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INTRACLUTCH VARIATION IN EGG APPEARANCE CONSTRAINS REJECTION OF BROWN-HEADED COWBIRD (*MOLOTHRUS ATER*) EGGS IN COMMON GRACKLES (*QUISCALUS QUISCULA*)

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ABSTRACT.—Variation in the appearance of eggs within a clutch has been hypothesized to decrease the likelihood of rejection of brood-parasite eggs, but tests of the hypothesis have produced mixed results among cuckoo (*Cuculus canorus* and *Clamator glandarius*) hosts. The hypothesis has not been tested in cowbird hosts because they typically show little intraspecific variation in responses to cowbird eggs. However, the Common Grackle (*Quiscalus quiscula*) is unusual among potential hosts of the Brown-headed Cowbird (*Molothrus ater*) because it shows both acceptance and rejection of cowbird eggs and it demonstrates high intraclutch variation in egg appearance, which makes it one of the few potential cowbird hosts suitable for a test of the intraclutch variation–host rejection hypothesis. We tested whether intraclutch variation in the appearance of Common Grackle eggs influenced the likelihood of egg rejection and found that Common Grackles with greater variation in intraclutch egg appearance were more likely to accept cowbird eggs when these were added prior to clutch completion. These results are the first to indicate that even when a host has eggs that are dramatically different from those of a parasite, variation in its own eggs may increase the threshold required to elicit egg rejection. Received 24 October 2008, accepted 17 June 2010.

Key words: brood parasitism, Brown-headed Cowbird, coevolution, Common Grackle, egg rejection threshold, egg variation, *Molothrus ater*, *Quiscalus quiscula*, recognition systems.

La Variación en la Apariencia de los Huevos de una Nidada Limita el Rechazo de Huevos de *Molothrus ater* por parte de *Quiscalus quiscula*

RESUMEN.—Existe la hipótesis de que la variación en la apariencia de los huevos de una nidada disminuye la probabilidad de rechazo de los huevos de aves parásitas de cría, pero las pruebas de esta hipótesis han arrojado resultados mixtos entre los hospederos de *Cuculus canorus* y *Clamator glandarius*. La hipótesis no ha sido puesta a prueba en los hospederos de *Molothrus* pues éstos típicamente muestran poca variación intraespecífica en la respuesta ante los huevos del parásito. Sin embargo, la especie *Quiscalus quiscula* es inusual entre los hospederos potenciales de *Molothrus ater* debido a que muestra tanto aceptación como rechazo de los huevos del parásito y a que exhibe amplia variación en la apariencia de los huevos de una nidada. Estas características hacen de esta especie una de las pocas hospederas potenciales de *M. ater* apropiadas para probar la hipótesis de variación intra-nidada y rechazo de huevos. Evaluamos si la variación en la apariencia entre los huevos de las nidadas de *Q. quiscula* afecta la probabilidad de rechazo de huevos parásitos. Encontramos que los individuos con mayor variación en la apariencia de sus huevos fueron más propensos a aceptar huevos de *M. ater* cuando estos fueron añadidos antes de que la nidada se completara. Estos resultados son los primeros en indicar que incluso cuando un hospedero pone huevos dramáticamente diferentes de los de un parásito, la variación entre sus propios huevos puede incrementar el umbral necesario para provocar el rechazo de huevos parásitos.

LAYING A CLUTCH that has minimal variation in the appearance of the eggs may facilitate recognition of brood-parasitic eggs, especially when a brood parasite lays eggs that resemble those of its host. Conversely, if a female's own eggs are variably pigmented, it may be difficult for it to learn to recognize its eggs and express rejection, or at least it may require more time to learn the range

of variation in its eggs (Lotem et al. 1995). More importantly, a female with eggs of variable appearance will also likely demonstrate greater tolerance of foreign eggs (Rothstein 1982). Therefore, even if a female has eggs that are different in appearance from those of a brood parasite, it may be more likely to accept foreign eggs when its own are variable in appearance, because of proximate

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constraints on the recognition system (e.g., Moskát and Hauber 2007). Studies that have examined whether intraclutch egg variability influenced the likelihood of rejection have yielded mixed results. Only two demonstrated that females with higher degrees of intraclutch egg variability were more likely to accept parasite eggs (Stokke et al. 1999, Soler et al. 2000). Others have shown that intraclutch variability did not influence rejection (Karcza et al. 2003, Procházka and Honza 2003, Lovászi and Moskát 2004), and two studies have demonstrated that hosts with higher intraclutch variation tended to reject foreign eggs more frequently (Lotem et al. 1995, Avilés et al. 2004).

All these studies tested hosts of the Common Cuckoo (*Cuculus canorus*) or Great Spotted Cuckoo (*Clamator glandarius*). Whether intraclutch egg variation influences the likelihood of rejection has not been directly tested in hosts of the Brown-headed Cowbird (*Molothrus ater*; hereafter “cowbird”), in part because many of these species reject or accept close to 100% of nonmimetic eggs placed in their nests (i.e., there is relatively little or no variation in behavior to explain; Rothstein 1975a, b; Peer and Sealy 2004a). Variation in hosts’ intraclutch egg appearance may not be important in rejection by North American birds because many cowbird hosts have eggs that are easily distinguishable from cowbird eggs (Peer and Sealy 2004a; but see Peer et al. 2000). However, one of the best-studied North American hosts, the Common Grackle (*Quiscalus quiscula*; hereafter “grackle”), is highly unusual in showing a low level of unambiguous ejection and therefore an appreciable level of intraspecific variation in behavior (Rothstein 1975a, Peer and Bollinger 1997b, Peer and Sealy 2004b, Peer and Rothstein 2010). Grackles differ from accepters whose occasional “rejections” are typically cases of nest desertion (Rothstein 1975b), which occur for a variety of reasons, whereas responses by grackles are bona fide cases of ejection. The grackle is also unique among members of its own clade because it has the lowest frequency of egg rejection among the five congeners that have been tested (~12% vs. 63–100%) but the highest variation in intraclutch egg appearance (Peer and Sealy 2004b, Peer and Rothstein 2010). Indeed, grackles appear to have among the most variable eggs, from both interclutch and intraclutch perspectives, of any North American passerine examined to date (B. D. Peer and S. I. Rothstein unpubl. data). Selection may favor grackles that reject only in response to very dramatic differences between a potentially foreign egg and the rest of a clutch (Rothstein 1982) because of this species’ high intraclutch variation in egg appearance and because of the weak selection pressure from the low rate of parasitism and low cost when parasite eggs are accepted (Peer and Bollinger 1997b). These factors—high intraclutch variation in egg appearance and weak selection—could explain why grackles may be in the process of losing rejection behavior (Peer and Rothstein 2010).

We examined whether intraclutch egg variation is related to egg rejection behavior in grackles. Although cowbird eggs are easily distinguishable from grackle eggs, intraclutch variation in egg appearance may influence rejecters’ tolerance of foreign eggs (Rothstein 1982; see also Moskát and Hauber 2007), such that they may be more likely to accept. We predicted that if intraclutch variation in egg appearance is a constraint on egg rejection, individuals with high intraclutch variability will be more likely to accept cowbird eggs than conspecifics with less variable eggs.

METHODS

We studied grackles in Warren County, Iowa, from 2004 to 2005 and in McDonough County, Illinois, in 2006. Most grackle nests were located in Scotch Pine (*Pinus sylvestris*) on Christmas tree farms and occasionally in Blue Spruce (*Picea pungens*), Norway Spruce (*Picea abies*), and Eastern White Pine (*Pinus strobus*) in suburban habitats. Eggs were numbered daily to determine laying order and photographed on a Kodak Gray Card the day after clutch completion. Nests were parasitized with artificial plaster cowbird eggs that are effective mimics of real cowbird eggs (Rothstein 1975a) during the laying and incubation stages of the nesting cycle because these are the stages during which cowbirds lay their eggs. Cowbird eggs were considered accepted if they remained in a nest for at least 5 days (Rothstein 1975a, Peer and Bollinger 1997b) and rejected if they were ejected from the nest or pecked. In a previous study (Peer and Rothstein 2010), we found that grackles desert and bury eggs in experimentally parasitized nests at a similar frequency as in control nests; therefore, deserted nests and buried eggs—relatively rare responses that occurred at 7.7% of nests—were not considered rejections (Rothstein 1975a, Peer and Bollinger 1997b).

Variation in intraclutch egg appearance was scored by two volunteers who were not aware of the hypothesis being tested. Although eggs reflect ultraviolet (UV) light and we did not measure UV light, the patterns of intraclutch egg variation that we observed are supported by spectral reflectance data (B. D. Peer unpubl. data). We scored intraclutch egg variation in clutches of 2 to 7 eggs (2-egg clutches, $n = 2$; 3-egg clutches, $n = 12$; 4-egg clutches, $n = 62$; 5-egg clutches, $n = 157$; 6-egg clutches, $n = 26$; 7-egg clutches, $n = 1$). The scoring scheme was a modification of that first used by Braa et al. (1992) and Moksnes (1992), and subsequently by Peer and Sealy (2004b) and Peer et al. (2007), and was as follows: 1 = all eggs within a clutch looked the same, 2 = at least one egg was moderately different from the other eggs within a clutch, 3 = at least one egg was dramatically different from the other eggs within a clutch, and 4 = all eggs in the clutch differed. There was a highly significant correlation between variation scores of the two volunteers (Kendall’s rank correlation, $\tau = 0.56$, $z = 9.62$, $P < 0.0001$). Grackle eggs are pearl gray, or sometimes brown, with blackish scrawls or rarely with black spots, and average 29×21 mm (Peer and Bollinger 1997a). Cowbird eggs have a white background with brown and some gray spots that are usually concentrated at the larger end of the egg, and average 21×16 mm (Lowther 1993).

Statistical analysis.—We used an information-theoretic approach (Burnham and Anderson 2002) to determine which factors influenced egg rejection in grackles. We developed 11 candidate models (Table 1), including a null model, a global model, and models that examined the interactive and additive effects of (1) variation in intraclutch egg appearance, (2) whether a cowbird egg was added before or after clutch completion, (3) date of clutch initiation, (4) clutch size, and (5) year. Date of clutch initiation may play a role if older females are more likely to reject and tend to breed earlier in the season (e.g., Lotem et al. 1992), and clutch size may be a factor if it influences variation in intraclutch egg appearance. It is possible that the Common Grackle’s high variability in appearance of eggs within a clutch is related to its relatively large modal clutch size ($n = 5$; Peer and Bollinger 1997a; see above) compared to its

TABLE 1. Results of 11 candidate models that we used to determine the effects of variation in intraclutch egg appearance (= variation) on egg rejection by Common Grackles. Completion = whether cowbird egg was added before or after clutch completion; year = year when experiment was conducted; initiation date = date of clutch initiation; and clutch size = clutch size of grackle. Interactions between predictors are denoted by an asterisk. The best model is highlighted in bold. K indicates the number of parameters; Δi and w_i represent the change in AIC_c in relation to the best model and Akaike weights, respectively.

Candidate model	K	AIC_c	Δi	w_i
1. Variation*completion	3	210.04	0	0.30
2. Variation*completion + year	4	210.79	0.75	0.21
3. (Null)	1	211.44	1.39	0.15
4. Initiation date	2	212.14	2.10	0.11
5. Clutch size	2	213.33	3.28	0.06
6. Variation	2	213.41	3.36	0.06
7. Clutch size + year	3	213.85	3.81	0.04
8. (Global) variation + initiation date + completion + clutch size + clutch size*variation + clutch + initiation date*variation + variation*completion	9	214.89	4.85	0.03
9. Variation + clutch size	4	214.91	4.86	0.03
10. Variation + year	3	215.48	5.44	0.02
11. Variation + initiation date + initiation date*variability	4	215.72	5.67	0.02

North American congeners, the Boat-tailed Grackle (*Q. major*) and Great-tailed Grackle (*Q. mexicanus*), which both have modal clutch sizes of only 3 eggs (Post et al. 1996, Johnson and Peer 2001).

We determined the fit of each model using a generalized mixed model (PROC GLIMMIX; SAS, version 9.2; SAS Institute, Cary, North Carolina) fitted to a binomial distribution with year entered as a random variable. Models were evaluated using ΔAIC_c , the relative difference from the smallest AIC_c (Akaike's information criterion, corrected for small sample size) and Akaike weights (w_i) (Burnham and Anderson 2002). We considered models that were ≤ 2 AIC_c units from the best model and better than the null model to be competing models, and models > 2 and ≤ 4 AIC_c units from the best model to be plausible. We disregarded models > 4 AIC_c units from the best model as an unlikely representation of the data (Burnham and Anderson 2002). We calculated parameter estimates and 95% confidence intervals (CI) for all models ≤ 4 AIC_c units from the best model (Burnham and Anderson 2002).

RESULTS

There was no significant geographic variation in rejection by grackles; they rejected 12.1% of 66 eggs in Illinois and 13.4% of 201 eggs in Iowa ($\chi^2 = 0.10$, $df = 1$, $P = 0.78$; Peer and Rothstein 2010), for a combined rejection frequency of 13.1%. The most common method of rejection was ejection, which made up 85.7% of the 35 rejections, with pecking the parasitic egg comprising the remaining 14.3% of rejections (Peer and Rothstein 2010). There was also no geographic variation in intraclutch egg appearance between Illinois and Iowa, which had mean (\pm SE) intraclutch variation scores of 1.49 ± 0.07 and 1.50 ± 0.04 (Mann-Whitney test, $U = 28,840$, $P = 0.74$), resulting in a combined intraclutch variation score of 1.5 ± 0.04 .

The AIC_c values indicated that the interactive model of variation in intraclutch egg appearance and clutch completion was the best model (model 1; Table 1). We also considered the interactive model between variation in intraclutch egg appearance and clutch completion with year as a random effect (model 2; Table 1) a competing model (< 0.76 AIC_c units of the best model). Nonetheless, because model 3 was the same as model 1 with one

additional variable and similar log-likelihood values (model 1, -2 log likelihood = 203.95; model 2, -2 log likelihood = 202.64), it was not a competitive model and we removed it from consideration (Burnham and Anderson 2002). This suggested that year as a random variable did not improve the strength of the model. The best model (model 1) had $w_i = 0.30$, which suggests that it was twice as likely to explain the data as the null model. Confidence intervals for the parameter estimate for the best model did not include zero ($\beta = -0.29$, 95% CI: -0.56 to -0.19), which indicates that variation*completion was a relevant predictor of egg rejection. Specifically, grackles with more variable clutches were more likely to accept cowbird eggs than those with less variable clutches when the eggs were added prior to clutch completion, but variation did not affect the likelihood of rejection when cowbird eggs were added after clutch completion (Fig. 1). Grackles lost 1 or

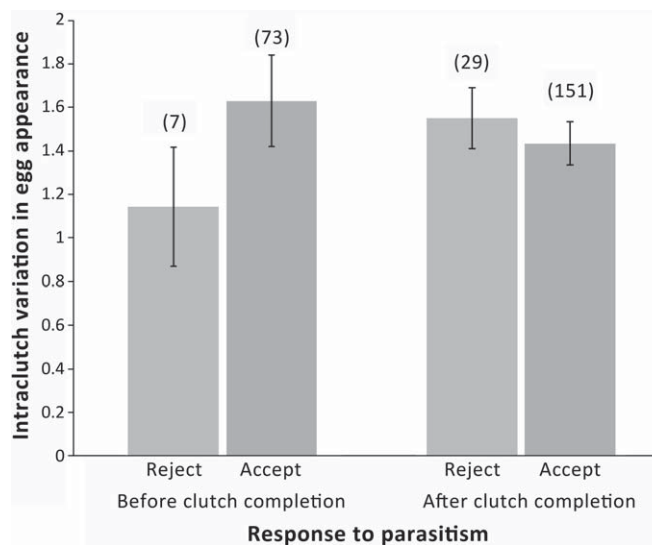


FIG. 1. Intraclutch egg variation scores (1–4) of Common Grackles and their response to artificial cowbird eggs added before clutch completion or after clutch completion. Sample Sizes are indicated in parentheses.

2 eggs from five (1.9%) experimentally parasitized nests (Peer and Rothstein 2010). In one nest an egg was missing following an ejection, which may have been a rejection error. In the remaining four cases, grackles lost 1 or 2 eggs and then deserted the nests without rejecting the cowbird eggs. The mean intraclutch variation score of these five clutches was 1.5 (range: 1.0–2.5).

DISCUSSION

Variation in intraclutch egg appearance and egg rejection in the grackle.—Despite the striking difference in appearance between grackle and cowbird eggs, variation in intraclutch egg appearance affected grackles' responses to cowbird eggs. Grackles with eggs of more variable appearance were more likely to accept experimentally added artificial cowbird eggs than were those with less variable eggs when artificial cowbird eggs were added prior to clutch completion. To our knowledge, this is the first study to demonstrate that variation in intraclutch egg appearance influenced egg rejection in a host with eggs that are radically different from those of its brood parasite. Acceptor individuals' tolerance for divergent eggs may be greater because it is based on the relatively high variation they detect in their present clutch (or, possibly, remember from past clutches) and because they cannot know the full range of their egg variation in the present clutch until laying is complete (Rothstein 1974, Lotem et al. 1995; see also Moskát and Hauber 2007). This uncertainty and weak selection may cause grackles with eggs of variable appearance to accept because it keeps them from rejecting their own oddly colored eggs (Lotem et al. 1995). Variation in intraclutch appearance may result in lower rejection levels even for strongly nonmimetic eggs because a divergent egg in a bird's own clutch could indicate that it is likely to lay even more divergent eggs (see also Moskát and Hauber 2007). In other words, grackles may not be able to set their discrimination threshold to an optimal level until they have finished laying. We suggest that variation in intraclutch egg appearance did not affect rejection when cowbird eggs were added after clutch completion because females were able to observe the range of phenotypic variation in their eggs at this time and because a cowbird egg is always outside the range of variation of grackle eggs. Thus, after a clutch is complete, rejection may be based solely on whether a grackle is a rejecter individual or whether some factor other than variation in intraclutch egg appearance has elicited rejection at that time (see Peer and Rothstein 2010).

The grackle's high threshold to reject foreign eggs is likely the result of the weak selection pressure to maintain rejection in the absence of parasitism and low costs when they are parasitized, in addition to variation in intraclutch egg appearance (Peer and Bollinger 1997b, Peer and Rothstein 2010). Similarly, Rothstein (1982) demonstrated that the American Robin (*Turdus migratorius*), whose eggs differ from cowbird eggs in three obvious ways (egg size, background color, and spotting pattern), also have a high rejection threshold. Although an egg that differs from their own eggs in any of the three parameters is highly divergent, American Robins tend to reject only if an egg differs in at least two parameters. Grackle eggs also differ from cowbird eggs in these parameters, and, unlike American Robins, grackles have high variation in intraclutch egg appearance (Peer and Rothstein 2010) that apparently increases their rejection threshold.

We recorded grackle egg loss from 2% of experimental nests, which could indicate a low level of rejection costs via either recognition errors or the damage of eggs during ejection attempts. However, the 2% rate was less than the 8% of control nests not subjected to experimental parasitism that lost one or more grackle eggs (Peer and Rothstein 2010) and, thus, there is no evidence of rejection costs.

Unlike in Great Reed Warblers (*Acrocephalus arundinaceus*) in Japan (Lotem et al. 1995), we found no relationship between clutch initiation date and variation in intraclutch egg appearance in grackles. Younger Great Reed Warblers initiate clutches after older ones, and the younger birds have higher variation in the appearance of their eggs (Lotem et al. 1995). It is not known whether young female grackles are more likely to lay clutches with more variably pigmented eggs. Indeed, nothing is known about the consistency in appearance of grackle eggs. Approximately 30% of grackle clutches have eggs of variable appearance (Peer and Rothstein 2010), but it is unknown whether a female that lays variable eggs will always do so. It is possible, for example, that clutches with variably pigmented eggs are limited mostly to first-time breeders (e.g., Lotem et al. 1995). It is also unclear whether there is an adaptive explanation for intraclutch variation in egg appearance. Although Common Grackles have larger modal clutch sizes than the other grackle species, which could deplete pigment reserves by the time females lay their last egg, there was no evidence that larger clutches had more variation, and clutch size did not affect rejection behavior. A lack of pigment for last-laid eggs might exert only weak selection pressures because females begin incubation after the penultimate egg has been laid in five egg clutches (Peer and Bollinger 1997a), and the last-laid egg will be covered by the female most of the time, unlike earlier-laid eggs.

Despite the effect of variation in intraclutch egg appearance on egg rejection, the amount of intraclutch variation we recorded in grackles in the Great Plains was less than that recorded in previous studies conducted farther east (see Peer and Sealy 2004b). It is possible that grackles in the Great Plains, where our study was conducted, were under greater selection to minimize intraclutch variation to recognize past cowbird parasitism—because this is within the original center of abundance of cowbirds before Europeans colonized North America (Mayfield 1965)—compared with grackles to the east that likely experienced less selection from parasitism. Indeed, there are very few records of cowbird parasitism on grackles, but the most recent records all come from the Great Plains (Peer et al. 2001). This raises the possibility that populations with greater variation have a higher discrimination threshold for rejection and are therefore less likely to reject cowbird eggs. In support of this possibility, there is a trend in our studies (Peer and Bollinger 1997b, Peer and Sealy 2004b, Peer and Rothstein 2010, present study) for rejection frequency to decline from the Great Plains to the east (Indianola, Iowa, 13.4%; Macomb, Illinois, 12.1%; Charleston, Illinois, 7.8%; Connecticut, 7.1%), and this requires further study.

Contrary to our findings, a comparative analysis across a range of species found no link between variation in intraclutch egg appearance and rejection in North American hosts (Stokke et al. 2002). This may, in part, be attributable to the fact that many hosts in North America, especially rejecter species, have relatively little within-clutch variation in the pigmentation and appearance

of eggs and there tends to be relatively little variation in host response, especially compared with European hosts (Peer and Sealy 2004a, B. D. Peer and S. I. Rothstein unpubl. data). More experimental studies on the influence of variation in intraclutch egg appearance on rejection in North American hosts, especially hosts whose eggs are similar to cowbird eggs (e.g., Burhans and Freeman 1997, Peer et al. 2000), are required to fully understand the importance of intraclutch egg variation.

The effects of variation in intraclutch egg appearance in other brood parasite–host systems.—In spite of the similarity between host and cuckoo (*Cuculus*, *Clamator*) eggs, the evidence that variation in intraclutch egg appearance affects host rejection is mixed (Øien et al. 1995, Soler and Møller 1996). Given the longer history of cuckoo parasitism (Rothstein et al. 2002), one might expect European hosts to have evolved eggs with minimal variation in the appearance of host eggs to facilitate recognition of cuckoo eggs if this was important, but variation in intraclutch egg appearance does not differ between North American and European hosts (Avilés et al. 2006).

Experimental tests also have not provided a consensus because hosts with less variable eggs are sometimes more likely to reject nonmimetic eggs (Stokke et al. 1999, Soler et al. 2000), and sometimes less likely to reject (Lotem et al. 1995, Avilés et al. 2004), whereas rejection in some hosts is not related to variation in egg appearance (Karcza et al. 2003, Procházka and Honza 2003, Lovászi and Moskát 2004). Finally, some studies have found indirect evidence that exposure to brood parasitism selects for reduced variation in intraclutch egg appearance compared with host populations that are not exposed to brood parasitism (Avilés and Møller 2003, Lahti 2005), whereas others have found no difference in parasitized and unparasitized populations (Davies and Brooke 1989, Moskát et al. 2002).

Implications for brood parasite–host coevolution.—Once hosts are parasitized and evolve defenses, their parasites may respond by evolving mimetic eggs (Davies and Brooke 1998). Hosts may counter parasitic egg mimicry by one or both of two mechanisms: evolving eggs with minimal variation in intraclutch egg appearance or maximum interclutch variation in egg appearance to facilitate recognition of parasitic eggs (Øien et al. 1995, Davies and Brooke 1998). Our results indicate the value of minimizing variation in intraclutch egg appearance, even in hosts whose eggs are very different from those of the parasite, to facilitate recognition of parasitic eggs.

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