16.7 (0.1)	30	2.7 (0.2)	30	3.2	1
Oversized Artificial	34.4 (0.1) x 22.7 (0.1)	15	6.7 (0.1)	15	9.0	1
Bronzed Cowbird	24.0 (0.2) x 18.9 (0.2)	16	4.2	61	4.4	1, 2
Brown-headed Cowbird	21.4 (0.2) x 16.1 (0.2)	13	3.2	40	2.8	1, 3
Giant Cowbird	32.5 x 26.3	12	11.7	6	11.4	4
Great-tailed Grackle	31.8 (0.3) x 22.4 (0.2)	52	8.2 (0.3)	8	8.1	1
Boat-tailed Grackle	31.9 (0.06) x 21.8 (0.03)	657	8.1 (0.03)	869	7.7	5

^a Standard errors are given in parentheses when known.

^b Volume calculated by the formula $V = 0.51 \times LB^2$, where L = egg length and B = egg breadth (Hoyt 1979).

^c References: 1 = this study, 2 = Rahn et al. 1988, 3 = Ankney and Johnson 1985, 4 = Haverschmidt 1967, 5 = Bancroft 1984.

were added to grackle nests from 05:00-12:00 (CST). No grackle eggs were removed in the experiments, because egg removal behavior varies in Brown-headed Cowbirds (Sealy 1992), and Bronzed Cowbirds puncture host eggs (Friedmann 1929, Carter 1986, see below). Whenever possible, the response of the adults was observed following parasitism. Nests were checked every 24 h for evidence of rejection, and also in some cases, one and nine hours following parasitism. Cowbird eggs were considered rejected if they were absent from an active nest, and accepted if they remained for at least five days. Host eggs that were damaged or missing following ejections were also noted. Control nests were treated in the same manner as experimental nests (i.e. eggs were numbered and nest contents checked daily) except no parasitic eggs were added.

Another experiment was performed to determine whether grackles recognize their own eggs and reject eggs that are sufficiently different from their own (true egg recognition), or whether they simply reject the discordant egg (rejection via discordancy; Rothstein 1982a). Grackle clutches were manipulated so that their own egg was the discordant element. After completion of the typical three-egg clutch, two grackle eggs were removed and replaced with two artificial, grackle-sized Bronzed Cowbird eggs (Table 2.1). The manipulated clutch consisted of two artificial cowbird eggs and one grackle egg. Oversized Bronzed Cowbird eggs were used to control for the effects of partial clutch reduction that often cause birds to desert their nests (Rothstein 1982a, 1986, Hill and Sealy 1994; see also Peer and Bollinger 1998). This experiment was otherwise conducted using the same protocol as that for the single-egg experiments described above.

Kansas Great-tailed Grackle population

A population of Great-tailed Grackles allopatric with Bronzed Cowbirds was tested for egg rejection behavior at the Quivira National Wildlife Refuge in Stafford County, Kansas (38°2' N, 98°5' W), in June, 1995 (Fig. 2.1). Brown-headed Cowbirds are present in Kansas (see Lowther 1993), but they are not likely to parasitize Great-tailed Grackles (see below). Nests were parasitized with artificial Bronzed Cowbird eggs following the same protocol used to test the Texas population.

Florida Boat-tailed Grackle population

A Boat-tailed Grackle (*Q. major*) population was tested for egg rejection behavior in Highlands County, FL (27°4' N, 81°4' W), near the Archbold Biological Station in March and April, 1996 (Fig. 2.2). Boat-tailed Grackles are similar in size to Great-tailed Grackles, thus they are also unlikely hosts of the Brown-headed Cowbird. Nevertheless, the study was conducted here because this area of Florida is mostly free of cowbirds (Woolfenden and Fitzpatrick 1996, Cruz et al. in press). Florida is being colonized from the north by Brown-headed Cowbirds, from the south by Shiny Cowbirds (*M. bonariensis*), and from the west by Bronzed Cowbirds (Robertson and Woolfenden 1992, Cruz et al. in press). No nests of any hosts in Florida had been found parasitized by either Bronzed or Shiny cowbirds at the time of this study. Artificial Bronzed Cowbird eggs were added to Boat-tailed Grackle nests following the same protocol used for the Great-tailed Grackle populations.

ANALYSIS OF INTRACLUTCH EGG VARIATION

I subjectively ranked the differences in appearance of eggs within clutches for all of the extant grackle species, including the Boat-tailed, Carib

Figure 2.2. Breeding range of the Boat-tailed Grackle and location of the Archbold Biological Station (after Post et al. 1996).



Archbold Biological Station

(*Q. lugubris*), Common, Great-tailed, and Greater Antillean (*Q. niger*) grackles. The one species that was not ranked was the Nicaraguan Grackle (*Q. nicaraguensis*), a threatened species that occurs in Nicaragua and northern Costa Rica, of which little is known. Great-tailed Grackle eggs were ranked in the field in Texas and from a museum collection, and the other grackle eggs were ranked using museum collections. Clutches were ranked using a method similar to Møller and Petrie (1991; see also Braa et al. 1992, Moksnes 1992, Moksnes and Røskft 1992): (1) all eggs appeared the same, (2) at least one egg was moderately different, (3) at least one egg was dramatically different, and (4) all eggs differed.

STATISTICAL ANALYSES

A Fisher exact test was used to compare the number of Great-tailed Grackles and Boat-tailed Grackles that rejected cowbird eggs within 24 h . An approximate *t*-test was used to test for differences between cowbird and grackle mass, gape width, culmen length, and tarsometatarsus length at hatching. This *t*-test does not assume equality of variances. The degrees of freedom are approximated and are conservative relative to *t*-tests in which equal variances are assumed (Zar 1996). The Kruskal-Wallis test was used to analyze intraclutch egg variation and nonparametric multiple comparisons for unequal samples corrected for ties were used to test for differences between the species (Zar 1996:227). Standard errors were used as measures of variance, and $P < 0.05$ was the accepted level of significance. All tests were two-tailed unless otherwise indicated.

RESULTS

FREQUENCY OF COWBIRD PARASITISM

There was no evidence of either Bronzed or Brown-headed cowbird parasitism on the 797 Great-tailed Grackle nests monitored in Texas (Table 2.2). Seven host species were parasitized by at least one cowbird species (Table 2.2).

CROSS-FOSTERING EXPERIMENTS

Six Brown-headed Cowbird nestlings were cross-fostered into Great-tailed Grackle nests and all died at a mean age of 3.7 d, presumably due to starvation. Two died before any grackles hatched, and the remaining four "hatched" the same day as their grackle nestmates up to two days before any grackles. At least four of the six foster nests produced grackle fledglings; the final outcome of two nests was undetermined. Great-tailed Grackle nestlings weighed more, had larger gape widths, culmen lengths, and tarsometatarsus lengths than Brown-headed Cowbirds at hatching (Table 2.3).

Ten Bronzed Cowbird nestlings were cross-fostered into Great-tailed Grackle nests and two fledged. Great-tailed Grackle nestlings also weighed more, had larger gape widths, culmen lengths, and tarsometatarsus lengths than Bronzed Cowbird nestlings at hatching, but the differences were less compared to those with Brown-headed Cowbird nestlings (Table 2.3). The Bronzed Cowbird in nest 94-1 "hatched" one day prior to its only grackle nestmate. Both nestlings fledged. The Bronzed Cowbird weighed 46.2 g on day 12 when it fledged (adult male Bronzed Cowbirds average 66.7 g, females 57.4 g; Dunning 1993). The Bronzed Cowbird in nest 95-30 "hatched" 2.5 d prior to the first grackle nestling and 4.5 d prior to the second. The second grackle nestling was gone two days later. The remaining grackle nestling and Bronzed

Table 2.2. Frequency of Brown-headed Cowbird and Bronzed Cowbird parasitism on hosts at the Welder Wildlife Refuge, Sinton, TX, from 1994-1996. Nomenclature is according to Sibley and Monroe (1990).

Host	<u>Percent of nests parasitized</u>		
	Brown-headed Cowbird	Bronzed Cowbird	Total Nests
Killdeer <i>Charadrius vociferus</i>	0	0	3
Mourning Dove <i>Zenaida macroura</i>	0	0	22
Common Ground Dove <i>Columbina passerina</i>	0	0	3
Yellow-billed Cuckoo <i>Coccyzus americanus</i>	0	0	11
Greater Roadrunner <i>Geococcyx californianus</i>	0	0	4
Scissor-tailed Flycatcher <i>Tyrannus forficatus</i>	0	0	279 ^a
Verdin <i>Auriparus flaviceps</i>	25	0	4
Northern Mockingbird <i>Mimus polyglottos</i>	0	0	40
White-eyed Vireo <i>Vireo griseus</i>	100	0	2
Northern Cardinal <i>Cardinalis cardinalis</i>	27.8	27	115
Painted Bunting <i>Passerina ciris</i>	50	50	2
Olive Sparrow <i>Arremonops rufivirgatus</i>	33.3	33.3	3
Lark Sparrow <i>Chondestes grammacus</i>	0	0	2
Red-winged Blackbird <i>Agelaius phoeniceus</i>	12.5	0	8
Great-tailed Grackle <i>Quiscalus mexicanus</i>	0	0	797
Bullock's Oriole <i>Icterus bullockii</i>	25	0	4

^a One nest contained a Mourning Dove egg.

Table 2.3. Measurements (mean \pm SE) at hatching for Brown-headed Cowbirds ($n = 6$), Bronzed Cowbirds ($n = 10$), and Great-tailed Grackles ($n = 27$).

Measurement	Brown-headed Cowbird	Bronzed Cowbird	Great-tailed Grackle	<i>t</i>	<i>P</i>	df
Mass (g)	2.20 \pm 0.13	3.54 \pm 0.11	6.21 \pm 0.13	-21.89	<0.001	15*
				-16.15	<0.001	30**
Gape (mm)	8.03 \pm 0.13	9.84 \pm 0.26	12.85 \pm 0.17	-22.12	<0.001	23*
				-9.61	<0.001	17**
Culmen (mm)	2.10 \pm 0.11	2.64 \pm 0.06	3.15 \pm 0.05	-8.92	<0.001	7*
				-6.76	<0.001	22**
Tarsometatarsus (mm)	5.40 \pm 0.11	6.77 \pm 0.13	8.85 \pm 0.14	-19.3	<0.001	23*
				-10.67	<0.001	28**

* *t*-test comparing Brown-headed Cowbirds and Great-tailed Grackles

** *t*-test comparing Bronzed Cowbirds and Great-tailed Grackles

Cowbird nestling fledged. This Bronzed Cowbird weighed 37.6 g on day 10 after which it fledged. Five Bronzed Cowbird nestlings died at a mean age of 3.4 d, also presumably as a result of starvation. Two died before any grackles had hatched, and the other three "hatched" the same day as their nestmates, up to three days prior to any grackles. Of these five foster nests two produced grackle fledglings, two were later depredated, and one failed for an unknown reason. Three Bronzed Cowbird nestlings were taken by predators in other nests.

RESPONSES TO EXPERIMENTAL COWBIRD PARASITISM

Texas Great-tailed Grackle population

Great-tailed Grackles ejected 100% of artificial Bronzed ($n = 77$) and Brown-headed ($n = 74$) cowbird eggs, and real cowbird eggs ($n = 3$ Bronzed Cowbird; $n = 6$ Brown-headed Cowbird). One grackle egg was missing following an ejection, so it is possible it was damaged during ejection. Cowbird eggs were ejected almost immediately; the longest a cowbird egg remained was 72 h (Table 2.4). I witnessed 34 ejections, all of which were performed by females. Each female typically looked into the nest, grasped the foreign egg between her mandibles, flew away with the egg and gently placed it into the water or on a lily pad. Once, a male returned to a nest before the female. He repeatedly stuck his head into the nest, but did not eject the egg. The female immediately ejected the egg upon returning. In the egg recognition experiments in which grackle eggs were made the discordant element, each of the 10 oversized Bronzed Cowbird eggs was ejected within 24 h, leaving the single grackle eggs in the nest.

Table 2.4 Time required for Great-tailed Grackles to eject cowbird eggs from experimentally parasitized nests. One-hundred sixty nests were observed every 24 h, 89 of which were also observed one and nine hours after parasitism.

Time	% Rejection^a
1 h	77.5
9 h	88.9
24 h	95.0
48 h	98.1
72 h	100.0

^a Cumulative percent

Kansas Great-tailed Grackle population

Thirteen grackle nests were artificially parasitized. All 13 Bronzed Cowbird eggs were ejected within 24 h, and no grackle eggs were damaged in the process.

Florida Boat-tailed Grackle population

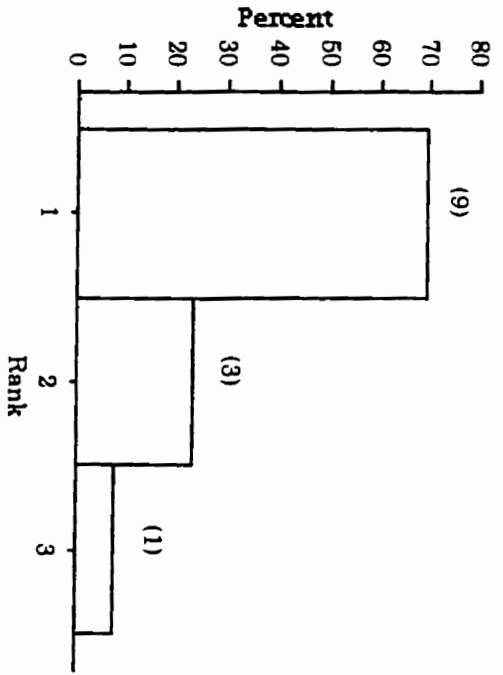
Twenty Boat-tailed Grackle nests were artificially parasitized. All Bronzed Cowbird eggs were ejected within 48 h (16 within 24 h, 3 within 48 h) with no damage to any grackle eggs. One cowbird egg was present at one nest at the 24-h check; the nest was found depredated at the 48 h check. Great-tailed Grackles tended to eject more eggs within 24 h (165/173) compared to Boat-tailed Grackles (16/19) and the difference approached significance (Fisher exact test, $P = 0.08$).

INTRACLUTCH EGG VARIATION

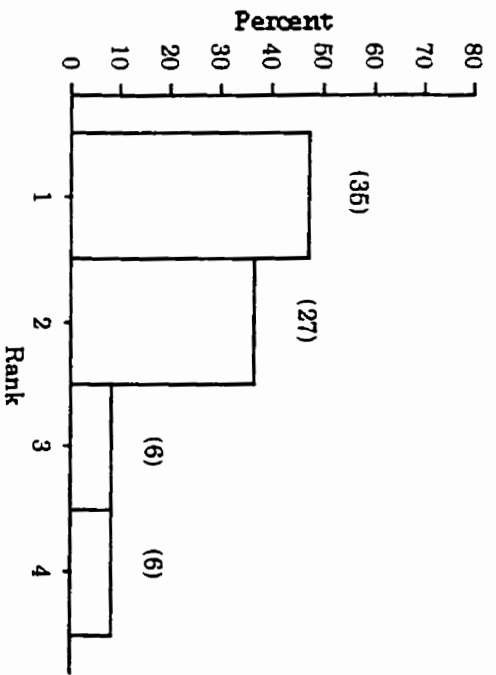
Common Grackles demonstrated the greatest amount of intr clutch egg variation, followed by Great-tailed Grackles, Carib Grackles, and Boat-tailed Grackles (Kruskal-Wallis one-way ANOVA, $H = 13.0$, $df = 3$, $P = 0.005$; Fig. 2.3). Common Grackle clutches had significantly more variation (multiple comparisons) than Boat-tailed ($P < 0.005$) and Great-tailed grackles ($P < 0.05$), but the sample was too small to demonstrate differences with Carib Grackles ($P > 0.05$). There were no significant differences between the other grackles. Only three clutches of the Greater Antillean Grackle were observed (all three demonstrated no variation), so these data were not included in the analysis.

Figure 2.3. Intraclutch egg variation in the grackles (see text for ranking system). Sample sizes for each rank are given above the bars.

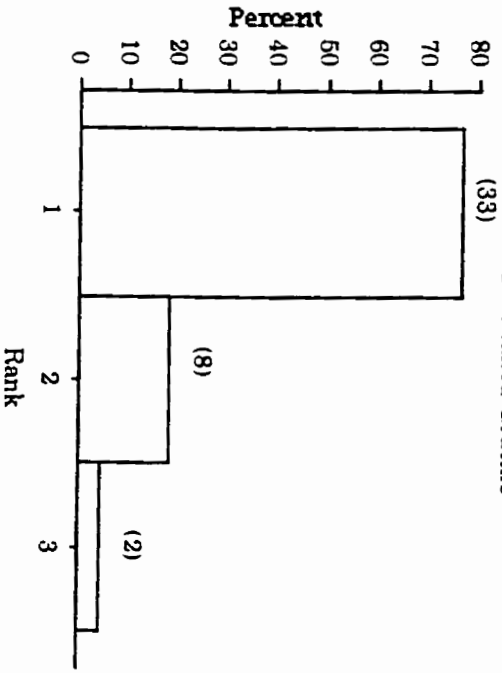
Caribb Grackle



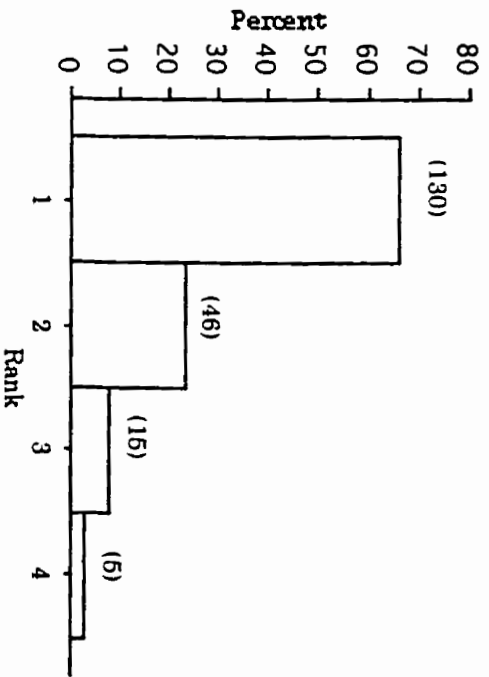
Common Grackle



Bont-tailed Grackle



Great-tailed Grackle



DISCUSSION

LACK OF COWBIRD PARASITISM ON GREAT-TAILED GRACKLES

Neither Bronzed nor Brown-headed cowbirds parasitized Great-tailed Grackles in this study and there are no previous records of parasitism, though the Great-tailed Grackle is sympatric with four cowbird species in different parts of its range (Friedmann 1963, Friedmann and Kiff 1985, Carter 1986). Despite the rapidity with which experimentally added cowbird eggs were rejected, I am confident that Great-tailed Grackles at the Welder Refuge are rarely if ever parasitized by either cowbird species. First, I found no cowbird eggs in grackle nests, despite checking nests just after the time at which cowbirds lay. Using this method, Scott (1977) found 44% of Gray Catbird (*Dumetella carolinensis*) nests were parasitized compared to only 11.4% when nests were checked later in the day. Second, cowbirds were present in the vicinity of grackle colonies only when the cowbirds roosted. Approximately 300 cowbirds roosted each evening at Big Lake in the bulrushes near grackle nests. They left each morning prior to, or just after sunrise; females typically left before sunrise, presumably to parasitize other hosts, whereas the males sometimes left after sunrise. During the remainder of the day, cowbirds were found foraging and searching for host nests elsewhere, and hosts nesting in these areas were parasitized.

Third, Bronzed Cowbirds punctured host eggs, which were found below and in nests of three host species: Northern Cardinals ($n = 24$), Olive Sparrows ($n = 1$), and Yellow-billed Cuckoos ($n = 1$). All hosts that suffered egg puncture were also parasitized by Bronzed Cowbirds, or are known hosts of this cowbird (Clotfelter and Brush 1995), whereas species that were not observed parasitized had no eggs punctured, including the grackle.

SUITABILITY OF GREAT-TAILED AND BOAT-TAILED GRACKLES AS COWBIRD HOSTS

Common Grackles are near or at the uppermost size limit for suitable hosts of the Brown-headed Cowbird (Peer and Bollinger 1997a), hence as predicted, Brown-headed Cowbird nestlings could not compete with the considerably larger Great-tailed Grackle nestlings. Common Grackle nestlings are 2.2 times the mass of Brown-headed Cowbird nestlings at hatching, and Great-tailed Grackles are 2.8 times larger. Boat-tailed Grackles are similar in size to Great-tailed Grackles (Dunning 1993), therefore, Boat-tailed Grackles are also too large to be appropriate hosts of Brown-headed Cowbirds.

Brooker and Brooker (1989) noted that Australian cuckoos (*Cuculus*, *Chrysococcyx*, *Eudynamis*, *Scythrops* spp.) do not parasitize hosts with egg volumes more than 2.3 times that of the cuckoos, because such species are too large to be suitable hosts. The volume of Great-tailed Grackle eggs is 2.9 times that of the Brown-headed Cowbird, and the volume of Boat-tailed Grackle eggs is 2.8 times that of the Brown-headed Cowbird (Table 2.1). Thus, parasitism by this cowbird does not maintain rejection in the allopatric Great-tailed or Boat-tailed grackle populations because these hosts are unsuitable for parasitism and such hosts are typically avoided (Davies and Brooke 1989a, Moksnes et al. 1990; but see Rothstein 1976b, Kozlovic et al. 1996).

The Bronzed Cowbird is the largest of the Molothrine cowbirds (Dunning 1993) and its nestlings weighed 1.8 times less than Great-tailed Grackle nestlings at hatching. Apparently, this size difference was not too large to overcome as 28.6% of Bronzed Cowbird nestlings that were not depredated fledged. This is not surprising because Bronzed Cowbirds parasitize larger hosts more frequently than Brown-headed Cowbirds presently do (Friedmann and Kiff 1985, Carter 1986). Among these is the Chestnut-headed Oropendola

(*Psarocolius wagleri*; Friedmann et al. 1977) (males = 214 g, females = 113 g; Dunning 1993) which is larger than the Great-tailed Grackle (males = 191 g, females = 107 g; Dunning 1993). Great-tailed Grackle eggs are also 1.9 times the volume of Bronzed Cowbird eggs (Table 2.1), and thus are less than the maximum size difference noted by Brooker and Brooker (1989). Therefore, the Great-tailed Grackle is a suitable host for the Bronzed Cowbird.

EGG REJECTION BEHAVIOR IN GREAT-TAILED AND BOAT-TAILED GRACKLES

Egg rejection by Great-tailed Grackles confirms the results of Carter (1986) who found that real Bronzed Cowbird eggs were rejected from the four nests he experimentally parasitized. Like other rejecter species, Great-tailed Grackles apparently learn their own egg types and reject eggs that are sufficiently different from their own (Rothstein 1975c, 1982a, Lotem et al. 1995, Sealy and Bazin 1995). Great-tailed Grackles did not reject their own eggs even when they were the discordant element, but rather displayed true egg recognition behavior. Rejection by Boat-tailed Grackles is contrary to Post et al. (1996) who stated that these grackles "accept the eggs of other species" in South Carolina. Red-winged Blackbird (*Agelaius phoeniceus*) and Shiny Cowbird eggs were added to grackle nests during incubation in the context of other experiments, but apparently none of these eggs was rejected (Post pers. comm). Acceptance of Red-winged Blackbird eggs is expected because these eggs are essentially smaller versions of grackle eggs.

Although Great-tailed Grackles are suitable hosts for Bronzed Cowbirds, parasitism by Bronzed Cowbirds is probably not the most significant factor selecting for egg rejection in this grackle species. This does not mean that Bronzed Cowbirds do not occasionally, or have not parasitized Great-tailed

Grackles in the past. However, rejecters demonstrate a tolerance toward foreign eggs that is directly proportional to the degree of divergence between the appearance of their eggs and the eggs of the cowbirds that parasitize them (Rothstein 1975c, 1982b). In other words, if a rejecter species' eggs are similar in appearance to those of the cowbird, the rejecter will require more discriminatory ability to recognize and reject the cowbird egg compared to rejecters whose eggs are very different from cowbird eggs. A rejecter with highly divergent eggs can afford to be more tolerant because it can reject the cowbird egg and still avoid rejecting its own eggs, whereas hosts with eggs that resemble cowbird eggs must be more intolerant to ensure the cowbird egg is rejected (Rothstein 1982b).

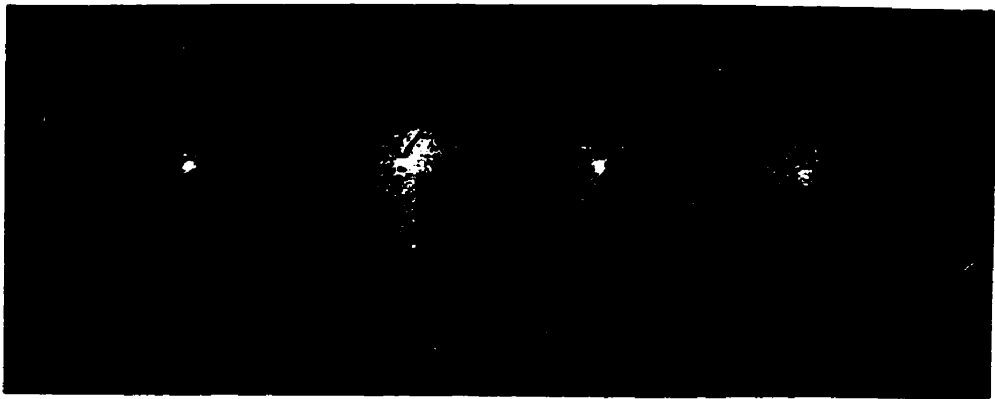
Rothstein (1982b) demonstrated this by recording the responses of Gray Catbirds and American Robins (*Turdus migratorius*) to variations in three egg parameters: background color, maculation pattern, and size. Robin eggs differ from cowbird eggs in every respect, whereas catbird eggs resemble cowbird eggs in size, and as a result catbirds were more intolerant of foreign eggs than robins. One measure of this intolerance was how fast the foreign eggs were rejected. Robins rejected 57.8% of cowbird eggs from artificially parasitized nests within 24 h, whereas catbirds rejected 76.9%. Great-tailed Grackles in both the Texas and Kansas populations rejected 95.4% (165 of 173) of cowbird eggs within 24 h, indicating that this grackle is even more intolerant of foreign eggs than the catbird. Boat-tailed Grackles demonstrated similar intolerance as 84.2% (16 of 19) of rejections occurred within 24 h. Great-tailed Grackle eggs (and Boat-tailed Grackle eggs) differ from those of the Bronzed Cowbird in all three parameters. Bronzed Cowbird eggs are smaller, pale blue, and immaculate, whereas grackle eggs are larger, light blue with brownish-black scrawls that sometimes resemble spots. If Bronzed Cowbird parasitism was

the selective pressure responsible for egg rejection, then the Great-tailed Grackle could afford to be much more tolerant, like the robin.

The intolerance of Great-tailed Grackles is further evident in that some individuals eject conspecific eggs (Chapter 1). There is no reason for Great-tailed Grackles to recognize and eject conspecific eggs unless they are parasitized by a species with eggs that resemble their own. In fact, such refined ability would be more harmful than beneficial as they would be more likely to commit recognition errors (e.g. Lotem et al. 1992, 1995). I suggest egg rejection in Great-tailed and Boat-tailed grackles evolved in response to Giant Cowbird (*Scaphidura oryzivora*) parasitism. Giant Cowbirds parasitize almost exclusively large-bodied, colonial icterines that build pendant nests (Friedmann 1929, Robinson 1988, Webster 1994). Great-tailed and Boat-tailed grackles are large-bodied, colonial icterines, but they build open-cup nests. This does not preclude parasitism, because there is a record of Giant Cowbird parasitism on the open-cup nesting Green Jay (*Cyanocorax yncas*; Friedmann 1963).

Most significantly, the eggs of the Giant Cowbird resemble those of Great-tailed and Boat-tailed grackles (Fig. 2.4a, b, c). Kuschel (1896) noted that the eggs of the Giant Cowbird resembled those of grackles more than the eggs of the *Molothrus* cowbirds. Variability in the eggshell pattern of Giant Cowbirds exists (see Smith 1968:290); however, they are similar to Great-tailed and Boat-tailed grackle eggs in size (Table 2.1), background color, and scrawling pattern, with the exception of the "dumper" egg type that is immaculate, pale blue or white (Smith 1968). Parasitism by Giant Cowbirds would necessitate the refined recognition ability exhibited by these two grackles. This is similar to Bramblings (*Fringilla montifringilla*), Chaffinches (*F. coelebs*), and Reed Buntings (*Emberiza schoeniclus*) which reject conspecific eggs, yet this form of parasitism does not regularly occur in these species

Figure 2.4. Clutches of the (a) Giant Cowbird, (b) Great-tailed Grackle, and (c) Boat-tailed Grackle.



(Braa et al. 1992, Moksnes and Røskoft 1992, Moksnes 1992). Instead, these hosts may have evolved this ability because they were parasitized by Common Cuckoos (*Cuculus canorus*) that laid mimetic eggs (Moksnes 1992).

Giant Cowbirds are sympatric with Great-tailed Grackles from southern Mexico to northern South America (Sibley and Monroe 1990), but Giant Cowbird parasitism on Great-tailed Grackles has not been recorded (Friedmann 1963). This may be because there have been no in-depth studies of this grackle in Central or South America. It is also possible that cowbird eggs are ejected before grackle nests are observed (see above), or that the Great-tailed Grackle, or its ancestor, may have been parasitized by Giant Cowbirds in the past and is now avoided because it is a rejecter (Sealy and Bazin 1995, Peer and Bollinger 1997a). Similar to grackles and cowbirds throughout the western hemisphere, Great-tailed Grackles and Giant Cowbirds occupy the same habitats (Post and Post 1987, Post et al. 1990, Skutch 1996, this study, Peer pers. obs.). They forage together on the ground and also in association with large mammals (Skutch 1996), hence Giant Cowbirds could easily locate Great-tailed Grackle nests by following them back from their common feeding grounds (Post and Post 1987). Furthermore, Great-tailed Grackles nest in large colonies, which would make them obvious targets for parasitism (Post and Wiley 1977, this study).

Giant Cowbirds are not sympatric with Boat-tailed Grackles. The most parsimonious explanation for rejection in Boat-tailed Grackles is that rejection behavior was inherited from a common ancestor with the Great-tailed Grackle. Boat-tailed and Great-tailed Grackles are sibling species (Avisé and Zink 1988) that were considered the same species until it was demonstrated that there is no introgression in the zone of sympatry (Selander and Giller 1961). Rejection may have evolved in the ancestor of these two species prior to their split during

the Pleistocene (see Selander and Giller 1961), and has been maintained by the Boat-tailed Grackle for at least 10,000 years in the absence of parasitism. This is a very conservative estimate because the Pleistocene ended 10,000 years ago and began 1.8 million years ago (Futuyma 1998), so rejection has likely been maintained in the absence of parasitism for some length of time in between these two extremes. There are no records of cowbird parasitism on Boat-tailed Grackles (Friedmann and Kiff 1985, Post et al. 1996). Hence, the Boat-tailed Grackle has probably never been parasitized, but its common ancestor with the Great-tailed Grackle was ostensibly parasitized. Possibly, Boat-tailed Grackles evolved rejection in response to parasitism by a large-bodied brood parasite that has subsequently gone extinct. If this was true, then I would expect that many hosts in eastern North America would also reject foreign eggs as a result of past parasitism. However, relatively few North American hosts display rejection (Rothstein 1975a, 1992, Chapter 3).

Rejection also has been maintained in the two Great-tailed Grackle populations I studied, despite the fact they are not parasitized. It is unknown how long these populations have been free from parasitism. Great-tailed Grackles may be parasitized by Giant Cowbirds in the southern portion of their range and gene flow from these populations may help to maintain rejection in the unparasitized populations. This seems improbable though, as rejection occurs at 100% of nests and if gene flow was responsible the level of rejection would likely be more variable (Rothstein 1975a, Järvinen 1984, Briskie et al. 1992).

EVOLUTION OF EGG REJECTION BEHAVIOR IN GRACKLES

Egg rejection behavior has most commonly evolved in response to interspecific brood parasitism (IBP; Rothstein 1990). CBP also selects for egg

rejection; however, it is much more difficult to recognize conspecific eggs (Sealy et al. 1989, Peer and Bollinger 1997a; but see Jackson 1990, Moksnes and Røskaft 1992, Chapter 1). The only other circumstances under which egg recognition and rejection are selected are dense colonial nesting and nest usurpation. Species that nest colonially on the ground or on cliffs, typically seabirds, recognize their eggs to avoid confusing them with those of nearby conspecifics (Tschanz 1959, Buckley and Buckley 1972). At least one species that lays its eggs in nests it usurps, the Mourning Dove (*Zenaida macroura*), also rejects the eggs of the former nest owner (Peer and Bollinger 1998). If birds have not been subjected to one of these four selection pressures, they should not exhibit egg rejection behavior. Otherwise, the only eggs rejected would be their own, and the only circumstance when removal of one's own eggs is beneficial is when they are broken or damaged (Kemal and Rothstein 1988). This is the very reason why brood parasites such as the Brown-headed Cowbird and Shiny Cowbird are currently so successful, to the detriment of many of their hosts (Post and Wiley 1977, Robinson et al. 1995a, b). As the breeding ranges of these two cowbirds expanded, they have come into contact with new hosts that have never experienced brood parasitism and as a consequence possess no anti-parasite behaviors, unless they have inherited rejection from ancestors (see above).

All five grackle species that have been tested exhibit rejection behavior (Table 2.5). It is unknown whether the threatened Nicaraguan Grackle rejects cowbird eggs or whether it is parasitized. There is little doubt that rejection in all grackles has evolved in response to cowbird parasitism, because there is direct evidence that three of these species are at least occasionally parasitized (Table 2.5). The three other selection pressures responsible for egg rejection do not apply to grackles because they are not conspecific brood parasites (Post et

Table 2.5. Frequency of observed cowbird parasitism and egg rejection in the grackles.

Grackle Species	% Parasitism	% Rejection	Reference ^a
Common	$n = 21^b$	12; 17 ^c	1-3
Carib	0-100	69.2	4-8
Greater Antillean	4.1-21.5	85.7	7-10
Boat-tailed	0	100	11, 12
Great-tailed	0	100	12, 13
Nicaraguan	?	?	no information
Slender-billed ^d	?	?	no information

^a References: 1 = Rothstein 1975a, 2 = Peer and Bollinger 1997a, 3 = Peer and Bollinger 1997b, 4 = Friedmann and Smith 1955, 5 = Ramo and Busto 1981, 6 = Cruz and Andrews 1989, 7 = Post et al. 1990, 8 = Cruz et al. 1995, 9 = Pérez-Rivera 1986, 10 = Cruz et al. 1985, 11 = Post et al. 1996, 12 = this study, 13 = Carter 1986.

^b Common Grackles have only been reported parasitized 21 times (Peer and Bollinger 1997b; see also Fleischer 1986)

^c Common Grackles are more likely to reject cowbird eggs during the prelaying stage (17.0%) versus the laying and incubation stages (12.0%) of the nesting cycle (Peer and Bollinger 1997a).

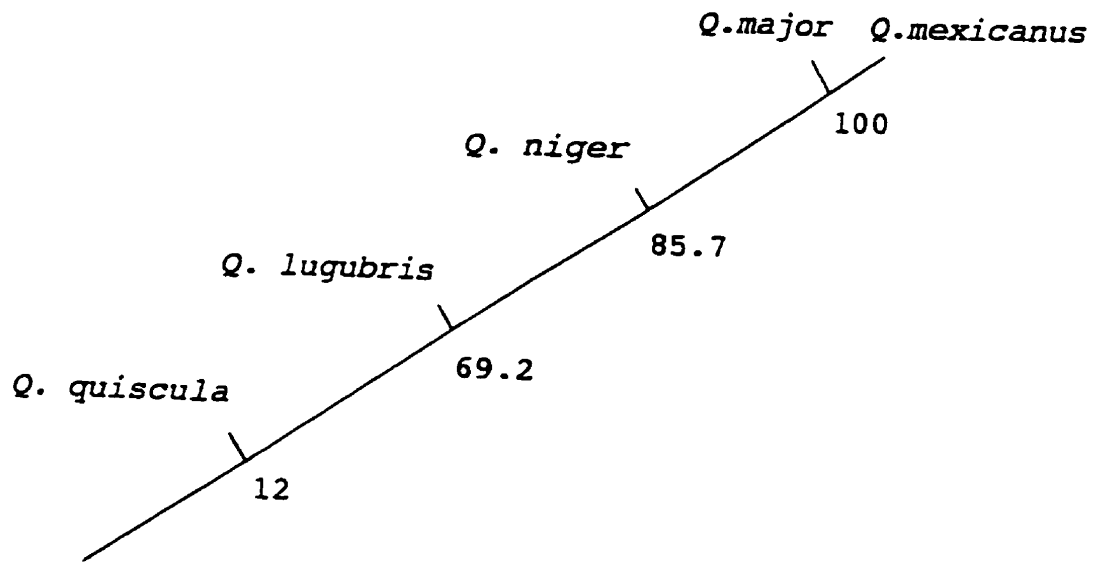
^d The Slender-billed Grackle (*Q. palustris*) is extinct.

al. 1996, Peer and Bollinger 1997a, b, see above, Chapter 1), they do not typically nest on the ground or on cliffs, and they do not usurp the nests of other species.

Peer and Bollinger (1997a) suggested that rejection is either an easily evolved trait in *Quiscalus*, or it evolved once and it is lost so slowly because of the small costs in maintaining it that evidence of it can be found in all members of this genus. The phylogeny of five of the six extant grackle species is known and indicates that they are monophyletic (Lanyon 1994, Lanyon pers. comm.; Fig. 2.5). The rate of rejection is consistent with the phylogeny (Fig. 2.5). The most parsimonious explanation is that rejection evolved once, possibly in the Common Grackle, and the remaining grackles inherited some level of rejection from the Common Grackle depending on the percentage of the Common Grackle population that exhibited rejection when speciation occurred. Rejection probably then increased and reached fixation (e.g. Great-tailed Grackles) when the different grackle species were parasitized by their respective cowbirds.

It is possible that the Common Grackle was never parasitized that often and simply inherited this low level of rejection from an ancestor (Peer and Bollinger 1997a). However, Common Grackles are unique in that they demonstrate this low level of true egg rejection behavior (Peer and Bollinger 1997a). All other Brown-headed Cowbird hosts either reject close to 0% or 100% of cowbird eggs (Rothstein 1975a). Like Peer and Bollinger (1997a), I believe that Common Grackles were parasitized more often in the past and evolved a high level of rejection prior to losing it in the absence of parasitism. In fact, I suggest the Common Grackle was among the first, if not the first host of the Brown-headed Cowbird (see also Fretwell 1973). Common Grackles responded more aggressively to cowbird mounts compared to control mounts

Figure 2.5. Phylogeny and rejection frequencies of five of the six extant grackle species. Numbers indicate rejection frequencies (%). Phylogeny from Lanyon (1994, pers. comm.). Rejection frequencies from Rothstein (1975a), Cruz et al. (1985), Carter (1986), Post et al. (1990), Cruz et al. (1995), Peer and Bollinger (1997a), and this study.



(Peer and Bollinger 1997a), which suggests past interactions between the species. Hamilton and Orians (1965) suggested that brood parasites probably first parasitized colonial species that were closely related to themselves, as often occurs at present (Post and Wiley 1977). Grackles and cowbirds are both members of the tribe Icterini (Sibley and Monroe 1990), and grackles typically nest in colonies (Peer and Bollinger 1997b).

In the initial stages of the evolution of parasitism, cowbirds were probably much less proficient at finding nests of other species. The Common Grackle builds large easily found nests, typically located in colonies, and it has a large population (Peer and Bollinger 1997b). Consequently, there would have been a large supply of easily found grackle nests available for parasitism. Larger hosts in general, were ostensibly parasitized more frequently in the past, because most rejecters of Brown-headed Cowbird eggs are larger species (Rothstein 1975a, Chapter 3). Once these hosts evolved rejection, cowbirds were seemingly forced to parasitize smaller hosts that accept their eggs (Rothstein 1975a, Mason 1980, Peer and Bollinger 1997a, in press, Chapter 3). Indeed, Common Grackles are among the largest of the Brown-headed Cowbird's hosts (Friedmann and Kiff 1985). Common Grackles and Brown-headed Cowbirds also migrate, forage, and roost together (Peer and Bollinger 1997b). Cowbirds could easily locate grackle nests by following them back to their nests from foraging or roosting sites (Post and Wiley 1977, and above).

Finally, the almost complete lack of parasitism on Common Grackles today may be further evidence that this grackle was one of the first hosts of the Brown-headed Cowbird. Rothstein (1976b) suggested that cowbirds may have readily avoided the first few hosts that evolved rejection, but as more and more species evolved rejection, it may have become difficult to avoid these hosts as North American rejecters are such a diverse group (see Chapter 3).

Species that have recently evolved rejection may continue to be parasitized (Rothstein 1976b, Scott 1977, Neudorf and Sealy 1994), whereas those that were among the first to evolve rejection are avoided (Sealy and Bazin 1995).

INFLUENCE OF INTRACLUTCH EGG VARIATION ON THE RETENTION OF REJECTION IN GRACKLES

Rejection has been maintained at approximately 70% or higher in four of the five grackle species largely in the absence of parasitism (Table 2.5). The three grackles breeding in North America are rarely if ever parasitized by cowbirds (Table 2.5). The Greater Antillean and Carib grackles became exposed to parasitism only during the middle of this century after the Shiny Cowbird expanded into the Caribbean (Cruz et al. 1985, Post et al. 1990). It is unlikely that rejection evolved and increased in these populations to their present levels in the 50 or so years since the invasion of this cowbird.

Rejection should spread slowly through these populations because the costs to the reproductive success of larger hosts is small (Rothstein 1975b, Peer and Bollinger 1997a, this study). Cruz et al. (1985) speculated that rejection in Greater Antillean Grackles evolved in response to CBP, but this is doubtful (see above and Chapter 1). It is possible that rejection in the Carib Grackle has been maintained by gene flow with populations in Venezuela that are heavily parasitized by Shiny Cowbirds (Table 2.5), but rejection in the Greater Antillean Grackle cannot be a result of gene flow as this species is confined to the Greater Antilles. In addition to these grackles, almost half of the hosts tested in the Caribbean rejected at least 60% of experimentally introduced cowbird eggs (Cruz et al. 1985, Post et al. 1990, Baltz and Burhans 1998). Four of the seven species are endemic to these islands, which rules out gene flow from parasitized populations. This area may have been inhabited by a

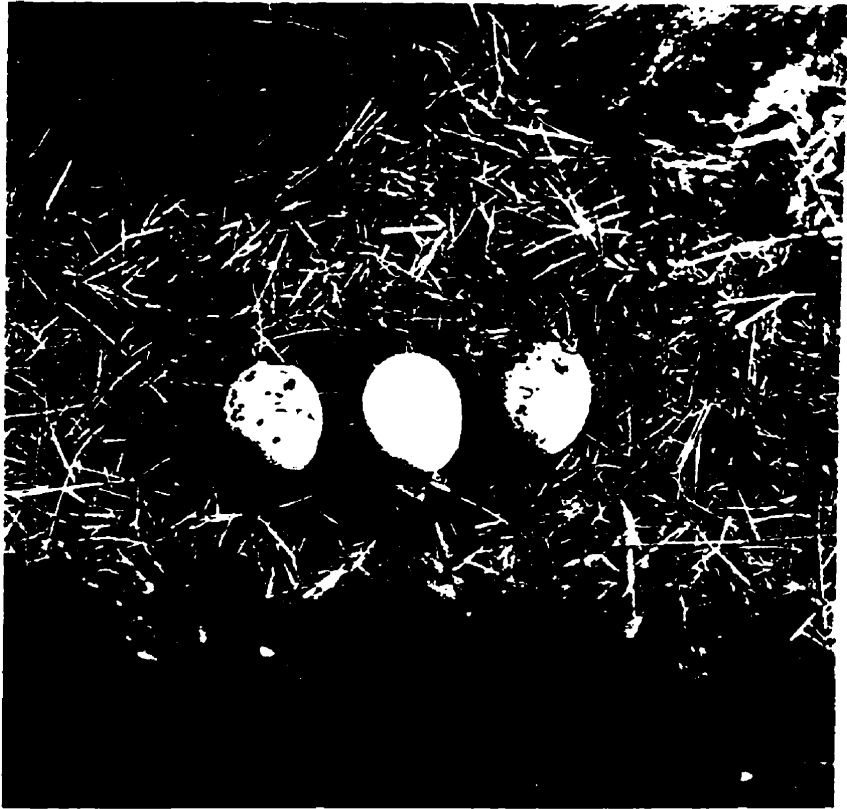
brood parasite in the past and these hosts evolved and also retained rejection at moderate-to-high levels in the absence of parasitism (see also Rothstein 1992).

Presumably, the most significant factor selecting against rejection in the absence of parasitism is rejection of one's own aberrant eggs (e.g. Davies and Brooke 1989b). Recognition errors have been recorded in experimentally and naturally parasitized nests (Davies and Brooke 1988, Marchetti 1992, Lotem et al. 1995, Sealy 1995); however, recognition errors at unparasitized nests are required for rejection to be selected against (Rothstein and Robinson in press). Marchetti (1992) and Lotem et al. (1995) proposed the commission of such errors but other explanations can account for these observations (Chapter 1). Stronger evidence of such errors comes from Yellow Warblers (*Dedroica petechia*) and Great Reed Warblers (*Acrocephalus arundinaceus*) that have mistakenly buried only their own eggs. However, both of these hosts are parasitized frequently (Lotem et al. 1995, Sealy 1995).

There is strong indirect evidence that recognition errors have occurred in the Common Grackle. Peer and Bollinger (1997a) suggested that the reason most Common Grackles lost rejection in the absence of parasitism was due to the high level of intraclutch egg variation in this species (see Fig. 2.6). Indeed, the Common Grackle shows the greatest level of intraclutch egg variation among the grackles I tested (see also Møller and Petrie 1991). Common Grackle clutches are probably also more variable than Greater Antillean Grackles, as the eggs in the few clutches I examined of this species showed no variation.

Rothstein (1982b) found that species avoid committing recognition errors by rejecting an egg only when it deviates from their own in at least two of three parameters (e.g. background color, size, spotting pattern). Birds may

Figure 2.6. Example of intraclutch egg variation in a Common Grackle clutch from Coles County, Illinois.



lay an egg that occasionally differs in one of these parameters, but rarely do they differ in two or more (Rothstein 1982b). The Common Grackle seems to be an exception. Common Grackle eggs tend to vary in the following three parameters (S. I. Rothstein pers. comm.; see also Rothstein 1974a): they increase in size with laying sequence (see also Howe 1978), the eggshell of the last-laid egg is thinner than the earlier-laid eggs, and the last-laid egg is usually lighter in color than the remainder of the clutch in 20-30% of clutches. Thus, the last-laid egg tends to be the largest, thinnest, and a different color. Therefore, these eggs sometimes differ in two of the three parameters necessary to elicit egg rejection - background color and size. Because rejecters imprint on the first eggs they lay, Common Grackles should reject the last egg laid (Rothstein 1974b, 1978, Lotem et al. 1995). In the absence of parasitism, such behavior would be selected against. Presumably, variation must reach the extreme level observed in Common Grackles before rejection is lost, because all grackles tend to demonstrate some intraclutch egg variation (see Fig. 2.3), yet the other grackle species have retained rejection. Thus, it would seem that rejection behavior should be retained in the absence of parasitism in most species.

IMPLICATIONS FOR HOST-PARASITE CYCLES

According to the evolutionary equilibrium hypothesis, rejection behavior is costly and is lost in the absence of parasitism, thereby allowing parasites to switch from exploiting well-defended hosts to accepters, until the rejecters lose the behavior (Marchetti 1992, Thompson 1994). The result is an endless cycle of exploitation and avoidance in which the parasites and their hosts continue to coexist indefinitely. Loss of rejection by the Common Grackle potentially is support for this hypothesis. The Common Grackle can be re-exploited by the

Brown-headed Cowbird. However, there is no need for cowbirds to parasitize this host again because most cowbird hosts are still accepters (Rothstein 1992, Chapter 3). Once the remaining hosts become rejecters, the cowbird will then be forced to switch back to parasitizing species such as the Common Grackle.

The only other apparent example of a host that has lost rejection is the Village Weaver (*Ploceus cucullatus*). This weaver is a host of the Didric Cuckoo (*Chrysococcyx caprius*) in Africa and has apparently lost most of its rejection after it was introduced to the parasite-free island of Hispaniola two centuries ago (Cruz and Wiley 1989). However, there are problems with this study because of a lack of controls on the African populations and the weavers are conspecific brood parasites (see Payne 1997). Rejection in Northern Masked Weavers, for example, is largely a result of CBP rather than cuckoo parasitism (Freeman 1988, Jackson 1992b). Presumably, CBP still occurs in the Hispaniola population, so the loss of rejection is unusual. Possibly, rejection was lost in this population as a result of genetic drift, rather than due to the costs in maintaining it. The effects of genetic drift can significantly affect gene frequencies in small populations (Russell 1986). Thus, the Village Weavers that established the Hispaniola population may not have exhibited the same level of rejection as the African population.

There are also Brown-headed Cowbird and Common Cuckoo hosts that display decreased levels of rejection in allopatric populations compared to those sympatric with the parasites (Davies and Brooke 1989a, Brown et al. 1990, Soler and Møller 1990, Briskie et al. 1992; but see Zuñiga and Redondo 1992). These data were presented as evidence that egg rejection has evolved in response to IBP, with the intent to show that only parasitized populations need to display the behavior. If rejection once existed at higher levels in the

allopatric populations, as it does in sympatric populations, then these too are examples of the loss of rejection. However, individuals in allopatric populations do not require rejection, thus it does not necessarily indicate loss of rejection (Briskie et al. 1992). Furthermore, in none of these examples has rejection been lost completely. Brooke et al. (1998) suggest that these may be examples of phenotypic plasticity. In other words, when hosts are not exposed to parasitism they demonstrate decreased levels of rejection. Rejection is not lost, but rather, the hosts are displaying adaptive phenotypic flexibility in response to environmental conditions.

In contrast to the Common Grackle, the Boat-tailed, Carib, Great-tailed, and Greater Antillean grackles have maintained rejection at high levels. This supports the evolutionary lag hypothesis that rejection behavior should become a neutral trait in the absence of parasitism (Rothstein 1976b, 1990, 1996). Retention of rejection in the absence of parasitism also appears to be the norm for most rejecters of Brown-headed Cowbird eggs (see Rothstein 1975a, b, 1982a, 1996, Friedmann and Kiff 1985, Sealy and Bazin 1995, Murphy 1996, Woolfenden and Fitzpatrick 1996, G.E. Woolfenden pers. comm.), cowbird hosts in the Caribbean (see above), and Common Cuckoo hosts (see Jourdain 1925, Davies and Brooke 1989a, Moksnes et al. 1990, Braa et al. 1992, Moksnes and Røskoft 1992, Nakamura et al. in press). Thus, it appears that most hosts retain rejection which should force brood parasites to specialize on relatively few hosts. For example, once most cowbird hosts become rejecters, cowbirds will be forced to evolve mimetic eggs for only one or a few hosts with similar eggs, similar to Common Cuckoo genets (Wyllie 1981). In response, hosts should improve their discriminatory ability or perhaps evolve less intraclutch egg variation and higher interclutch egg variation (Davies and Brooke 1989b, Øien et al. 1995, Soler and Møller 1996).

CHAPTER 3

CORRELATES OF EGG REJECTION BEHAVIOR IN HOSTS OF THE BROWN-HEADED COWBIRD

INTRODUCTION

One of the most controversial issues surrounding avian brood parasitism is why many birds accept parasitic eggs to the detriment of their reproductive success. Two opposing hypotheses have been proposed to explain this behavior. The evolutionary equilibrium hypothesis suggests that acceptance of parasitism is more adaptive than rejection, because rejection entails costs that outweigh the benefits of this behavior (Zahavi 1979, Lotem et al. 1992, 1995, Marchetti 1992, Soler et al. 1995, Brooker and Brooker 1996). In contrast, the evolutionary lag hypothesis suggests that there may be some time lag after parasitism begins and before egg rejection evolves, but rejection is almost always more adaptive than acceptance (Rothstein 1975a, b, 1990, Davies and Brooke 1989a, b, Davies et al. 1996, Sealy 1996). It is difficult to test these two alternatives, especially evolutionary lag because support for it is usually by default (Sealy 1996, Rothstein and Robinson in press).

Instead of directly testing the evolutionary lag and equilibrium hypotheses, I use a comparative approach to determine which characteristics distinguish accepters and rejecters of Brown-headed Cowbird (*Molothrus ater*) eggs. Rothstein (1975a) concluded that six factors probably were most important in the evolution of egg rejection by birds: (1) eggs that differ in appearance from those of the cowbird, (2) long history of contact with the cowbird, (3) large population size, (4) well-developed nest sanitation, (5) large

bill size, and (6) large, easily-found nests. Rothstein suggested that bill size and easily found nests were the most important, but he did not statistically analyze these correlates. Since Rothstein's (1975a) study, numerous other hosts have been tested for egg rejection. I use the characteristics suggested by Rothstein (1975a), plus characteristics that I identified as being potentially important, including egg predation and taxonomic affiliation, and compare the presence of these traits in rejecters and accepters to determine which are important in the evolution of cowbird egg rejection.

METHODS

I examined eight potential correlates of egg rejection in Brown-headed Cowbird hosts that have been tested experimentally for rejection at a minimum of four nests. There are 23 potential hosts known to reject cowbird eggs at a frequency of $\geq 80\%$ ("rejecters"), five that reject 26-79% ("intermediate rejecters"), and 25 that reject $\leq 25\%$ ("accepters"; Table 3.1). For these analyses, I classified the Common Grackle as a rejecter species (Table 3.1), because Peer and Bollinger (1997a) suggested that this host once rejected close to 100% of cowbird eggs, but has subsequently lost most of this behavior in the absence of parasitism (see also Chapter 2). Thus, it possesses any correlates required for the evolution of rejection. I also classify two intermediate rejecters as rejecters for the analyses. Northern Mockingbirds reject 50% of Brown-headed Cowbird eggs, 75% of Bronzed Cowbird (*M. aeneus*) eggs, and 77.8% of Shiny Cowbird (*M. bonariensis*) eggs (Table 3.1). Eastern Meadowlarks reject 35.7% of Brown-headed Cowbird eggs and 40% of nonmimetic eggs (Table 3.1).

Table 3.1. Rejection status of potential Nearctic hosts of the Brown-headed Cowbird. Only hosts that have been tested experimentally at \geq four nests are included. Nomenclature is according to Sibley and Monroe (1990).

Species	% Rejection	Source ^a
REJECTERS (> 80%)		
Eastern Kingbird <i>Tyrannus tyrannus</i>	100	1, 2
Western Kingbird <i>T. verticalis</i>	100	1, 3
Cassin's Kingbird <i>T. vociferans</i>	100	4
Couch's Kingbird <i>T. couchii</i>	100 ^b	5
Scissor-tailed Flycatcher <i>T. forficatus</i>	100	6, 7
Florida Scrub-Jay <i>Aphelocoma coerulescens</i>	100	8
Western Scrub-Jay <i>A. californica</i>	100	4
Blue Jay <i>Cyanocitta cristata</i>	100	1
American Robin <i>Turdus migratorius</i>	97.8	1
Loggerhead Shrike <i>Lanius ludovicianus</i>	100	9
Gray Catbird <i>Dumetella carolinensis</i>	94.3	1
Sage Thrasher <i>Oreoscoptes montanus</i>	100	10
Brown Thrasher <i>Toxostoma rufum</i>	96.3	1
Curve-billed Thrasher <i>T. curvirostre</i>	100 ^b	5
Crissal Thrasher <i>T. dorsale</i>	100	11
Cedar Waxwing <i>Bombycilla cedrorum</i>	87.5; 40 ^c	1, 12
Eastern Warbling-Vireo <i>Vireo gilvus</i>	100	13
Western Meadowlark <i>Sturnella neglecta</i>	81.8	14
Common Grackle <i>Quiscalus quiscula</i>	17; 12 ^d	1, 15

Boat-tailed Grackle <i>Q. major</i>	100	16
Great-tailed Grackle <i>Q. mexicanus</i>	100	5, 16
Baltimore Oriole <i>Icterus galbula</i>	100	1, 17, 18
Bullock's Oriole <i>I. bullockii</i>	100	17, 19

INTERMEDIATE REJECTERS (26-79%)

Mourning Dove <i>Zenaida macroura</i>	49.4	1, 20
Black-billed Cuckoo <i>Coccyzus erythrophthalmus</i>	41.7	1
Northern Mockingbird <i>Mimus polyglottos</i>	50 ^e	7, 21
Yellow Warbler <i>Dendroica petechia</i>	77; 56.6 ^f	22
Eastern Meadowlark <i>S. magna</i>	35.7 ^g	14

ACCEPTERS (0-25%)

Eastern Phoebe <i>Sayornis phoebe</i>	6.0	1
Least Flycatcher <i>Empidonax minimus</i>	0	23
Barn Swallow <i>Hirundo rustica</i>	7.7	1
House Wren <i>Troglodytes aedon</i>	0	24
Wood Thrush <i>Hylocichla mustelina</i>	0	1
LeConte's Thrasher <i>T. lecontei</i>	0	4
California Thrasher <i>T. redivivum</i>	20	4
Western Warbling-Vireo <i>V. swainsonii</i>	0	13, 25
Yellow-breasted Chat <i>Icteria virens</i>	9.1 ^h	26
Rose-breasted Grosbeak <i>Pheucticus ludovicianus</i>	0	1
Northern Cardinal <i>Cardinalis cardinalis</i>	14.3	1
Grasshopper Sparrow <i>Ammodramus savannarum</i>	0	14
Vesper Sparrow <i>Pooecetes gramineus</i>	0	1, 14
Song Sparrow <i>Melospiza melodia</i>	11.1	1

Lark Sparrow <i>Chondestes grammacus</i>	0	14
Field Sparrow <i>Spizella pusilla</i>	0 ⁱ	27
Chipping Sparrow <i>Spizella passerina</i>	15.8	1
Clay-colored Sparrow <i>Spizella pallida</i>	0	29
Dickcissel <i>Spiza americana</i>	11.1	14
Lark Bunting <i>Calamospiza melanocorys</i>	20	28
Yellow-headed Blackbird	0 ^j	1, 30
<i>Xanthocephalus xanthocephalus</i>		
Red-winged Blackbird <i>Agelaius phoeniceus</i>	3.3	1
Brewer's Blackbird <i>Euphagus cyanocephalus</i>	18.2	28
Orchard Oriole <i>Icterus spurius</i>	25 ^k	28
American Goldfinch <i>Spinus tristis</i>	20.0	1

^a Sources: 1 = Rothstein 1975a, 2 = Sealy and Bazin 1995, 3 = Rohwer and Spaw 1988, 4 = Rothstein unpubl. data, 5 = Carter 1986, 6 = Regosin 1994, 7 = Peer unpubl. data, 8 = Woolfenden unpubl. data, 9 = Rothstein 1982a, 10 = Rich and Rothstein 1985, 11 = Finch 1982, 12 = Rothstein 1976a, 13 = Sealy 1996, 14 = Peer et al. unpubl. data, 15 = Peer and Bollinger 1997a, 16 = Chapter 2, 17 = Rothstein 1977, 18 = Sealy and Neudorf 1995, 19 = Rothstein 1978, 20 = Peer and Bollinger 1998, 21 = Mason unpubl. data *in* Friedmann and Kiff 1985, 22 = Sealy 1995, 23 = Briskie and Sealy 1987, 24 = Pribil and Picman 1997, 25 = Sealy et al. unpubl. data, 26 = Burhans and Freeman 1997, 27 = Burhans 1996, 28 = Sealy unpubl. data, 29 = Hill and Sealy 1994, 30 = Ortega and Cruz 1991.

^b Couch's Kingbirds and Curve-billed Thrashers reject 100% of Bronzed Cowbird eggs (Carter 1986).

^c Cedar Waxwings reject cowbirds eggs more frequently during the laying period or shortly thereafter compared to later in the nesting cycle (Rothstein 1976a, b).

d Common Grackles reject eggs more often when parasitized during the prelaying stage of nesting compared to later stages (Peer and Bollinger 1997a). Common Grackle is considered a rejecter, because it is likely that it once rejected close to 100%, but has subsequently lost most of this behavior (Peer and Bollinger 1997a, Chapter 2).

e Northern Mockingbirds reject 75% of artificial Bronzed Cowbird eggs (Peer unpubl. data).

f Yellow Warblers bury cowbird eggs under new nests and they are more likely to do so when two or fewer host eggs are present (Sealy 1995). Yellow Warblers are also less likely to respond to artificial parasitism compared to natural parasitism (Sealy 1995), therefore, I report responses to natural parasitism.

g Eastern Meadowlarks also reject 40% of nonmimetic eggs (Peer et al, unpubl. data).

h Yellow-breasted Chats reject 54.5% of immaculate eggs (Burhans and Freeman 1997).

i Field Sparrows are more likely to desert parasitized nests if they observe cowbirds at their nests (Burhans in press).

j Yellow-headed Blackbirds reject 33.3% of experimentally added Red-winged Blackbird eggs in at least one population (Dufty 1994).

k Orchard Orioles are parasitized at > 90% of nests in central Illinois (Robinson pers. comm.).

Couch's Kingbirds and Curve-billed Thrashers are included in the analyses although they have been tested only with Bronzed Cowbird eggs (Table 3.1). Rejecters remove any eggs that differ sufficiently from their own (Rothstein 1982a, b, Sealy and Bazin 1995, Chapter 2). It is probable that these two species also reject Brown-headed Cowbird eggs, because their eggs differ from those of the cowbird (Appendix 1). Both of these hosts are sympatric with Brown-headed and Bronzed cowbirds, thus it is possible that parasitism by both cowbirds selected for rejection. Great-tailed and Boat-tailed grackles reject Brown-headed Cowbird eggs (Chapter 2; Table 3.1) and occur in sympatry with Brown-headed Cowbirds. However, rejection in these two species has apparently evolved in response to Giant Cowbird (*Scaphidura oryzivora*) parasitism and they are also unsuitable hosts for Brown-headed Cowbirds (Chapter 2). As a consequence, these two hosts are not included in the analyses.

Mourning Doves, Black-billed Cuckoos, Barn Swallows, House Wrens, and American Goldfinches are all unsuitable hosts because of diets, inappropriate feeding methods, or inaccessible nests, and are rarely parasitized (Friedmann 1963, Rothstein 1975a, Friedmann et al. 1977, Friedmann and Kiff 1985, Middleton 1991, Pribil and Picman 1997, Peer and Bollinger 1998). There is no need for these species to evolve rejection in response to cowbird parasitism, thus they are excluded from the analyses. Although Mourning Doves and Black-billed Cuckoos are intermediate rejecters, they are also not included in the analyses (Table 3.1). Rejection in Mourning Doves has apparently evolved as a manifestation of nest usurpation (Peer and Bollinger 1998). Black-billed Cuckoos are parasitized by conspecifics and Yellow-billed Cuckoos (*Coccyzus americanus*) (Nolan and Thompson 1975, Fleischer et al. 1985, Hughes 1997), so rejection in this species may have evolved in response

to these forms of parasitism. Cedar Waxwings are also unsuitable hosts due to diet; however, they are frequently parasitized and they have evolved rejection (Rothstein 1976a, b). For this reason, Cedar Waxwings are included in the analyses.

Ejection of eggs from nests, pecking the eggs, egg burial, and desertion of parasitized nests have been considered methods of "rejection". However, birds desert nests for a variety of reasons (Rothstein 1975a), and without carefully controlled experiments (e.g. Hill and Sealy 1994) it is impossible to know whether desertion is in response to parasitism or some other disturbance. The significance of egg burial is also questionable as it is often just a continuation of the nest-building process (Rothstein 1975a, Hobson and Sealy 1987). The one apparent exception is the Yellow Warbler, which is unique in its burial of parasitized clutches (Sealy 1992, 1995). In contrast, ejection and pecking parasitic eggs are directly in response to the egg and are "true" rejections (Rothstein 1975a, Peer and Bollinger 1997a). Most "rejections" recorded in accepter species are via nest desertion, whereas those by rejecters are through ejection (Rothstein 1975a). Therefore, I am most concerned with ejection (and pecking in the context of puncture-ejection) of parasitic eggs.

I make two assumptions in these analyses. The first is that all birds see well enough to distinguish cowbird eggs from their own, as long as their eggs differ adequately in appearance from cowbird eggs. The visual ability of each cowbird host species is unknown, but it is known that birds' color vision exceeds that of humans in both spectrum and acuity (Sillman 1973, Gill 1990). Therefore, all hosts probably have the potential to recognize cowbird eggs. The second assumption is that hosts that accept cowbird eggs do not possess other defenses that deter parasitism. Egg rejection is seemingly the most effective adaptation against brood parasitism. Defense of nests against parasites has

been thoroughly studied (Sealy et al. in press), but the effectiveness of this strategy appears to be limited as cowbirds parasitize nests even when hosts are present at their nests (Neudorf and Sealy 1994).

The data were analyzed using the pairwise comparative method (Møller and Birkhead 1992). Closely related species frequently inherit traits from common ancestors, thus treating species as independent data points incorrectly inflates the number of degrees of freedom potentially leading to erroneous conclusions (Harvey and Pagel 1991). The pairwise comparative method controls for phylogeny by comparing pairs of closely related species that differ in the trait that is expected to influence the trait of interest. I used this method because some of my data were discrete and the phylogenies for many of these species were unresolved. Other comparative analyses require continuous data and/or resolved phylogenies (Harvey and Pagel 1991), however these conditions are not necessary to use the pairwise comparative method (Møller and Birkhead 1992). Rejecters were compared to the most closely related accepter species, according to Sibley and Monroe (1990), or if this was not clear, pairs were chosen at random. Pairs were compared using a sign test and all tests were one-tailed because I predicted *a priori* that these correlates would affect rejection. One correlate that was not analyzed using the comparative method was taxonomic affiliation. I wanted to determine whether rejection was common to members of a taxonomic unit (see below), therefore, controlling for phylogeny would defeat the purpose. The correlates I used were as follows:

Correlate 1: Hosts with the longest history of contact with cowbirds should be more likely to reject cowbird eggs. Brown-headed Cowbirds were largely confined to the Great Plains of North America prior to European settlement (Friedmann 1929, Mayfield 1965, Rothstein 1994; but

see Ward and Smith 1998). Cowbirds also prefer open areas and typically avoid large tracts of unfragmented habitat, whether it is forested (Robinson et al. 1995b) or grasslands (Johnson and Temple 1990). Therefore, hosts in the Great Plains and those in relatively open habitats have been in contact with cowbirds the longest and have had the most time to evolve rejection (Rothstein 1975a).

Correlate 2: Large hosts were parasitized more frequently in the past, and as a consequence should be more likely to display rejection.

Hosts approximately the same size as the cowbird (male: 49.0 g, female: 38.8 g; Dunning 1993) or larger were apparently parasitized more frequently in the past as most hosts that display rejection are larger hosts (Rothstein 1975a, Mason 1980, Peer and Bollinger 1997a, in press). It is unclear whether this is a result of large species being superior hosts (Fretwell *in* Rothstein 1975a) or simply because these hosts build larger nests that are easier for cowbirds to locate (Rothstein 1975a). Host masses were obtained from Dunning (1984, 1993).

Correlate 3: Hosts that practice nest sanitation should be more likely to evolve rejection. Rothstein (1975a) suggested that nest sanitation (i.e. fecal sac removal and removal of eggshells from nests) may be a preadaptation for the evolution of egg rejection because the same mechanics are utilized in both behaviors.

Correlate 4: Egg predators should be more likely to evolve egg rejection. Rothstein (1975a) suggested that egg predators may be more likely to evolve rejection because the mechanics involved in this behavior are also similar to those in egg ejection (see also Ortega and Cruz 1988, Peer and Bollinger 1997a).

Correlate 5: Hosts with large populations should have larger and hence, more variable gene pools, which make them more likely to evolve rejection. Species with larger populations (i.e. more diverse gene pools) may have a greater likelihood of evolving rejection (Rothstein 1975a). Population status was determined using Peterjohn et al. (1994) and Price et al. (1995) both based on Breeding Bird Survey (BBS) data. Species that were observed on < 14 BBS routes were classified as small populations. Peterjohn et al. (1994) determined this as the minimum sample required to analyze short-term population trends and this method largely agreed with my subjective assessment of large versus small populations based on the figures from Price et al. (1995). The exceptions were Couch's Kingbird, Crissal Thrasher, and Curve-billed Thrasher, the ranges of which extend into Mexico and Central America where there are no BBS routes. I classified these as having large populations. Peterjohn et al. (1994) made no distinction between the Florida and Western scrub-jays. I classified the Florida Scrub-Jay population as small, because its population size is estimated at 10,000 individuals (Woolfenden and Fitzpatrick 1996).

Correlate 6: Rejection should be common to the members of a taxonomic unit. Rejection may evolve once within a lineage and be retained in the ancestors even through speciation events (Rothstein 1996, Chapter 2; see also Rothstein 1975a). I compared species at the lowest possible taxon above the genus, according to Sibley and Monroe (1990), and considered rejection to be common to a taxonomic unit if ≥ 2 species exhibited it.

Correlate 7: Hosts with eggs that differ in appearance from cowbird eggs should be more likely to recognize and reject cowbird eggs. Presumably it is more difficult for hosts with eggs similar to cowbirds to

recognize cowbird eggs (Rothstein 1975a, Burhans and Freeman 1997, Peer et al. unpubl. data). Eggs were compared using Baicich and Harrison (1997).

Correlate 8: Hosts with large bills can handle eggs more efficiently than those with smaller bills. Species with large bills may be more able to manipulate and eject parasitic eggs (Rothstein 1975a, Rohwer and Spaw 1988). Rothstein (1975a) compared the ratio of bill lengths of hosts to the width of the cowbird egg to determine whether hosts could grasp cowbird eggs. Rohwer and Spaw (1988) attempted to improve this measure with a "grasp index" by multiplying bill length times bill width, measured at the base of the bill. This index is problematic because the width of the bill at its base is of little significance, considering that eggs are grasped at the tip of the bill (Rothstein unpubl. ms.). This results in index values that are misleading in terms of rejection abilities. This is evident in a comparison of the Cedar Waxwing and Gray Catbird (Rothstein unpubl. ms.). Both species have essentially the same grasp indices as calculated by Rohwer and Spaw (1988), 230 and 232, respectively. Therefore, both should have similar ejection abilities. However, the catbird is a grasp-ejecter and the waxwing is a puncture-ejecter. Hosts with larger bills grasp cowbird eggs between their mandibles and remove them, whereas smaller hosts are forced to puncture-eject cowbird eggs and remove them in their open beaks (e.g. Bullock's and Baltimore orioles; Rothstein 1977, Sealy and Neudorf 1995) or remove them on their closed beaks or piecemeal (e.g. Eastern Warbling-Vireos, Sealy 1996). In contrast to their similar grasp indices, the bill lengths differ markedly between these two hosts. Catbird bills are 17% longer than waxwings', thus explaining why they grasp-eject instead of puncture-eject cowbird eggs. Therefore, bill length is the superior predictor of rejection ability (Rothstein unpubl. ms.) and I use bill length to compare the rejection abilities of accepters and rejecters.

Nevertheless, as Rothstein (1975a) noted, this method is only a crude estimate of a host's ability to eject cowbird eggs.

Here I report bill lengths of the species measured by Rohwer and Spaw (1988). For species not measured by Rohwer and Spaw (1988), I measured tomial length from the commissure to the tip of the upper mandible (Rothstein 1975a, Rohwer and Spaw 1988) for five adult females of each species. These measurements were taken at the Field Museum of Natural History, Chicago, and the Zoology Museum of the University of Manitoba.

RESULTS AND DISCUSSION

Historic contact with cowbirds

Clearly, hosts must be parasitized before they evolve rejection (Davies and Brooke 1989b), unless they have inherited rejection from an ancestor (Chapter 2 and below). Hosts whose breeding ranges include the Great Plains have been in contact with the Brown-headed Cowbird the longest (Friedmann 1929, Mayfield 1965, Rothstein 1994; but see Ward and Smith 1998). Presumably, these hosts have had the longest time to evolve rejection (Mayfield 1965, Rothstein 1975a) and there was a strong trend between historic contact and egg rejection (Sign test, $P = 0.06$; Table 3.2). This correlation is strengthened when considering the Eastern and Western meadowlarks and the Blue-gray Gnatcatcher. The Western Meadowlark rejects cowbirds eggs at a higher frequency than the Eastern Meadowlark (see Table 3.1), which may be due to the cowbird having longer contact with the Western Meadowlark (Peer et al. unpubl. data). Likewise, Blue-gray Gnatcatchers (*Polioptila caerulea*) may desert nests in response to parasitism (see below). Populations in Illinois desert 80% of parasitized nests (Helton and Bollinger unpubl. data), whereas populations in New Mexico that have

Table 3.2. Pairwise comparisons between acceptor and rejecter species with respect to historic contact with the Brown-headed Cowbird.

Host Species	Historic Contact^a
LeConte's Thrasher	-
Brown Thrasher	+
California Thrasher	-
Crissal Thrasher	+
Wood Thrush	-
American Robin	+
Western Warbling-Vireo	-
Eastern Warbling-Vireo	+

^a Species with a long history of contact with cowbirds received a "+", and those with a short history of contact received a "-".

seemingly had less contact with cowbirds desert only 45% of parasitized nests (Goguen and Mathews 1996). Despite these results, there are 15 accepter species that ostensibly have been in contact with cowbirds throughout much of their evolutionary histories, and have eggs that differ from cowbirds (see below and Appendix 1). Thus, this correlate can be used to explain why hosts that have recently come into contact with cowbirds accept parasitism, but it cannot be used to explain why some hosts that have had long histories of contact are accepters.

Host mass and nest visibility

Host mass and, hence, nest size and visibility, was also correlated with rejection behavior (Sign test, $P = 0.02$; Table 3.3). Because historic contact with cowbirds affects rejection, I did not include the Wood Thrush, LeConte's and California thrashers, and Western Warbling-Vireo in this, or the remaining analyses. This result suggests that large hosts were parasitized more frequently in the past. This is similar to both Shiny and Bronzed cowbirds that tend to parasitize hosts that are as large or larger than themselves, and consequently most rejecters of the eggs of these cowbird species' tend to be larger (Mason 1986, Carter 1986). Brown-headed Cowbirds may have parasitized large hosts more frequently because they are superior hosts (S. Fretwell unpubl. data *in* Rothstein 1975a, Trine in press), or because their larger nests are easier to locate (Rothstein 1975a). Cowbirds were probably not as adept at finding nests early in their evolutionary history compared to the present, and thus they may have parasitized nests most easily found (Chapter 2).

This also supports the role of historic contact in the evolution of rejection. Just because species were sympatric with the cowbird, does not

Table 3.3. Pairwise comparisons between acceptor and rejecter species with respect to body mass. Masses are from Dunning (1984, 1993).

Host Species	Mass (g)
Eastern Phoebe	19.8
Scissor-tailed Flycatcher	43.2
Least Flycatcher	10.3
Cassin's Kingbird	45.6
Yellow-headed Blackbird	64.5
Eastern Meadowlark	89.0
Red-winged Blackbird	52.6
Western Meadowlark	100.7
Brewer's Blackbird	62.6
Common Grackle	113.5
Orchard Oriole	19.6
Baltimore Oriole	33.8

mean they were parasitized at the same frequencies. For example, parasitism frequencies vary significantly in different regions of North America for the Red-winged Blackbird, Wood Thrush, and numerous grassland hosts (reviewed in Robinson et al. 1995a). Therefore, once the frequently parasitized large hosts evolved rejection, cowbirds may have been forced to switch to new hosts, i.e. smaller hosts (Rothstein 1975a, Mason 1980, Peer and Bollinger 1997a, in press). Accordingly, these small hosts would have had less time to evolve rejection, hence, the large number of small accepter species. Therefore, historic parasitism, in the context of host body mass and nest size, may account for the presence or absence of rejection and is support for evolutionary lag.

Nest sanitation

Rothstein (1975a) suggested that nest sanitation may be a preadaptation for the evolution of egg rejection (see also Ortega and Cruz 1988). Heightened nest sanitation may be manifested in the removal of foreign objects, such as cowbird eggs, and the mechanics involved in nest sanitation are similar to those used in egg rejection (Rothstein 1975a). However, Rothstein (1975a) found no pattern based on this criterion. A pairwise comparative analysis was not possible for this correlate because all accepter and rejecter hosts whose nest sanitation status is known, practice this behavior (Appendix 1). Thus this correlate does not appear to influence egg rejection behavior. Moreover, the Black-billed Cuckoo demonstrates a low level of true egg rejection behavior, yet it does not always remove eggshells from its nest (Rothstein 1975a).

Egg predation

Rothstein (1975a), Ortega and Cruz (1988), and Peer and Bollinger (1997a) speculated that egg predators may evolve rejection more readily because of the similarities between these behaviors. There was no apparent correlation between egg predation and egg rejection; only one pair differed, Orchard and Baltimore orioles (Appendix 1). Thus, despite the similarity in mechanics between the two behaviors, egg predators are not more likely to have evolved egg rejection (see also Yom-Tov 1976, Soler and Møller 1990).

Population size

Pairwise comparisons were not possible for this trait because most hosts had large populations (Appendix 1). The exceptions were the Florida Scrub-Jay and the LeConte's and California thrashers. The Florida Scrub-Jay apparently inherited rejection from an ancestor as it is isolated from parasitism (see Chapter 2 and below) and the thrashers were excluded from this analysis because of their short history of contact with cowbirds. Population size and, hence, gene pool, may be a constraint on the two thrasher species. However, the remaining accepters all have large populations and therefore this correlate cannot explain acceptance.

Taxonomic affiliation

Taxonomic affiliation was significantly correlated with rejection behavior; 20 of 23 rejecters were members of the same taxon, whereas only eight of 15 accepters were affiliated with rejecters (Fisher exact test, $P = 0.0004$; Appendix 1). The 23 rejecter species are represented by eight taxa. Rejection is common to all of the kingbirds, jays, and most of the mimids and icterines that have been tested. The Loggerhead Shrike appears to have

inherited rejection from its ancestors that are parasitized by Common Cuckoos (*Cuculus canorus*) (Rothstein 1996; see also Moksnes and Røskoft 1995). This suggests that once rejection evolves in a lineage it is usually retained even through speciation events (Rothstein 1990, 1996, Chapter 2). This correlate also is support for evolutionary lag because it suggests rejection behavior is not costly in the absence of parasitism (see Chapter 2); however, it does not explain why rejection evolves in the first place.

Egg appearance

There is little doubt that egg appearance is a significant constraint on the evolution of rejection. However, no comparison was possible for this correlate, because only four hosts have eggs that match cowbird eggs: Yellow-breasted Chat, Rose-breasted Grosbeak, Northern Cardinal, and Song Sparrow (Appendix 1). Presumably, this makes recognition of cowbird eggs very difficult as all are accepters (see also Rothstein 1975a). This is evident in Yellow-breasted Chats which reject immaculate eggs (54.5%) more frequently than spotted cowbird eggs that resemble their own (9.1%; Burhans and Freeman 1997). At least five other hosts are also more likely to reject cowbird eggs that differ the most from their own eggs: Northern Mockingbirds (Peer unpubl. data), Chalk-browed Mockingbirds (*M. saturninus*; Fraga 1985), Brown-and-Yellow Marshbirds (*Pseudoleistes virescens*; Mermoz and Reboreda 1994), and Yellow-winged Blackbirds (*Agelaius thilius*; Fraga 1985). Grasshopper Sparrows, Yellow Warblers, and Eastern and Western meadowlarks also have eggs that resemble cowbird's but differ in size. Apparently, Western Meadowlark eggs differ enough for them to recognize cowbird eggs because they eject cowbird eggs at a high frequency (Table 3.1).

There may be an evolutionary equilibrium in these hosts that have eggs that resemble cowbird eggs depending on the costs of rearing cowbirds (see also Rothstein and Robinson in press). For example, Northern Cardinals suffer small losses when parasitized (Scott and Lemon 1996). Therefore, it may be more beneficial for cardinals to accept cowbird eggs than risk ejecting their own eggs (e.g. Lotem et al. 1992, 1995, Davies et al. 1996).

Bill size

Rothstein (1975a) and Rohwer and Spaw (1988) found that rejecters had larger bills than accepters, but these authors did not conduct statistical analyses to corroborate their conclusions. Pairwise comparisons, nevertheless, confirm their conclusions (Sign test, $P = 0.002$; Table 3.4, Appendix 1). Rohwer and Spaw (1988) argued that small bill size is a significant constraint in the evolution of rejection, and suggested that it is less costly for smaller hosts to accept parasitism and raise cowbirds than to attempt to puncture-eject the cowbird eggs. The host's bill may deflect off the thick-shelled cowbird egg (see Spaw and Rohwer 1987, Picman 1989), thereby damaging some of the host's own eggs. According to the "puncture-resistance" hypothesis (Rohwer and Spaw 1988), bill size constraints have resulted in an evolutionary equilibrium that accounts for the acceptance of cowbird eggs. However, Sealy (1996) found that the 15 g Eastern Warbling-Vireo rejects cowbirds eggs via puncture-ejection. Sealy (1996) compared the damage incurred by the vireo and the larger Baltimore Oriole (34 g), also a puncture-ejecter, and found that vireos lost only 0.29 eggs for every cowbird egg ejected, whereas orioles lost 0.38 eggs. The cost of acceptance clearly exceed those of rejection in warbling vireos, which typically raise none of their own young when they accept parasitism (Rothstein et al. 1980).

Table 3.4. Pairwise comparisons between accepter and rejecter species with respect to bill length.

Host species	Bill length (mm \pm SD)	Reference ^a
Eastern Phoebe	20.2 \pm 0.5	1
Scissor-tailed Flycatcher	25.6 \pm 1.2	2
Least Flycatcher	15.9 \pm 1.0	2
Cassin's Kingbird	26.4 \pm 1.4	2
Yellow-headed Blackbird	20.8 \pm 1.1	2
Eastern Meadowlark	28.5 \pm 1.9	1
Red-winged Blackbird	19.1 \pm 0.9	1
Western Meadowlark	31.0 \pm 3.2	2
Brewer's Blackbird	21.1 \pm 0.8	1
Common Grackle	34.2 \pm 1.2	2
Orchard Oriole	17.3 \pm 0.6	2
Baltimore Oriole	21.7 \pm 0.9	2

^a References: 1 = Rohwer and Spaw 1988, 2 = this study.

Sealy (1996) noted that the Western Warbling-Vireo, which is slightly smaller than the Eastern Warbling-Vireo in both bill size ($16.2 \text{ mm} \pm 0.93$ vs. $17.6 \text{ mm} \pm 0.94$, respectively) and mass (12 g vs. 15 g), may be below the minimum size requirement to evolve rejection. There is little doubt that large bills are beneficial in the evolution of egg rejection. Nevertheless, desertion is always an option for the Western Warbling-Vireo. Indeed, the 5-7 g Blue-gray Gnatcatcher appears to desert parasitized nests (Helton and Bollinger unpubl. data; see also Goguen and Mathews 1996). Gnatcatchers incur costs by deserting nests, because re-nesting attempts are significantly less successful than first nests (Helton and Bollinger unpubl. data). However, the decreased chance of success in re-nesting is still the better option because no gnatcatcher young fledge from parasitized nests (Helton and Bollinger unpubl. data). Three other smaller hosts also appear to desert in response to parasitism: Prothonotary Warblers (*Protonotaria citrea*; Petit 1991), Yellow Warblers desert parasitized clutches by burying them (Sealy 1992, 1995), and Field Sparrows frequently desert parasitized clutches after they observe cowbirds at their nests (Burhans in press).

Considering that the Eastern Warbling-Vireo is the smallest known ejector of cowbird eggs, it is reasonable to expect that all species with bills as large or larger than the vireo should have the ability to eject cowbird eggs. However, eight acceptor species have bills larger than the vireo (Appendix 1). Therefore, the puncture-resistance hypothesis (i.e. evolutionary equilibrium) does not account for acceptance by these species.

The tendency for rejecters to have larger bills can be explained by the fact that larger hosts, which tend to have larger bills (Appendix 1), were parasitized more frequently in the past and have had more time to evolve rejection (see correlate 2), thereby supporting evolutionary lag. This is further

supported by hosts of the Common Cuckoo. In contrast to hosts of the Brown-headed Cowbird, most cuckoo hosts in Europe and Africa demonstrate rejection and show no such relationship between bill size and acceptance (see Rothstein 1992). Large hosts are typically grasp-ejecters, medium-sized hosts puncture-eject, and small hosts desert parasitized nests (Davies and Brooke 1989a, Moksnes et al. 1991). Similar to cowbird eggs, cuckoo (*Cuculus*, *Clamator*) eggs are also unusually strong (Brooker and Brooker 1991, Picman and Pribil 1997).

The difference between cuckoo-host systems and cowbird-host systems is likely due to the longer history of association between the former compared to the latter. Cuckoo-host systems are more highly evolved; cuckoos and their hosts may have interacted longer than cowbirds and their hosts (Rothstein 1990, 1992, Rothstein and Robinson in press). For example, most cuckoo hosts exhibit rejection and in response cuckoos have evolved egg mimicry (Brooke and Davies 1988). In contrast, relatively few cowbird hosts reject cowbird eggs (Table 3.1) and cowbirds apparently do not lay mimetic eggs. Cowbirds and their hosts may have interacted for a shorter period of time. Given enough time, perhaps cowbird hosts will also evolve rejection similar to cuckoo hosts in Europe and Africa which would support the evolutionary lag hypothesis.

GENERAL DISCUSSION

Egg rejection in Great-tailed Grackles has not evolved in response to CBP. I found no evidence of this behavior despite the close proximity of grackle nests, and I was unable to induce CBP by removing nests during grackle laying periods. Great-tailed Grackles also do not lay indeterminately, which is often characteristic of species that exhibit CBP (Hamilton and Orians 1965, Kendra et al. 1988, McRae 1998). Despite the absence of CBP, some Great-tailed Grackles rejected experimentally added conspecific eggs. They also rejected all cowbird eggs, yet I found no evidence of IBP on this grackle species. It appears that egg rejection behavior in Great-tailed Grackles has evolved in response to Giant Cowbird parasitism. The Giant Cowbird parasitizes mainly large, colonial icterines and this cowbird's eggs are very similar to Great-tailed Grackle eggs, which would necessitate the enhanced discriminatory ability exhibited by Great-tailed Grackles. Great-tailed Grackles are suitable hosts for the Bronzed Cowbird. However, Bronzed Cowbird parasitism has probably not selected for egg rejection in Great-tailed Grackles in part because Bronzed Cowbird eggs are very different from grackle eggs. As a result, Great-tailed Grackles could demonstrate more tolerance towards parasitic eggs than they do. Great-tailed Grackles are too large to be suitable hosts of the Brown-headed Cowbird. Therefore, this also eliminates Brown-headed Cowbird parasitism as the factor selecting for egg rejection.

The most parsimonious explanation for the existence of egg rejection in Boat-tailed Grackles is that this behavior was inherited from a common ancestor with the Great-tailed Grackle. Rejection has been maintained by Boat-tailed Grackles in the absence of parasitism since it split with the Great-tailed Grackle during the Pleistocene, at least 10,000 years ago. Retention of rejection by the Boat-tailed Grackle, as well as the Great-tailed, Greater

Antillean and Carib grackles, all largely in the absence of parasitism, indicates that this behavior does not incur significant costs. This supports Rothstein's (1976b, 1990, 1996) contention that rejection should be maintained for long periods of time in the absence of parasitism because brood parasitism is the only circumstance in which passerine birds are regularly exposed to foreign eggs in their nests. The one grackle that has apparently lost rejection is the Common Grackle. The Common Grackle exhibits a high degree of intraclutch egg variation, which may have resulted in this species rejecting its own discordant eggs (Peer and Bollinger 1997a). Such behavior would be selected against in the absence of parasitism, hence, the low level of rejection in this species.

Loss of rejection in hosts such as the Common Grackle (Peer and Bollinger 1997a, this study) and Village Weaver (Cruz and Wiley 1989) would allow parasites to switch from parasitizing well defended hosts to new hosts that have no antiparasite defenses, or those that have lost antiparasite defenses. In this manner, hosts and parasites can coexist indefinitely through a cyclical process of parasitism and avoidance (Marchetti 1992, Thompson 1994). In contrast, if most hosts retain rejection in the absence of parasitism, which appears to be the case (e.g. Jourdain 1925; Rothstein 1975a, b; Friedmann and Kiff 1985; Davies and Brooke 1989a; Moksnes et al. 1990; Sealy and Bazin 1995; Nakamura et al. in press), parasites will be forced to specialize on relatively few hosts. This appears to be occurring with the Common Cuckoo genges. In order to circumvent host rejection, cuckoo genges have evolved eggs that mimic those of specific hosts (Wyllie 1981). In time, cowbirds may also be forced to become specialized once most hosts evolve rejection. Testing other species that are closely related to rejecters but which are not parasitized themselves (i.e. similar to my study of Great-tailed and

Boat-tailed grackles) is warranted to determine whether these closely related species have retained rejection.

The comparative analyses of correlates of egg rejection in Brown-headed Cowbird hosts tend to support evolutionary lag as the explanation for the acceptance of cowbird eggs. Larger species and, hence, those with large nests, were more likely to demonstrate rejection. These hosts were seemingly parasitized more frequently in the past, whether due to their more easily found nests or superiority as hosts. Hosts that have been parasitized the longest are more likely to exhibit rejection. Rejection was also correlated with taxonomic affiliation indicating that once rejection evolves it is often maintained, which also supports lag. However, taxonomic affiliation does not explain why rejection evolved in the first place.

Large bill size appears to facilitate the evolution of rejection. There is no doubt that larger bills make the removal of cowbird eggs easier, but small bills are not necessarily a constraint because all hosts have the option of deserting parasitized nests. The fact that hosts with larger bills are more likely to exhibit rejection may simply be a result of large hosts tending to have larger bills and these hosts were ostensibly parasitized more frequently in the past. There is no evidence that acceptance is more adaptive than rejection in any cowbird host (Rothstein 1990), with the possible exceptions of hosts that have eggs that match cowbird eggs. Such hosts are clearly constrained as this makes the recognition of cowbird eggs very difficult. Thus, an evolutionary equilibrium may exist between these hosts and cowbirds depending on the costs to host reproductive success and the likelihood of committing recognition errors. Nevertheless, there are still some hosts that have been in contact with cowbirds for a long time, have large nests, large bills, "favorable" phylogeny, and eggs that differ from those of cowbirds, yet they accept cowbird eggs (e.g.

Red-winged Blackbird). Random chance may play a role in the accumulation of the necessary recombinants and mutations necessary for the evolution of rejection (Rothstein 1975a). More species need to be tested to resolve these issues further because less than half of the hosts known to have successfully reared cowbirds have been tested. These tests should concentrate on nest desertion as an anti-parasite strategy by smaller hosts because it is unclear the extent to which this nebulous behavior is used as an antiparasite defense.

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Appendix 1. Status of rejecters and accepters of Brown-headed Cowbird eggs with respect to eight correlates of egg rejection behavior.

	Correlates								References ⁱ
	Hist ^a	Mass ^b	San ^c	Pred ^d	Pop ^e	Tax ^f	Egg ^g	Bill ^h	
REJECTERS									
<i>T. tyrannus</i>	+	43.6	+	-	+	+	+	25.8 ± 1.4	1-6, 8
<i>T. verticalis</i>	+	39.6	+	-	+	+	+	26.5 ± 0.9	1-6, 9
<i>T. vociferans</i>	+	45.6	?	-	+	+	+	26.4 ± 1.4	1-5, 7, 10
<i>T. couchii</i>	+	45.0	?	-	+	+	+	29.8 ± 1.5	1-5, 7, 10
<i>T. forficatus</i>	+	43.2	?	-	+	+	+	25.6 ± 1.3	1-5, 7, 10
<i>A. coerulescens</i>	-	80.2	+	+	-	+	+	30.9 ± 2.7	1-5, 7, 11
<i>A. californica</i>	+	77.0	?	+	+	+	+	32.0 ± 0.8	1, 5, 7, 12, 13
<i>C. cristata</i>	+	86.8	?	+	+	+	+	30.7 ± 1.0	1-6, 12
<i>T. migratorius</i>	+	77.3	+	-	+	-	+	26.1 ± 0.6	1-6, 14, 15

<i>L. ludovicianus</i>	+	47.4	?	-	+	+	+	+	22.0 ± 1.2	1-6, 16
<i>D. carolinensis</i>	+	36.9	+	+	+	+	+	+	23.2 ± 0.9	1-6, 18-20
<i>M. polyglottos</i>	+	48.5	+	-	+	+	+	+	25.3 ± 0.7	1-5, 7, 17
<i>O. montanus</i>	+	43.3	?	-	+	+	+	+	23.9 ± 0.6	1-6, 21
<i>T. rufum</i>	+	68.8	?	-	+	+	+	+	31.7 ± 1.4	1-6, 21
<i>T. curvirostre</i>	+	79.4	+	-	+	+	+	+	36.0 ± 1.6	1-5, 7, 22
<i>T. crissale</i>	+	62.7	?	+	+	+	+	+	39.1 ± 3.4	1-6, 21, 23
<i>B. cedrorum</i>	+	31.8	+	-	+	-	+	+	19.8 ± 0.6	1-6, 24
<i>V. gilvus</i>	+	14.8	?	-	+	-	+	+	17.6 ± 0.9	1-5, 7, 25
<i>S. magna</i>	+	89.0	+	+	+	+	+	+	28.5 ± 1.9	1-6, 26
<i>S. neglecta</i>	+	100.7	+	+	+	+	+	+	31.0 ± 3.2	1-5, 7, 27
<i>Q. quiscula</i>	+	113.5	+	+	+	+	+	+	34.2 ± 1.2	1-5, 7, 28
<i>I. galbula</i>	+	33.8	?	+	+	+	+	+	21.7 ± 0.9	1-5, 7, 19, 29
<i>I. bullockii</i>	+	33.6	?	+	+	+	+	+	21.4 ± 1.2	1-5, 7, 29

ACCEPTERS

<i>S. phoebe</i>	+	19.8	+	-	+	+	+	+	20.2 ± 0.5	1-6, 30
<i>E. minimus</i>	+	10.3	+	-	+	+	+	+	15.9 ± 1.0	1-5, 7, 31

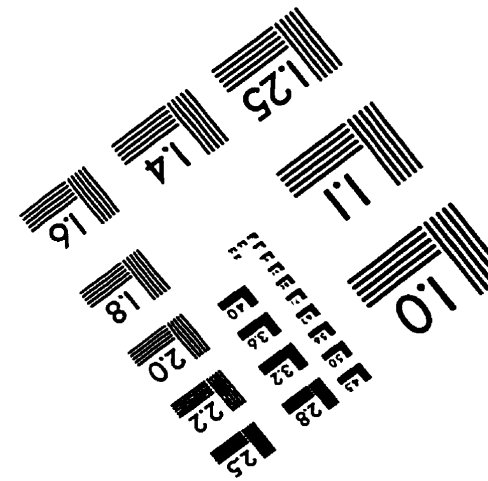
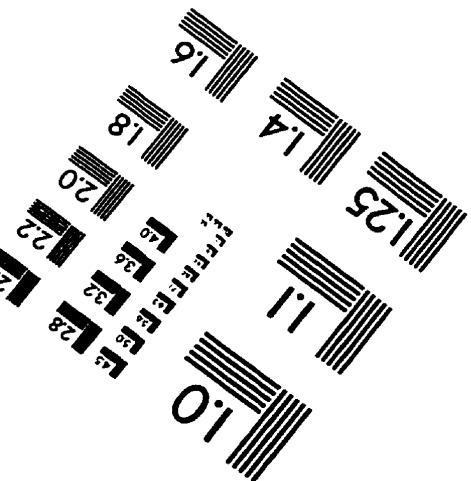
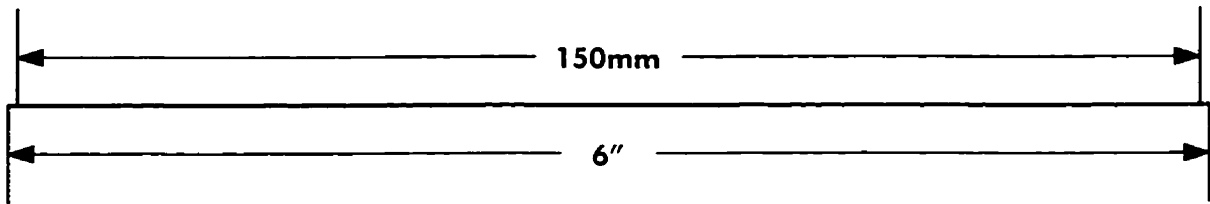
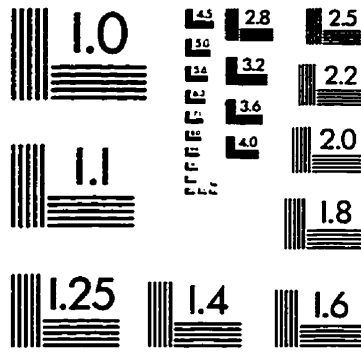
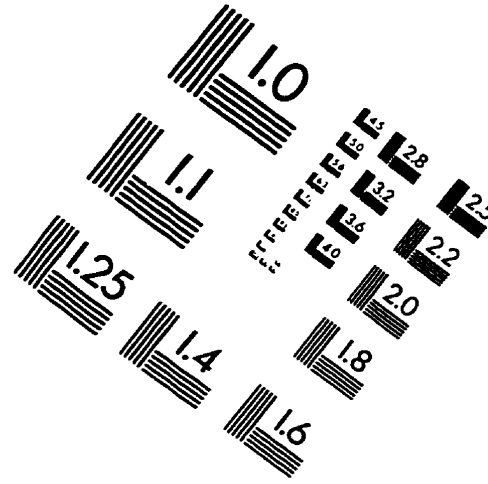
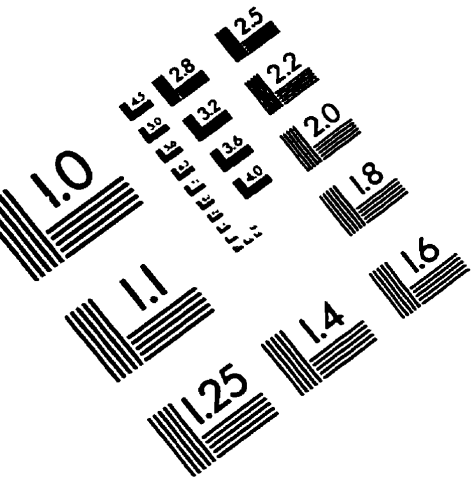
<i>H. mustelina</i>	-	47.4	+	-	+	-	+	24.7 ± 0.4	1-5, 7, 32
<i>T. lecontei</i>	-	61.9	+	-	-	+	+	38.2 ± 1.5	1-5, 7, 33
<i>T. redivivum</i>	-	84.4	?	-	-	+	+	44.5 ± 1.2	1-5, 7, 34
<i>D. petechia</i>	+	9.5	?	-	+	-	+	13.4 ± 1.1	1-6, 35
<i>I. virens</i>	+	25.3	?	-	+	-	-	19.1 ± 0.5	1-6, 35
<i>V. swainsonii</i>	-	12.0	?	-	+	-	+	16.2 ± 0.9	2-5, 7, 25, 36
<i>P. ludoviciana</i>	-	45.6	?	-	+	-	-	16.8 ± 0.5	1-5, 7, 37
<i>C. cardinalis</i>	+	44.6	+	-	+	-	-	17.0 ± 1.2	1-6, 14, 37
<i>A. savannarum</i>	+	17.0	+	+	-	+	+	11.1 ± 0.1	1-6, 38
<i>P. gramineus</i>	+	25.7	?	-	+	-	+	12.0 ± 0.5	1-6, 37
<i>M. melodia</i>	+	20.8	?	-	+	-	-	13.5 ± 0.5	1-6, 37
<i>C. grammacus</i>	+	29.0	?	-	+	-	+	12.8 ± 0.6	1-6, 37
<i>S. pusilla</i>	+	12.5	+	-	+	-	+	9.7 ± 0.5	1-6, 39
<i>S. passerina</i>	+	12.3	?	-	+	-	+	11.3 ± 0.5	1-6, 37
<i>S. pallida</i>	+	12.0	+	-	+	-	+	10.0 ± 0.0	1-6, 40
<i>S. americana</i>	+	26.9	+	-	+	-	+	13.8 ± 0.9	1-6, 37
<i>C. melanocorys</i>	+	37.6	?	-	+	-	+	14.2 ± 0.9	1-6, 37
<i>X. xanthocephalus</i>	+	64.5	+	+	+	+	+	20.8 ± 1.1	1-5, 7, 19, 41

<i>A. phoeniceus</i>	+	52.6	+	+	+	+	+	19.1 ± 0.9	1-6, 42
<i>E. cyanocephalus</i>	+	62.6	?	+	+	+	+	21.1 ± 0.8	1-6, 29
<i>I. spurius</i>	+	19.6	+	-	+	+	+	17.3 ± 0.6	1-5,7,43

a = Historic contact, **b** = Mass, **c** = Nest sanitation, **d** = Egg predator, **e** = Population size, **f** = Taxonomic affiliation, **g** = Egg difference, **h** = bill length.

i References: 1 = Dunning 1993, 2 = Peterjohn et al. 1994, 3 = Price et al. 1995, 4 = Sibley and Monroe 1990, 5 = Baicich and Harrison 1997, 6 = Rohwer and Spaw 1988, 7 = this study, 8 = Murphy 1996, 9 = Gamble and Bergin 1996, 10 = Bent 1942, 11 = Woolfenden and Fitzpatrick 1996, 12 = Bent 1946, 13 = Wootton 1996, 14 = Bent 1949, 15 = pers. obs., 16 = Yosef 1996, 17 = Derrickson and Breitwisch 1996, 18 = Cimprich and Moore, 19 = Sealy 1994, 20 = Spooner et al. 1996, 21 = Bent 1948, 22 = Tweit 1996, 23 = Tweit and Finch 1994, 24 = Witmer et al. 1997, 25 = Bent 1950, 26 = Lanyon 1995, 27 = Lanyon 1994, 28 = Peer and Bollinger 1997b, 29 = Bent 1958, 30 = Weeks 1994, 31 = Briskie 1994, 32 = Roth et al. 1996, 33 = Sheppard 1996, 34 = Cody 1998, 35 = Bent 1953, 36 = Dunning 1984, 37 = Bent 1968, 38 = Vickery 1996, 39 = Carey et al. 1994, 40 = Knapton 1994, 41 = Twedt and Crawford 1995, 42 = Yasukawa and Searcy 1996, 43 = Scharf and Kren 1996.

IMAGE EVALUATION TEST TARGET (QA-3)



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