



PHENOTYPIC PLASTICITY IN COMMON GRACKLES (*QUISCALUS QUISCULA*) IN RESPONSE TO REPEATED BROOD PARASITISM

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ABSTRACT.—Many North American bird species either accept or reject all Brown-headed Cowbird (*Molothrus ater*) eggs, but the Common Grackle (*Quiscalus quiscula*) is unusual in that it rejects a small proportion of experimentally introduced cowbird eggs. We tested whether individual Common Grackles and eight typical rejecter species were consistent in their responses by parasitizing nests a second time after initial cowbird eggs were ejected. We also assessed intraclutch variation in egg appearance in Common Grackles to determine whether it may influence phenotypic plasticity in rejection frequency. Rejections were recorded at 11.9% of 337 experimentally parasitized Common Grackle nests. Only 6 (33.3%) of 18 Common Grackles that ejected initial cowbird eggs also ejected a second experimentally added cowbird egg, however, which suggests that individuals that possess rejection behavior express it only 33.3% of the time. By contrast, the other eight rejecter species rejected between 91% and 100% of initial cowbird eggs ($n = 302$) and rejected 100% of second cowbird eggs ($n = 125$). Common Grackles are unique in three ways: they reject eggs at a low frequency, they have a high rate of intraclutch variation in egg appearance, and they exhibit phenotypic plasticity in response to repeated parasitism. It is difficult to ascertain the significance of these attributes, but combined with the fact that Common Grackles are rarely parasitized by cowbirds but may have been parasitized more frequently in the past, they suggest that egg rejection has no current adaptive value and may incur a cost such that Common Grackles may be losing rejection via drift or direct selection. Received 7 January 2009, accepted 31 October 2009.

Key words: brood parasitism, Brown-headed Cowbird, coevolution, Common Grackle, egg recognition, *Molothrus ater*, phenotypic plasticity, *Quiscalus quiscula*.

Plasticidad Fenotípica como Respuesta al Parasitismo de Cría Recurrente en *Quiscalus quiscula*

RESUMEN.—Muchas especies de aves de Norteamérica aceptan o rechazan todos los huevos de *Molothrus ater*, pero *Quiscalus quiscula* presenta un patrón inusual porque sólo rechaza una pequeña proporción de los huevos de *M. ater* que son colocados en sus nidos experimentalmente. Probamos si los individuos de *Q. quiscula* y de ocho especies que típicamente rechazan huevos presentan respuestas consistentes ante una segunda introducción de huevos al nido realizada después de que los huevos de *M. ater* introducidos inicialmente han sido rechazados. También evaluamos la variación en la apariencia de los huevos dentro de una misma nidada de *Q. quiscula* para determinar si ésta puede influenciar la plasticidad fenotípica en la frecuencia de rechazo. Observamos rechazos en el 11.9% de 337 nidos de *Q. quiscula* parasitados experimentalmente. Sólo seis (33.3%) de 18 individuos de *Q. quiscula* que expulsaron los huevos de *M. ater* puestos inicialmente en sus nidos también expulsaron el segundo huevo de *M. ater* adicionado experimentalmente. Esto sugiere que los individuos que tienen comportamiento de rechazo lo expresan sólo en un tercio de las veces. De modo contrastante, las otras ocho especies que rechazan los huevos del parásito rechazaron entre el 91% y el 100% de los huevos de *M. ater* iniciales ($n = 302$) y rechazaron el 100% de los huevos de las segundas adiciones ($n = 125$). La especie *Q. quiscula* es única en tres aspectos: los individuos rechazan huevos con frecuencias bajas, tienen una alta tasa de variación en la apariencia de los huevos dentro de una misma nidada y exhiben plasticidad fenotípica en respuesta al parasitismo recurrente. Es difícil determinar la relevancia de estos atributos, pero al considerarlos en combinación con el hecho de que los nidos de *Q. quiscula* rara vez son parasitados por *M. ater* pero podrían haber sido parasitados con mayor frecuencia en el pasado, sugieren que el rechazo de huevos no tiene un valor adaptativo y que puede representar un costo. Así, los individuos de *Q. quiscula* podrían estar perdiendo la capacidad de rechazar huevos por deriva o por selección directa.

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OBLIGATE AVIAN BROOD parasitism is an alternative breeding strategy in which birds lay eggs in the nests of other species and rely on these hosts to care for their young. Brood parasites have evolved various features that increase the likelihood that their young will survive in these nests (Rothstein 1990, Davies 2000, Avilés 2008). These adaptations make parasitism costly to hosts, which typically raise fewer of their own offspring when parasitized, which in turn selects for host countermeasures to circumvent parasitism (Rothstein 1990, Peer et al. 2005). In spite of these costs, relatively few hosts of the parasitic Brown-headed Cowbird (*Molothrus ater*; hereafter “cowbird”) remove the parasite’s eggs from their nests (Rothstein 1975a, Peer and Sealy 2004a). Host species demonstrate a dichotomy in their response to experimentally simulated parasitism in that they either accept or reject nearly 100% of cowbird eggs, with relatively few suitable hosts demonstrating intermediate rates of rejection (Rothstein 1975a, Peer and Sealy 2004a). In this they differ from hosts of the Common Cuckoo (*Cuculus canorus*; hereafter “cuckoo”), which exhibit a wide range of rejection frequencies (Davies and Brooke 1989, Moksnes et al. 1990, Stokke et al. 2008).

We know that a small percentage of cowbird hosts reject parasitism, but no studies have determined whether these hosts are phenotypically plastic in their response to parasitism and, if so, the significance of such plasticity. If hosts are phenotypically plastic, it may indicate that rejection behavior is in some way costly and that responses are altered according to conditions, such as the perceived risk of parasitism (Davies et al. 1996). These costs may include recognition errors when hosts reject their own eggs instead of the parasitic egg or when hosts damage their own eggs in attempting to eject the parasitic egg (Rothstein 1976; Lotem et al. 1995; Sealy 1995, 1996). If hosts are phenotypically plastic, recognition and rejection of parasitic eggs are not synonymous, and although hosts may recognize that they have been parasitized, they do not always act to rid themselves of this parasitism (e.g., Moskat and Hauber 2007).

We compared the responses to repeated parasitism of eight “typical” rejecter species that usually reject cowbird eggs and one “atypical” species, the Common Grackle (*Quiscalus quiscula*), which rejects cowbird eggs at a low frequency of 11.9%. Common Grackles, which are rarely if ever parasitized, are unique among potential North American cowbird hosts in that they demonstrate a low frequency of unambiguous rejection of cowbird eggs and have a high level of intraclutch variation in egg appearance, although their eggs are always easily distinguished from those of the cowbird (Rothstein 1975a, Peer and Bollinger 1997b, Peer and Sealy 2004b). Because rejection behavior in Common Grackles has no apparent current utility, it has been hypothesized that the species is in the process of losing rejection (Peer and Bollinger 1997b, Peer and Sealy 2004a; see also Rothstein 2001). If Common Grackles expressed rejection as strongly as typical rejecter species, they could suffer net costs because their high level of intraclutch egg variation might cause them to reject their own divergently colored eggs (Peer and Bollinger 1997b, Peer and Sealy 2004a). It is unclear whether 11.9% of Common Grackles reject all of the time or whether all individuals reject 11.9% of the time. If the latter is true, Common Grackles are phenotypically plastic in their response to parasitism, and this might give us insight into the current utility, if any, of rejection behavior in this species.

METHODS

Common Grackles were tested for egg rejection in Iowa (Warren and Dallas counties), Illinois (McDonough County), and Connecticut (New Haven and Fairfield counties). Experiments on Great-tailed Grackles (*Q. mexicanus*) and Northern Mockingbirds (*Mimus polyglottos*) were conducted in the same Iowa counties. Gray Catbirds (*Dumetella carolinensis*) were tested at the same Iowa, Illinois, and Connecticut locations, and in Michigan (Cheboygan and Emmet counties). Warbling Vireos (*Vireo gilvus*) were tested in Illinois; Brown Thrashers (*Toxostoma rufum*) in Iowa, Illinois, Connecticut, Michigan, and Nebraska (Douglas and Dodge counties); Eastern Kingbirds (*Tyrannus tyrannus*) in Michigan, Connecticut, Iowa, and Illinois; American Robins (*Turdus migratorius*) in Iowa, Illinois, Michigan, Connecticut, and New Brunswick; and Blue Jays (*Cyanocitta cristata*) in Connecticut, Michigan, and Nebraska. Experiments were conducted in Iowa in 2004 and 2005, in Illinois in 2006 and 2007, and at all other locations from 1966 to 1969. Although our studies were conducted throughout the eastern half of North America, there is no evidence that these hosts exhibit geographic variation in rejection behavior (Rothstein 1975a, Peer and Sealy 2004a; see below).

Our procedure was to determine the responses of hosts to two parasitism events. After an initial egg was ejected, whether it was an artificial egg or a naturally laid cowbird egg, we parasitized the nest a second time. It is possible that we underestimated phenotypic plasticity because we did not add a second egg to nests of individuals that accepted the initial one. If we had added a second cowbird egg to those nests, there would have been two eggs present, and this would have been a different experiment than the single-egg experiment. In addition, an individual that accepts a cowbird egg has allowed its nest contents to be altered by the continuing presence of a foreign egg, and this may affect its recognition and rejection behavior in unknown ways. The most conclusive way to test the responses of individuals that accept would be to test them at a new nest (e.g., Alvarez 1996), but this would require extensively banded populations of both Common Grackles and numerous rejecter species, and this was not feasible.

The second parasitism event occurred later in the nesting cycle, but the one North American host that is more likely to accept cowbird eggs the later parasitism occurs, the Cedar Waxwing (*Bombycilla cedrorum*; Rothstein 1976), was not involved in the study. All other North American hosts that have been tested, except possibly the Bullock’s Oriole (*Icterus bullockii*; Rothstein 1977), also a species not involved in our study, reject eggs at the same frequency regardless of the timing of parasitism, as does the Common Grackle (Rothstein 1975a, Peer and Bollinger 1997b; see below).

We did not control for previous experience with parasitism. Although previous experience has been demonstrated to affect rejection in some hosts of the cuckoo (Lotem et al. 1992), it is not known to do so in cowbird hosts (e.g., Sealy 1995) except in situations where rejecter hosts may misimprint on cowbird eggs (see Strausberger and Rothstein 2009). Moreover, the only host that varied in its response to double parasitism was the Common Grackle, and, given that it is among the most rarely used suitable hosts of the cowbird, prior experience is unlikely to be an important factor in its response.

TABLE 1. Responses of rejecter species to experimental multiple parasitism.

Species	Location ^a	Egg type	Host egg removed?	Percent rejection of first parasitism (<i>n</i>)	Percent rejection of second parasitism (<i>n</i>)
Common Grackle	CT, IA, IL	Artificial cowbird	No, yes	11.9 (337)	33.3 (18)
Eastern Kingbird	CT, IA, IL, MI	Artificial cowbird; artificial cowbird-sized blue ^b	No, yes	100 (36); $\chi^2 = 156$, $df = 1$, $P < 0.001^d$	100 (6); Fisher's exact test, $P = 0.01^d$
Blue Jay	CT, MI, NE	Artificial cowbird; 2 cowbird-sized blue with polka dots; 1 robin-sized blue with polka dots; 1 real robin	Yes	92 (25); Fisher's exact test, $P < 0.001^d$	100 (4); Fisher's exact test, $P = 0.03^d$
American Robin	CT, IA, IL, MI, NE, NB	Artificial cowbird	No, yes	91.0 (100); $\chi^2 = 230$, $df = 1$; $P < 0.001^d$	100 (50); Fisher's exact test, $P < 0.001^d$
Gray Catbird	CT, IA, IL, MI	Artificial cowbird	No, yes	95.5 (67); $\chi^2 = 205$, $df = 1$, $P < 0.001^d$	100 (14); Fisher's exact test, $P < 0.001^d$
Brown Thrasher	CT, IA, IL, MI, NE	Artificial cowbird; 2 robin-sized cowbird; Eastern Meadowlark ^c	No, yes	97.5 (40); $\chi^2 = 158$, $df = 1$, $P < 0.001^d$	100 (17); Fisher's exact test, $P < 0.001^d$
Great-tailed Grackle	IA	Artificial cowbird	No	100 (32); $\chi^2 = 144$, $df = 1$, $P < 0.001^d$	100 (32); Fisher's exact test, $P < 0.001^d$

^aCT = Connecticut, IA = Iowa, IL = Illinois, MI = Michigan, NE = Nebraska, NB = New Brunswick.

^bIn three experiments, after an initial cowbird egg was ejected, another cowbird egg and a blue cowbird egg were inserted simultaneously.

^cRobin-sized cowbird eggs were ejected from two nests after initial ejection of standard cowbird eggs. One of these nests was parasitized again with a real Eastern Meadowlark (*Sturnella magna*) egg that was ejected. At an additional nest, a third standard cowbird egg was ejected.

^d*P* value for the comparison between each species and the comparable rejection frequency of the Common Grackle.

All experiments performed in Iowa and Illinois used artificial cowbird eggs. Those conducted elsewhere used artificial cowbird eggs in addition to real cowbird and robin eggs, cowbird-sized blue eggs, and robin-sized polka-dot eggs, and retests in these locations were sometimes conducted with a second egg-type (see Table 1 for details). Artificial cowbird eggs were made of plaster with white backgrounds and brown and gray spots (for details, see Rothstein 1975a). Controls demonstrate that hosts do not respond to the artificiality of these eggs (Rothstein 1975a, 1982). There was no variation in host response in relation to the different egg types (see below), which is expected given that all experimentally inserted eggs are highly nonmimetic with respect to host eggs (Rothstein 1974, 1975a). All experiments conducted on Common Grackles, the species that varied the most in its response to parasitism, used artificial cowbird eggs. Common Grackle eggs are typically light blue with black scrawls, although their background color ranges from almost white to brown (Peer and Bollinger 1997a). Eggs were added to nests during the laying or incubation stages of the nesting cycle. Eggs were removed in conjunction with initial parasitism events in some of the experiments (see Table 1), but this variation in the experimental procedure also had no apparent effect on host response (see below). All nests were checked within 24 h of the two experimental parasitism events and every 1 to 3 days thereafter.

Eggs were considered rejected if they were removed from the nest or pecked. We checked all eggs inserted into host nests for pecks, whether the host species was a grasp-ejecter or puncture-ejecter. Peck marks could be observed on the plaster eggs and are a direct response to the parasitic egg (Rothstein 1975a). It is sometimes unclear whether nest desertion and egg burial are responses to parasitic eggs or some other disturbance (Rothstein 1975a, Peer and Bollinger 1997b). We monitored control nests of Common Grackles, to which we did not add experimental eggs, in a similar

manner, including handling of eggs to determine whether desertion or a loss of some but not all Common Grackle eggs was related to the parasitic egg, because these events may occur even without addition of a foreign egg. Eggs were not removed from control nests. Eggs were considered accepted if they remained in a nest for at least 5 days. Most rejections occur within 1 day and almost all occur within 5 days (Rothstein 1975a, Peer and Sealy 2004b; but see Peer and Sealy 2000).

Common Grackle nests were also visited daily in 1972 in Anne Arundel County and Prince George's County, Maryland, to check for conspecific brood parasitism and to assess variation in appearance of eggs according to laying sequence. Intraclutch variation in egg appearance was examined only in Common Grackles because this is the only species that exhibited a variable response to repeated parasitism. In addition, intraclutch variation is markedly higher in Common Grackles than in any of the other study species, at least to human perception. We applied an intraclutch-variation scoring scheme similar to that used first by Braa et al. (1992) and Moksnes (1992) and subsequently modified by Peer and Sealy (2004b) and Peer et al. (2007), scoring clutches as follows: (1) all eggs within a clutch looked the same, (2) one egg was moderately different from the other eggs, (3) one egg was dramatically different from the other eggs, or (4) all eggs were different. Three individuals other than the authors scored clutch variability to determine the repeatability of this methodology, and there was no variation in their scores (Kruskal-Wallis one-way ANOVA, $H = 0.19$, $P = 0.91$).

RESULTS

Common Grackles rejected 12.1% of experimentally added cowbird eggs in Illinois ($n = 66$) and 13.4% in Iowa ($n = 201$). In previously reported work, Rothstein (1975a) found a 7.1% rejection rate

in Connecticut ($n = 70$). These three rejection rates did not differ ($\chi^2 = 2.0$, $df = 2$, $P = 0.37$), and the combined rejection frequency was 11.9%. The rate of desertion at experimentally parasitized Common Grackle nests (7.7% of 337) did not differ from that at control nests (10.5% of 105; $\chi^2 = 0.8$, $df = 1$, $P = 0.37$); thus, nest desertion was not considered a response to parasitism. One cowbird egg was buried in a Common Grackle nest, but whether this was a response to parasitism is questionable, and we did not consider it a rejection. Ejection of the parasitic egg was the most common means of rejection by Common Grackles (88%), followed by pecking the parasitic egg (12%), which we assume represented attempts to eject plaster eggs by piercing them.

Rothstein (1975a) found that rejection did not vary with the timing of parasitism in Common Grackles in Connecticut, and we had the same result in Illinois and Iowa. Eggs that were added during laying were rejected 13.1% ($n = 153$) of the time, and those added during incubation were rejected 13.2% of the time ($\chi^2 = 0.0$, $df = 1$, $P = 1.0$, $n = 114$). Common Grackles rejected initial parasitic eggs at a significantly lower frequency (11.9%) than the other eight rejecter species we tested (range: 91.0–100%; Rothstein 1975a, present study; Table 1). Common Grackles also rejected a second cowbird egg at a lower frequency (33.3%; $n = 18$) than the other eight species, which rejected 100% of second parasitic eggs ($n = 125$; Table 1). We also tested single nests of the Warbling Vireo and Northern Mockingbird, and both rejected the two cowbird eggs that were added to their nests; however, because of the small sample size, we did not include them in the statistical analyses in Table 1. All Common Grackles that were parasitized a second time had ejected the cowbird egg when they were parasitized the first time. One Common Grackle deserted a nest after a second parasitic egg was added. Nine American Robins and two Blue Jays deserted in response to initial parasitism events (Rothstein 1975a, present study), so second parasitic eggs could not be added to these nests, but all second rejections were via egg ejection.

Common Grackles lost eggs, 1 or 2 in all cases, from 1.4% of experimentally parasitized nests. In one case, a Common Grackle egg that went missing after a cowbird egg was rejected may have been a rejection error. In the remaining four cases, the host lost 1 or 2 eggs and then subsequently deserted the nest without rejecting the cowbird egg. However, this rate of egg loss was significantly less than that at control nests (5 of 337 vs. 8 of 95 nests; Fisher's exact test, $P = 0.002$), which makes it unlikely that partial clutch losses were related to recognition errors attributable to the foreign egg. In only one other host was a host egg damaged in conjunction with parasitism, and this was at an American Robin nest from which the cowbird egg was ejected and a host egg was punctured.

Nineteen Common Grackle clutches with known laying sequences were assessed for intraclutch egg variation. The last-laid egg in 28.1% of clutches had noticeably lighter pigmentation than previously laid eggs (Fig. 1). Two Common Grackle eggs never appeared in a single day among the 19 nests visited daily during laying, which indicates that there was no conspecific brood parasitism. There was also no evidence of naturally occurring cowbird parasitism at the Common Grackle nests we monitored ($n = 310$).

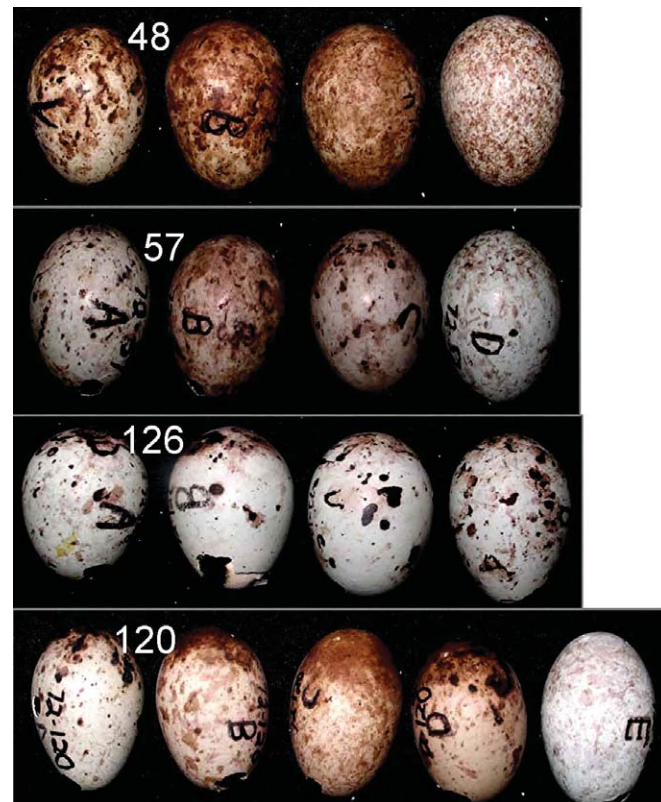


FIG. 1. Common Grackle eggs, showing clutches with and without a last laid egg that differs strongly in appearance from eggs laid earlier in the clutch sequence. All clutches are arranged with the order of laying going from left to right, as indicated by the letters visible on most eggs. Shown are 2 of the 3 four-egg clutches that had a highly divergent last egg (top two clutches) and 1 of the 9 four-egg clutches that did not have a highly divergent last egg. Shown on the bottom is the 1 five-egg clutch with a highly divergent last egg. There were 5 other five-egg clutches with known laying sequences, none of which had a highly divergent last egg. The frequency of clutches with a highly divergent last egg is 25.0% for four-egg clutches (3 of 12) and 16.7% for five-egg clutches (1 of 6).

DISCUSSION

Response to parasitism.—There was an extreme contrast in the behavior of Common Grackles compared with that of eight “typical” rejecter species. Common Grackles that rejected an initial cowbird egg rejected a second cowbird egg only about one-third of the time, whereas the other rejecters did so all of the time. The lower rejection rate of second cowbird eggs was not attributable to Common Grackles being more likely to accept cowbird eggs later in the nesting cycle, because Common Grackles, like most North American hosts, reject eggs at the same frequency regardless of when they are parasitized (Rothstein 1975a, Peer and Bollinger 1997b, present study). There is also no evidence that Common Grackles reject eggs at a higher frequency later in the nesting season when cowbirds are present (Peer and Bollinger 1997b), nor can

prior experience account for the differences in rejection, because Common Grackles are almost never parasitized (see below). The only other studies that have examined whether hosts respond consistently to parasitism involved hosts of the cuckoo, which were inconsistent in their responses to repeated parasitism (Lotem et al. 1995, Alvarez 1996, Soler et al. 2000, Honza et al. 2007). Thus, our results show that the consistent responses of most cowbird hosts make them quite different from cuckoo hosts but that Common Grackles are an exception. The uniqueness of Common Grackles among North American birds is further evident in that they differ from both rejecters and accepters in their response to repeated parasitism. Acceptor species demonstrate nearly 100% acceptance of experimentally placed cowbird eggs across a broad range of conditions involving variation in nest stage, seasonality, geography, and likely local cowbird abundance, and show no evidence of phenotypic plasticity (Rothstein 1975a, 1986; Peer and Sealy 2004a). Furthermore, the rare rejections that occur among acceptor species are mostly nest desertions (Rothstein 1975b), which are of unclear significance, unlike the clear-cut ejections observed in a small proportion of Common Grackles.

Intraclutch variation in egg appearance in the Common Grackle and its potential influence on rejection behavior.—Although the differences in rejection behavior between Common Grackles and typical rejecters are obvious, the reason for these differences is not. Why are Common Grackles phenotypically plastic, whereas other North American species that are potential cowbird hosts are not? Clearly, Common Grackles that we parasitized a second time could recognize that they had been parasitized, because they ejected the initial cowbird eggs. The costs of rejecting the second egg cannot account for the phenotypic plasticity, because rejection costs are very small in Common Grackles (see below).

Instead, rejection behavior sometimes declines in the absence of parasitism (Davies and Brooke 1989, Briskie et al. 1992, Marchetti 1992). The phenotypic plasticity demonstrated by Common Grackles may indicate the partial loss of some aspects of rejection behavior because Common Grackles are almost never parasitized by cowbirds (Peer and Bollinger 1997b, Peer et al. 2001, Peer and Sealy 2004b). In more than 1,002 Common Grackle nests that we have observed, we have never found a cowbird egg (Rothstein 1975a, Peer and Bollinger 1997b, present study; B. Peer unpubl. data). In one of the largest data sets on Common Grackles, parasitism was recorded in only 4 of 2,091 nests in Ontario, where many species experience parasitism rates of 20% or more (Peck and James 1987). Because of this virtual lack of selection, egg recognition and rejection has no current utility for Common Grackles, such that they may be in the process of slowly losing rejection through drift or even via direct selection if rejection incurs a cost. If loss is occurring, it may be through a decline in individuals with a genetic tendency to reject, a decline in the expression of rejection even in individuals with the rejecter trait, or both. The rejection rate of 33% for second cowbird eggs indicates that Common Grackles with the rejection trait express it only 33% of the time. Thus, the rate of rejection of a first cowbird egg in the overall sample of 337 nests, 11.9%, must be multiplied by 100/33.3 to yield the actual percentage of 35.7% for individuals that likely possess the rejection trait.

Unlike most North American species, Common Grackles may experience a source of selection against recognition and rejection in unparasitized nests; about 28% of Common Grackle clutches have a divergent egg that is much more lightly pigmented than the other eggs (Fig. 1; see also Peer and Sealy 2004b) and also differs in the amount of reflectance of ultraviolet light (B. Peer unpubl. data). These discordantly colored eggs look suspiciously like conspecific brood parasitism because Common Grackles also have a high level of interclutch variation in egg appearance (Peer and Bollinger 1997a). However, we found no evidence of conspecific brood parasitism, and it rarely if ever occurs in Common Grackles or other colonial icterines (Rothstein 1993; Peer and Bollinger 1997a, b; Johnson and Peer 2001; Peer and Sealy 2004b; B. Peer unpubl. data). Importantly, discordantly colored eggs are typically the last egg laid. They would therefore be especially likely to be rejected by the Common Grackles, because birds with rejection behavior tend to learn the appearance of their own egg from the first one or few eggs that appear in their nest (Rothstein 1974, Lotem et al. 1995). The occurrence of discordant eggs in a large proportion of clutches is a clear source of selection against finely tuned egg discrimination in the absence of parasitism. We suggest that the most probable explanation for our findings is that the Common Grackle was once a typical rejecter species but has lost most of its rejection tendencies as a result of selection against rejection after cowbirds—whether Brown-headed Cowbirds, other cowbird species whose ranges may have shifted over time, or a larger extinct cowbird species—stopped parasitizing it (Peer and Bollinger 1997b, Rothstein and Peer 2005). This could explain the finding that rejection costs rarely if ever occur, and it may further mean that selection is no longer acting against egg recognition and rejection in Common Grackles because expression of the trait has been reduced to the point at which it is neutral.

We detected a very low incidence (1.4%) of egg disappearance from experimentally parasitized Common Grackle nests, and 1 of the 5 clutches at which this occurred had a high amount of intraclutch egg variation; thus, it is possible that this and the other cases constituted rarely occurring recognition errors. However, we also found that Common Grackles lost 1 or 2 eggs from 8.4% of control nests ($n = 95$). It is unclear whether these losses were recognition errors as opposed to partial clutch reduction, a phenomenon in which some but not all eggs are lost from a nest through predation or accidental breakage. Some have argued that partial clutch reduction in unparasitized rejecter nests is evidence of recognition errors (Marchetti 1992, Lotem et al. 1995), but similar losses (9–11%) occur at the nests of species that have been shown experimentally to lack egg recognition (Finch 1983, Rothstein 1986). Thus, the occasional loss of part of a bird's clutch is not proof of recognition errors (Rothstein and Robinson 1998, Rothstein 2001), and it is unclear whether the losses we recorded represent such errors.

Alternative explanations for the low level of egg rejection in the Common Grackle.—Although a scenario of loss of rejection is a plausible explanation for the unique combination of traits possessed by the Common Grackle, it is also possible that the Common Grackle inherited its low level of rejection from an ancestor that was never parasitized frequently and never had a high rate of rejection. However, previous studies have argued that there are

compelling reasons to believe that the Common Grackle was parasitized more frequently in the past (see Peer and Bollinger 1997b, Peer and Sealy 2004b). Additionally, the species basal to *Quiscalus*, Brewer's Blackbird (*Euphagus cyanocephalus*) and Rusty Blackbird (*E. carolinus*), do not show strong evidence of egg rejection (Price et al. 2009, B. Peer et al. unpubl. data, S. G. Sealy pers. comm.), which suggests that rejection evolved independently in Common Grackles.

It is also possible that the Common Grackle was parasitized and started to evolve into a typical rejecter but the high level of intraclutch variation in egg appearance or cessation of parasitism prevented the fixation of rejection that has occurred in all rejecter species. It is impossible to determine whether cessation of parasitism resulted in rejection not becoming fixed in the population. However, we know that intraclutch variation in egg appearance can only partially account for the low level of rejection in Common Grackles in a proximate sense, because variation increases the likelihood of acceptance only when cowbird eggs are added before clutch completion (B. Peer and S. Rothstein unpubl. data).

We have demonstrated that Common Grackles are unique in that they exhibit (1) bona fide ejection at a low rate (Rothstein 1975a, Peer and Bollinger 1997b, present study), (2) the highest level of intraclutch variation in egg appearance among North American hosts (Peer and Sealy 2004b, present study), and (3) individual phenotypic plasticity in egg ejection behavior (present study). An additional factor that is not unique to Common Grackles is that they are rarely parasitized (Peer and Bollinger 1997b, Peer et al. 2001). The co-occurrence of these three unique features with a very low rate of parasitism is unlikely to be coincidental. Even if these features varied randomly, the odds are extremely small that all of them would occur in one species, given that they do not appear to occur in any other species in North America. Intraclutch variation in egg pigmentation may be related to the low level of ejection behavior, and the low level of ejection behavior plus individual phenotypic plasticity are compatible with the view that this is a system that is intermediate between a rejecter and an acceptor species. This reasoning (i.e., Common Grackles being intermediate) suggests that there may have been a source of selection that is no longer operating and appears to favor the hypothesis that Common Grackles have lost most of their rejection behavior.

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