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

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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 colour 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.

Antagonistic coevolution between species favours the reciprocal evolution of traits that mitigate the negative fitness effects of the interspecific interaction (Brandt, Foitzik, Fischer-Blass, & Heinze, 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 favours the evolution of counterdefensive traits in the brood parasites (Davies, 1999, 2000; Langmore, Hunt, & Kilner, 2003; Rothstein, 1990). For example, parasitic chicks in some taxa impose extreme fitness costs on their hosts (Davies & 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 favoured the evolution of highly sophisticated egg mimicry and host specialization in the brood parasites (Brooke & Davies, 1988; Gibbs et al., 2000). However, not all hosts of interspecific brood parasites show defences against the parasites: some lack antiparasite defences entirely. In some species, hosts show intermediate levels of defence 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, Brooke, & Kacelnik, 1996; Rothstein, 1982). Understanding why hosts vary in defences 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 & Hauber, 2007; Røskaft, Takasu, Moksnes, & Stokke, 2006; Rothstein, 1990; Underwood & Sealy, 2006).

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Brood parasitism within species also occurs in birds, having been documented in over 200 species (Andersson, 1984; Lyon & 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, McRae, Simmons, & Trewby, 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 & Eadie, 2004). In these taxa it has proven difficult to disentangle the relative roles of conspecific and interspecific brood parasitism as drivers of host defences (Freeman, 1988; Grendstad, Moksnes, & Røskaft, 1999; Jackson, 1992; Lahti, 2006; Peer, Rothstein, Delaney, & Fleischer, 2007; Rothstein, 2001; Samas, Hauber, Cassey, & Grim, 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 behaviour 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 behavioural 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.) (Fig. 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 & Eadie, 2004, 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 rufifrons* (Fig. 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 (Fig. 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, Hochachka, & Eadie, 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 (Fig. 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, Pompilio, Hauber, Reboreda, & Mahler, 2012; Lotem, Nakamura, & Zahavi, 1995; Rothstein, 1982; Spottiswoode & 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* (Fig. 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 bulrush grew in the middle of Kloe Lake, providing nesting cover for coots away from the shoreline.