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Interspecific egg rejection as ecological collateral damage from selection driven by conspecific brood parasitism

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Abstract

Distinguishing between interspecific and intraspecific coevolution as the selective driver of traits can be difficult in some taxa. A previous study of an avian obligate brood parasite, the black-headed duck, *Heteronetta atricapilla*, suggested that egg rejection by its two main hosts (two species of coot) is an incidental by-product of selection from conspecific brood parasitism within the hosts, not selection imposed by the interspecific parasite. However, although both species of coot can recognize and reject eggs of conspecific brood parasites, which closely resemble their own, they paradoxically also accept a moderate fraction of duck eggs (40–60%), which differ strikingly in shape and color from their own eggs. Here we test the key assumption of the incidental by-product hypothesis that natural selection for egg recognition solely from conspecific brood parasitism can result in intermediate levels of rejection of nonmimetic eggs. We repeated the same egg rejection experiments conducted previously with the two Argentine hosts in a third closely related species that experiences only conspecific brood parasitism, the American coot, *Fulica americana*. These experiments yielded the same intermediate rejection rates for nonmimetic duck eggs. Our results confirm that selection from conspecific brood parasitism can lead to counterintuitive intermediate rejection rates of nonmimetic interspecific eggs and further support the suggestion that selection from antagonism within species can incidentally affect interactions between species.

Keywords: coevolution, conspecific brood parasitism, egg rejection, geographical comparison, *Heteronetta*, interspecific brood parasitism

Antagonistic coevolution between species favors the reciprocal evolution of traits that mitigate the negative fitness effects of the interspecific interaction (Brandt et al., 2005; Rothstein, 1990; Thompson, 1994). Interspecific avian brood parasites, birds that lay their eggs in the nests of other species and then leave all parental care to the hosts, provide a model system for studying antagonistic coevolution. The reciprocally hostile interactions between brood parasites and their hosts may lead to the evolution of defensive traits in hosts, which then favors the evolution of counter-defensive traits in the brood parasites (Davies, 1999, 2000; Langmore et al., 2003; Rothstein, 1990). For example, parasitic chicks in some taxa impose extreme fitness costs on their hosts (Davies and Brooke, 1988; Rothstein, 1975) that have led to the evolution of egg recognition and rejection in a diversity of host taxa (Davies, 2000; Rothstein, 1990). Egg rejection by hosts negatively impacts the fitness of the brood parasites, which in some cases has favored the evo-

lution of highly sophisticated egg mimicry and host specialization in the brood parasites (Brooke and Davies, 1988; Gibbs et al., 2000). However, not all hosts of interspecific brood parasites show defenses against the parasites: some lack antiparasite defenses entirely. In some species, hosts show intermediate levels of defense whereby not all parasitic eggs are rejected (Davies, 2000; Rothstein, 1990). In these species, it is unclear whether this reflects variation among individuals in cognitive aspects of recognition or variation in the recognition cues or social environment that an individual happens to encounter (Davies et al., 1996; Rothstein, 1982). Understanding why hosts vary in defenses against parasitism remains an important area of inquiry, and a number of factors have been identified to explain why such traits are lacking in some species or individuals within species (Davies, 1999; Kruger, 2011; Moskat and Hauber, 2007; Røskaft et al., 2006; Rothstein, 1990; Underwood and Sealy, 2006).

Brood parasitism within species also occurs in birds, having been documented in over 200 species (Andersson, 1984; Lyon and Eadie, 2008; Yom-Tov, 1980, 2001). In some cases such conspecific parasitism can impose substantial costs on hosts, and the adaptive responses to these costs are often identical to those exhibited in response to interspecific brood parasites: egg recognition and rejection (Arnold, 1987; Jackson, 1992; Jamieson et al., 2000; Lyon, 2003, McRae, 2011; Sorenson, 1995). However, discrimination against conspecific brood parasite eggs may require much finer-scaled recognition cues because intraspecific variation in egg features is often much lower than interspecific variation, at least prior to the evolution of egg mimicry (Andersson, 1984; Jackson, 1992; Lyon, 1993a).

In some cases, hosts suffer from both conspecific and interspecific brood parasitism, which can complicate the interpretation of evolutionary causes of host adaptation. Although the tendency is to often assume that interspecific parasitism is the evolutionary driver of host traits, perhaps because interspecific parasitism is often more obvious and easily detected than conspecific parasitism, it is possible that some signatures of coevolution might instead be fuelled by the brood parasitism within the hosts themselves (Freeman, 1988; Lahti, 2006; Lyon and Eadie, 2004). In these taxa it has proven difficult to disentangle the relative roles of conspecific and interspecific brood parasitism as drivers of host defenses (Freeman, 1988; Grendstad et al., 1999; Jackson, 1992; Lahti, 2006; Peer et al., 2007; Rothstein, 2001; Samas et al., 2014). However, one potentially powerful method for distinguishing between conspecific and interspecific interactions as the agent of selection is a geographical comparison of egg rejection behavior in regions where hosts are sympatric versus allopatric with their interspecific brood parasites (Lahti, 2006). A similar approach is to compare closely related species that differ in the forms of contemporary brood parasitism: an approach we use in this study.

Here we compare the results of experiments conducted in British Columbia, Canada with those of similar experiments conducted previously in Argentina to determine whether natural selection caused by interactions within species can account for the behavioral interactions observed between species. Specifically, we sought to determine whether conspecific brood parasitism can provide an evolutionary explanation for the pattern of rejection of the eggs of the black-headed duck, *Heteronetta atricapilla*, by its main hosts, the two species of Argentine coot (*Fulica* spp.) (Figure 1).

Black-headed ducks are unique among the 101 species of avian obligate brood parasites in that their young are precocial and, unlike all other brood parasites, they leave the nest upon hatching and make no posthatching demands on the parental care of their hosts (Davies, 2000; Lyon and Eadie, 2004; Lyon and Eadie, 2013; Weller, 1968). Given this reduced parasitic virulence, one might expect somewhat benign interactions between the brood parasite and its hosts. However, our previous study in Argentina revealed that duck eggs are often rejected by the two main hosts, the red-gartered coot, *Fulica armillata*, and the red-fronted coot, *Fulica ruffifrons* (Figure 1), despite a lack of detectable costs of parasitism imposed by the ducks (Lyon & Eadie, 2004). Moreover, parasite and host eggs differ strikingly in appearance (Figure 2), yet an experimental study revealed that increasingly mimetic eggs do not alter rejection rates (Lyon & Eadie, 2004). These paradoxical findings, coupled with the subsequent discovery of conspecific brood parasitism and rejection of conspecific parasitic eggs in both species of hosts, led us to conclude that the rejection of duck eggs is likely to be an incidental by-product of natural selection on hosts to recognize and reject the eggs of conspecifics (Lyon & Eadie, 2004). Unlike the ducklings, which feed themselves, coot chicks are fed by their

parents. In American coots, posthatching mortality is often severe, due to limiting food (Lyon, 1993b; Lyon et al., 2002), and conspecific parasites compete for this food.

One element that remains unresolved by the hypothesis that conspecific parasitism drives these patterns is the curious pattern of egg rejection: intermediate rejection rates of the duck eggs, whereby approximately 40% and 60% of duck eggs are accepted by the two host species, respectively (Lyon & Eadie, 2004). Given that hosts are capable of the very fine-scale discrimination required to accurately distinguish among eggs of conspecifics, shouldn't they always be able to recognize and reject the extremely different duck eggs (Figure 2)? This assumption is based both on theoretical considerations of recognition systems (Sherman, Reeve, & Pfennig, 1997), plus empirical evidence that egg rejection rates correlate with the degree of difference between host and parasite eggs in some brood-parasitic systems (de la Colina et al., 2012; Lotem et al., 1995; Rothstein, 1982; Spottiswoode and Stevens, 2010). Thus a key question, and one on which the rejection as incidental by-product hypothesis depends, is whether the evolution of egg rejection driven solely by conspecific brood parasitism could result in the intermediate rejection rates that we observed for the highly nonmimetic eggs of *Heteronetta*.

To answer this question, we repeated identical egg addition experiments done previously in the two species of Argentina host coot (Lyon & Eadie, 2004) in a third species of coot, the American coot, *Fulica americana* (Figure 1), breeding in allopatry with the parasitic duck *Heteronetta*. Conspecific brood parasitism and egg rejection are frequent in American coots (Figure 1 in Lyon, 1993b; Lyon, 2003), but interspecific brood parasitism is virtually absent (we never observed it in our study of some 800 coot nests, and very rare instances have been reported for other populations; Ryder, 1959). Thus, our experiment contrasts rates and patterns of egg rejection in two species that suffer both conspecific and interspecific brood parasitism (Argentine coots) with the rates and pattern of egg rejection in a species that suffers only conspecific brood parasitism (American coot). The experiment focuses on two aspects of rejection. First, how do the hosts respond to white eggs that resemble real duck eggs? Finding that American coots show the same intermediate rejection rates as the Argentine coots would confirm that selection from conspecific brood parasitism alone can lead to the patterns of rejection observed in the Argentina hosts, given that our assumption of a lack of history of interspecific brood parasitism in American coots is true. Second, do American coots show the same lack of response to a series of increasingly mimetic eggs? Again, finding a similar response to this more detailed cognitive challenge would further support the hypothesis that conspecific brood parasitism alone has shaped the cognitive mechanisms that underlie egg recognition and rejection in the Argentine host coots.

Methods

We conducted the experiment on several wetlands in the Williams Lake area in British Columbia, Canada in May and June of both 2005 and 2006. We conducted the experiments in different areas across the 2 years, so individual hosts would have been involved only once. The wetlands include Kloe Lake and Pond S5 (names for the wetlands from Ducks Unlimited, Inc., Memphis, TN, U.S.A.) (20 nests combined) on the Chilco Ranch near Hanceville, several small wetlands on Beechers Prairie near Riske Creek (19 nests in total) and the Westwick Lakes close to Williams Lake (9 nests in total). Hardstem bulrush, *Schoenoplectus acutus*, the dominant emergent plant at all wetlands, was limited to a shoreline strip on most wetlands, but sparse patches of bul-



Figure 1. Brood parasites and hosts. (a) A pair of black-headed ducks, an obligate precocial brood parasite (female on left, male on right, and a main host, the red-gartered coot, in the center). (b) Red-fronted coot, one of the two main hosts of the ducks in Argentina. (c) Red-gartered coot, the second main host of the duck. The two Argentine coots also show brood parasitism within species. (d) American coot, a species with conspecific brood parasitism but no interspecific brood parasitism.

rush grew in the middle of Kloe Lake, providing nesting cover for coots away from the shoreline. Water levels were stable in these wetlands: an important detail, because rapid increases in water levels have been shown to affect egg rejection rates in both the South American species of coot (Lyon and Eadie, 2004; Weller, 1968) and in the American coot (Weller, 1971). Additional details about the study area are provided in Lyon (1993b).

The experiment in British Columbia was designed to be identical to the experiments previously conducted with the two coot species in Argentina. Accordingly, we created a series of three treatments that varied in the number of features by which they differed from the host eggs (see Results, Figure 3). Real parasitic duck eggs in Argentine coot nests are immaculate white and oval-shaped and differ from the host eggs in three key visual features: they have a rounder shape and a paler background color, and they lack spots (Figure 2a). We painted domestic chicken eggs and real host eggs with exterior semigloss latex paint to create a series of three egg treatments that increasingly resembled host eggs: the least mimetic 'white duck' eggs (experimental versions of real duck eggs) had a different shape and background color and lacked spots; the 'brown duck' eggs had a different shape and lacked spots but resembled the average coot egg in background color; the 'brown coot' eggs differed from coot eggs only by lacking spots (Figure 3). We used chicken eggs for the 'white duck' and 'brown duck' treatments (Figures 2 & 3) because the shape of chicken eggs was similar to the shape of duck eggs. We used fresh coot eggs painted with brown latex paint for the 'brown coot' treatment, which was meant to have the same shape as the host eggs. We added a single experimental egg to each host nest, either in the laying or early incubation stage, and we scored the fate of the egg after 10 days. Coots reject parasitic eggs by burial in the nest rather than ejection outside the nests (Figure 2). Eggs were scored as rejected if found buried in the nest or if observed at least half buried on the

final nest visit for nests that hatched or were preyed on before rejection was complete. We also scored eggs that simply disappeared as rejected, although most rejection was by burial. Non-rejected eggs were scored as accepted only if the nest remained active long enough for rejection to have occurred (≥ 10 days).

Paint typically lacks a UV component, confirmed in our case with spectrophotometer measures. Measures of unpainted coot and chicken eggs further revealed that these eggs do have a UV component to their color (Lyon & Shizuka, 2006). To ensure that our results were not driven by the lack of a UV component in our treatments, we added a single unpainted white chicken egg to 10 nests, of which four were rejected (40%), and added a single unpainted brown chicken egg to 10 other nests, of which three were rejected (30%). These results were not significantly different from each other, nor did they differ from their corresponding treatments involving paint that we report below (Fisher's exact test: all $P \geq 0.25$). Lack of UV in paint was not a confounding factor in our experiments.

We compared the rejection patterns of American coots with their South American relatives in three ways. First, we compared rejection rates of the white duck eggs, as this is the egg phenotype of the interspecific brood parasite in South America. We used a chi-square test to compare rejection rates of white duck eggs among species because this enabled us to then conduct post hoc tests based on additive partition of the degrees of freedom (Siegel & Castellan, 1988). Second, we determined whether American coots show the same indifference to degree of egg mimicry previously shown by the South American coots. In the previous study we used continuous logistic regression; here we use the more appropriate nominal logistic regression with egg phenotype represented in terms of rank number of different phenotypic characters differing from host eggs, 1, 2 or 3, respectively (the two different forms of logistic regression yield very similar results). Third, if American coots are indiffer-



Figure 2. Natural and experimental brood-parasitic eggs. (a) Two real black-headed duck eggs (white) in a red-gartered coot nest in Argentina. (b) American coot nest with nine host eggs and two conspecific brood-parasitic eggs (darker eggs) in British Columbia. (c) American coot nest with seven host eggs and two paler conspecific brood-parasitic eggs in the process of being buried in the edge of the nest. (d) American coot nest with an experimental brown duck egg.

ent to degree of mimicry, we can then pool all three treatments and compare overall rejection rates. This comparison serves the same function as the comparison of the white duck treatment but the much larger sample size increases the statistical power of the test.

Ethical Note

Unfertilized chicken eggs were used for the white duck and brown duck treatments. Fresh (undeveloped) real coot eggs were used for the brown coot egg treatment. Whenever possible (based on availability) we used conspecific brood-parasitic coot eggs rejected from a host nest (we used parasitic eggs rejected quickly after being laid to avoid the confounding effects of partially developed eggs). When rejected parasitic eggs were not available we used fresh coot eggs taken from a coot nest early in laying. Removing a single fresh coot egg from a nest has very little effect on the final brood size at the nest because coot chicks have very high rates of mortality due to posthatching brood reduction (Lyon, 1993a, 1993b; Shizuka and Lyon, 2013). Because painting the experimental coot eggs (to hide natural spotting) sealed the pores and prevented development, all experimental brown coot eggs that were not rejected by the coots (all three treatments) were removed from the nests and destroyed after the 10-day trial period. This research was conducted under a University of California, Santa Cruz IACUC protocol SC 2008044, and permits from the British Columbia and federal Canadian Wildlife Services.

Results

The pattern and rates of egg rejection in American coots, a species currently parasitized by conspecific but not interspecific brood parasites, were broadly similar to those observed in the two Argentine coot species. Although the rejection rates of the white duck eggs differed significantly among the three species of coot (Figure 3; chi-square test: $\chi^2_2 = 7.61$, $P = 0.02$), this was due to the higher rejection rates in one of the Argentine species, not to geographical differences between the two regions (Figure 3). Post hoc tests, based on additive partitioning of the degrees of freedom, showed no differences in the rejection rate of the white duck eggs between *F. americana* and *F. armillata* ($\chi^2_1 = 0.21$, $P > 0.5$), but the rejection rate for *F. rufifrons* differed from that of the other two species combined ($\chi^2_1 = 7.40$, $P = 0.01$). For comparison, the rejection rate of natural conspecific parasitic eggs in nests that receive only a single egg is 16% (note the rejection rates of experimental nests was over a limited period, here 10 days, whereas natural rejection rates are over the time period a host nest is observed).

The degree of similarity of the experimental eggs to the host's own eggs did not affect egg rejection rates in American coots (Figure 3). With degree of similarity entered as a ranked variable, nominal logistic regression revealed no effect of degree of similarity on the proportion of eggs rejected (Wald chi-square test: $\chi^2_2 = 1.14$, $P = 0.56$). This pattern is identical to that found in the two South American coots, in which rejection rate was not

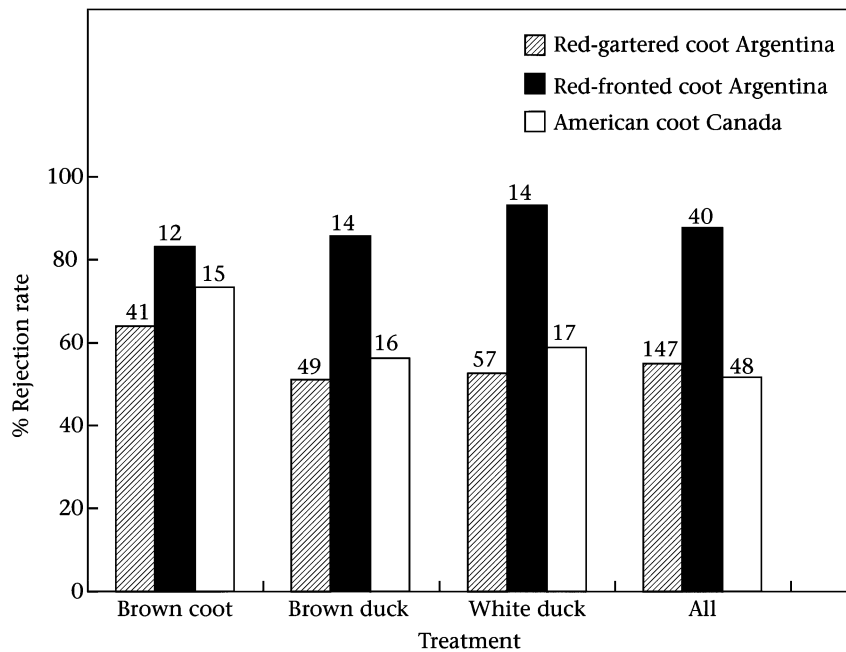


Figure 3. Egg rejection rates in three species of coots in the genus *Fulica* that all received the identical series of egg rejection experiments. Each species received three different egg phenotypes forming a graded mimetic series that increasingly differed from host eggs, as illustrated by the photograph. Two of the coots, the red-gartered and red-fronted coots of Argentina, experience both conspecific brood parasitism and interspecific brood parasitism by an obligately brood-parasitic duck whose eggs are very similar to the white duck treatment. The American coot studied in Canada experiences only conspecific brood parasitism. Numbers above the bars indicate sample size (number of nests).

influenced by degree of similarity (Lyon & Eadie, 2004). For consistency we repeated the two analyses for the South American coots using nominal rather than continuous logistic regression, as was used in the original article (Wald chi-square test: red-gartered coot: $\chi^2_2 = 1.63$, $P = 0.44$; red-fronted coot: $\chi^2_2 = 0.64$, $P = 0.73$).

Given that egg rejection was similar for the different egg treatments in all three species, we pooled the three treatments for each species and compared the rejection rates of all experimental eggs combined for a more powerful test. The rejection rates of all experimental eggs combined differed significantly among the three species of coot (chi-square test: $\chi^2_2 = 14.03$, $P = 0.001$; Figure 3) but, as with the white duck treatment, this was due to higher rejection rates in one of the Argentine species and not geographical differences (Figure 3). Post hoc tests, based on additive partitioning of the degrees of freedom, showed no differences between *F. americana* and *F. armillata* ($\chi^2_1 = 0.84$, $P > 0.25$), but the rejection rate for *F. rufifrons* differed from that of the other two species combined ($\chi^2_1 = 13.19$, $P = 0.001$).

Discussion

Our egg rejection experiments support the hypothesis that selection from conspecific brood parasitism alone can lead to the paradoxical patterns of duck egg rejection we previously observed in the two Argentine coot species (Lyon & Eadie, 2004). Several indirect lines of evidence all pointed to conspecific brood para-

sitism as the evolutionary driver of egg rejection behavior in the two main host species in Argentina, which implies that rejection of duck eggs is merely an incidental by-product of an egg rejection system geared towards conspecifics. A potential weakness of this hypothesis was that it did not explain why a reasonable fraction of hosts of both species failed to reject duck eggs (Lyon & Eadie, 2004). If an egg recognition and rejection system has been shaped by natural selection to distinguish subtle differences among the eggs of conspecifics, shouldn't it always allow a host to recognize and reject eggs like the duck eggs that differ so dramatically from the host eggs (Figure 1)? Our experiments here with American coots were designed to determine whether intermediate rejection rates could arise for a species in which egg rejection has evolved only in the context of conspecific parasitism. Our results show convincingly that a recognition system solely shaped by brood parasitism within species can lead to the same patterns of intermediate egg rejection of nonmimetic heterospecific eggs as we observed in the two South American coot species.

Our conclusions are further reinforced by experiments by Weller (1971). He wondered why the redhead, *Aythya americana*, a facultative interspecific brood parasite in North America, did not parasitize American coots, a question motivated by trying to understand why *Heteronetta* had become an obligate parasite while redheads remained facultative (Weller, 1968). Weller (1971) assessed the suitability of the American coot as a host for an obligate parasitic duck species by adding white nonmimetic

hen eggs to coot nests in Iowa. He observed intermediate rates of egg rejection, at least on wetlands with stable water levels (Weller, 1971), indicating that the intermediate rejection rates we observed in British Columbia are general.

An examination of the phylogeny of coots (genus *Fulica*; Livezey, 1998) reveals that American coots are more recently derived than the two Argentine hosts of *Heteronetta*. Based on this phylogenetic pattern, colleagues have suggested that egg rejection in American coots could be a relict trait inherited from an ancestor that was parasitized by the ducks and not an accurate reflection of rejection behavior driven solely by conspecific brood parasitism. The relict behavior hypothesis has recently been supported for several species in the context of interspecific brood parasitism: these species all show high levels of egg rejection, do not currently appear to suffer any form of brood parasitism (but are derived from ancestral species parasitized by interspecific brood parasites), and other explanations for egg rejection appear not to apply (Bolen et al., 2000; Peer et al., 2007, 2011; and Rothstein, 2001). However, one pattern in particular indicates that the relict behavior hypothesis is not a viable explanation for egg rejection behavior in American coots. Conspecific brood parasitism and conspecific egg rejection are widespread in rails (Rallidae), including two genera that are more basal than coots (*Porzana*: Sorenson, 1995; *Gallinula*: Jamieson et al., 2000 & McRae, 2011) according to Livezey's (1998) phylogeny. Thus, in the rails generally, conspecific brood parasitism and conspecific egg rejection are ancestral and widespread, whereas only two species of more recently derived taxa have been subjected to interspecific parasitism by *Heteronetta*. Thus, if relict behaviors were to occur in this clade, host responses to duck parasitism would have been influenced by relict behaviors driven by conspecific brood parasitism, not the other way around.

In fact, it seems very unlikely that any form of relict effects would influence egg rejection behavior in American coots due to the strength and specificity of contemporary natural selection driven by conspecific brood parasitism. Parasitism is very costly to American coot hosts (Lyon et al., 2002) because the food parents provide for the chicks is essential for survival and limiting. The high cost of raising a parasitic chick coupled with a high frequency of brood parasitism at the population level results in an estimated strength of selection for egg rejection that is similar to estimates for hosts of some interspecific parasites such as cuckoos (Lyon, 2003). Moreover, egg patterns and background colors differ considerably across the coot species we have studied, and across rails more generally, which requires the evolution of recognition mechanisms tailored to deal specifically with the egg features of their own species. In summary, relict behaviors cannot explain the fine-tuned cognitive responses that American coots show in recognizing and rejecting conspecific eggs. Our experiments thus provide much stronger support for the hypothesis that selection exclusively from conspecific parasitism can result in intermediate rejection rates of nonmimetic interspecific eggs.

Consideration of the proximate cues used for egg recognition could resolve further questions about the evolution of egg rejection in coots. For example, why do coots reject each of our egg types at roughly the same rate? One possibility is that our treatments did not vary in some important cue that hosts use to recognize eggs. Previous work showed that eggs of different females can be reliably distinguished based on a combination of egg background color, the density of spots of different size (spot color was not examined), and the length and width of the egg (but not shape) (Lyon, 1993a). In terms of what actually correlates with egg rejection, the difference in rank background color between host and parasite eggs was greater for rejected eggs than accepted eggs, indicating that background color serves as one recognition feature (Lyon, 2003). However, back-

ground color is not the only feature used in recognition, because coots reject many eggs that do not differ measurably in background color from the host's eggs. There is increasing evidence that spotting patterns may also be more important than background color in hosts of mimetic interspecific parasitic eggs (Lahti & Lahti, 2002; Stoddard, Kilner, & Town, 2014). The use of spots for egg recognition in coots could explain the seemingly paradoxical results of our mimicry experiment, whereby hosts treated all three treatments similarly despite the treatments representing a gradient of similarity in shape and background colour (Lyon & Eadie, 2004). If the colour and pattern of spots are particularly important for egg recognition, then the lack of difference in response to our three experimental mimicry treatments could reflect the fact that the treatments did not differ in the feature that is most important to hosts. It would be interesting to repeat this study with additional treatments that include spotting patterns.

The question remains as to why selection for the ability to recognize eggs of conspecific brood parasites would result in intermediate rejection rates for eggs that differ so strikingly from the host's eggs. More specifically, why aren't all duck eggs rejected? Intermediate levels of egg rejection are not unique to our study, and they remain a puzzling feature of brood parasite-host coevolution in general, including interspecific brood parasitism (de la Colina et al., 2012; Hauber et al., 2006; Rothstein, 1990; Takasu, 1998). We now review several hypotheses for intermediate rejection and discuss their relevance to coots. On a proximate level, these hypotheses involve two general mechanisms: (1) some hosts fail to recognize parasitic eggs despite drastic phenotypic differences in egg features, or (2) some hosts fail to reject parasitic eggs despite being able to recognize them.

With respect to either recognition or rejection, gene flow between parasitized and unparasitized populations could result in imperfect adaptations on a local level, and hence intermediate egg rejection rates (Briskie et al., 1992; Davies and Brooke, 1989). Alternatively, hosts may lag behind the parasites in the coevolutionary arms race such that the alleles for egg recognition or rejection have not completely swept through the population (Davies, 1999; Hosoi and Rothstein, 2000; Rothstein, 1990; Takasu, 1998). These genetic explanations cannot apply to our study of American coots because the species does not suffer interspecific parasitism by black-headed ducks in any part of its range.

The misimprinting hypothesis could explain why some birds are able to recognize parasitic eggs while others are not. With the assumption that egg patterns are learned the first time a bird breeds, any birds parasitized in their first breeding attempt are predicted to imprint on both their own eggs and the brood parasite's and, consequently, become lifelong acceptors (Lotem et al., 1992; Strausberger and Rothstein, 2009). This predicts that the ratio of acceptors is roughly proportional to the parasitism frequency of first-time breeders. This misimprinting hypothesis is rejected by our observation that all birds appear capable of recognizing parasitic eggs in some circumstances and, therefore, that lack of rejection does not stem from lack of recognition. For example, egg rejection rates in a few local populations of the two Argentina coots soared to 100% under extreme environmental conditions: rapidly rising water levels due to flooding or high waves on an open wetland with little vegetation (Eadie & Lyon, n.d.). Prior to flooding or high waves, rejection rates in these wetlands were intermediate to those typical of the broader population in general, but when the environment changed, all remaining duck eggs (real or experimental) in the population were rejected very quickly (Eadie & Lyon, n.d.). Weller also found that rejection rates of duck-like eggs (hen eggs) rose to near 100% during flooding in his experimental parasitism study of American coots in Iowa (Weller, 1971). That all birds appear

able to recognize eggs, but do not always reject them, indicates that the explanation for intermediate rejection rates lies in the factors that trigger egg rejection. The growing literature on context-dependent egg rejection, a characteristic that enables hosts to modulate the costs and benefits of egg rejection, indicates that the stimuli that trigger egg rejection can be numerous and complex (Davies et al., 1996; Hauber et al., 2006; Hoover and Robinson, 2007; Moskat and Hauber, 2007).

The observation that all birds reject duck eggs during flooding and high waves suggests two related explanations for why some coots might fail to reject parasitic eggs even when they are capable of recognizing them. One possibility is that coots have a 'life boat' response during floods and waves, whereby they ensure that their own eggs (and any eggs they cannot distinguish from their own eggs) are actively maintained inside the nest bowl while they rapidly build up their nest to avoid inundation of their clutch, while any eggs that fall outside the host's egg recognition template are treated as inert objects and the nest is incidentally built over them. Alternatively, coots may only discriminate against duck eggs when the ecological benefits of correct rejection outweigh the costs of false acceptance (Davies et al., 1996; Hauber et al., 2006; Sherman et al., 1997). Because the benefits of rejecting the relatively benign eggs from black-headed ducks are low (Lyon & Eadie, 2004), rejection may only pay under extreme conditions, such as when birds need to rapidly build up their nests to save their own eggs. Both hypotheses predict that egg rejection rates correlate with nest-building rates, but the cost-benefit hypothesis further predicts that parasitism by ducks is more costly when the risk of clutch inundation is high.

A third, but not mutually exclusive, explanation for the intermediate rejection rates of duck eggs by coots is suggested by consideration of the evolutionary basis of the egg recognition and rejection system that we discussed above. If evolution has molded egg recognition and rejection responses to target the relatively similar eggs of conspecific parasites, selection should favor the use of features that most reliably allow birds to distinguish their own eggs from the foreign eggs (Spottiswoode & Stevens, 2010), in this case the eggs of conspecifics, and these features are unlikely to be the same ones that differ most between the host's eggs and those of the interspecific parasite's eggs. Thus, the more extreme differences in phenotype we see in the interspecific parasitic eggs would not necessarily lead to a more extreme rejection response, such as rejection of all parasitic eggs.

Demonstrating that selection from conspecific brood parasitism alone can lead to the intermediate rejection rates for duck egg phenotypes reinforces the conclusion from our earlier work that the rejection of black-headed duck eggs by its two main hosts is an inadvertent consequence of selection from brood parasitism within the hosts, not antagonism between the host and interspecific brood parasite (Lyon & Eadie, 2004). This general phenomenon, selection from intraspecific interactions leading to the evolution of traits that can be confused with signatures of interspecific coevolution, may occur in contexts other than brood parasitism and should be considered as a feasible hypothesis where the natural histories of intraspecific and interspecific interactions would both lead to similar trait evolution.

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