



## Context-dependent response to eggs: egg retrieval versus egg rejection in a conspecific brood parasite



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Birds often need to distinguish their own eggs from those of others or from other objects that could be confused with their eggs. Egg recognition occurs in a variety of birds that retrieve eggs displaced from the nest. Egg recognition and rejection is also a particularly widespread defence against brood parasites. We studied egg retrieval and rejection in the American coot, *Fulica americana*, a species with high levels of conspecific brood parasitism. Previous work revealed that hosts recognize and reject many parasitic eggs. We conducted experiments to determine whether coots also show egg retrieval behaviour and, if they do, whether the same cues trigger retrieval and rejection. If these two responses share the same general cognitive mechanism, a given egg phenotype should elicit the same retrieval and rejection response (with the realization that failure to retrieve is analogous to rejecting eggs). Coots retrieved many eggs and objects placed on their nest rims. All coot eggs were retrieved, including eggs of other conspecific females, and most chicken eggs were also retrieved. The retrieval of a moderate proportion of non-egg-shaped objects like cubes and cylinders shows that an egg shape is not essential for retrieval. Two observations suggest that egg retrieval and rejection are triggered by different cues. The non-retrieval rates of parasitic eggs differed significantly from the corresponding egg rejection rates obtained in an earlier study. Moreover, a moderate fraction of retrieved eggs and objects were subsequently rejected soon after being retrieved. The rejection of the same eggs that were previously retrieved into the nest underscores the remarkable sensitivity of retrieval and rejection decisions to slight changes in an egg's location; a difference of a few centimetres triggers a very different response mechanism. Overall, our findings suggest that selection from brood parasitism has not shaped the evolution of egg retrieval in coots.

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Organisms that incubate their eggs often benefit from some level of egg recognition to deal with a variety of challenges. Depending on the context, however, egg recognition can vary in the degree of specificity, from general recognition of an egglike form to highly sophisticated discrimination between the eggs of conspecific females. One important context of recognition is egg retrieval. Various ground-nesting birds will retrieve eggs displaced from the nest bowl back into the nest (Baerends, 1982; Feare & Larose, 2014; Horák & Klvaňa, 2009; Lank, Bousfield, Cooke, & Rockwell, 1991; Noble & Lehrman, 1940). Egg retrieval behaviour was the focus of pioneering ethological work that investigated the stimuli that cause birds like geese and gulls to retrieve an egg placed outside of

the nest bowl (Baerends, 1982; Lorenz & Tinbergen, 1957). Egg retrieval is presumably an adaptive behaviour in ground-nesting birds because, without it, accidentally displaced eggs would perish. However, birds need to distinguish their eggs from other objects that might have similar size, shape and perhaps even colour, such as stones (Conover, 1985), so some form of recognition is required. Observations of a moderate frequency of inanimate objects in the nests of some species like ring-billed gulls, *Larus delawarensis*, and California gulls, *Larus californicus*, indicate that the recognition system involved in egg retrieval is not perfect (Conover, 1985).

Egg recognition occurs in two other social contexts where there is a high risk that parents might raise offspring that are not their own. In high-density colonial breeding species, the risk of accidental mixing of eggs or offspring can be high and egg recognition has evolved to reduce this risk in some species (Buckley & Buckley, 1972; Schaffner, 1990; Tschanz, 1968). Egg recognition is also commonly

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employed as a defence against brood parasitism, a common reproductive strategy in birds that can involve interspecific and intra-specific hosts (Davies, 2000; Lyon & Eadie, 2008). Brood-parasitic females lay their eggs in the nests of other individuals (hosts) and then leave all subsequent parental care to the hosts. Parasitism is often costly to hosts, which favours the evolution of egg rejection (Davies, 2000; Lyon & Eadie, 2008). Many experimental parasitism studies have investigated both the recognition mechanisms and the specific egg features birds use to recognize and reject foreign eggs (Rothstein, 1982; Spottiswoode & Stevens, 2010). Hosts in most species know their own eggs and do not simply reject the minority egg type (discordancy; Lyon, 2007; Moskat et al., 2010). In terms of specific egg features, egg size, egg colour and marking patterns have all been shown to play a role in recognition in some species, including hosts of interspecific brood parasitism (Lotem, Nakamura, & Zahavi, 1995; Rothstein, 1982; Spottiswoode & Stevens, 2010, 2011) and conspecific brood parasitism (Lyon, 2003). The level of egg discrimination required by hosts to recognize and reject parasite eggs differs across systems. Some hosts have evolved to recognize parasitic eggs that closely resemble their own, such as mimetic eggs laid by specialist interspecific brood parasites (e.g. cuckoo, *Cuculus canorus*) or parasitic eggs laid by members of their own species (i.e. conspecific brood parasites). In contrast, other hosts have evolved the ability to recognize nonmimetic parasitic eggs (e.g. brown-headed cowbird, *Molothrus ater*), although many hosts fail to reject these eggs as well.

In species with both egg retrieval behaviour and brood parasitism, egg retrieval can become intertwined with parasitic egg recognition. For example, when a parasitic female snow goose, *Chen caerulescens*, lays an egg sufficiently close to a potential host nest, the host will then retrieve the egg and treat it as her own (Lank et al., 1991). In the context of brood parasitism, retrieval of eggs of other females has been referred to as egg adoption (Lank et al., 1991). To date, egg retrieval and egg rejection behaviour have never been studied in the same species, so it is unclear whether these two behaviours ever co-occur and, if they do, whether the evolution of egg recognition for egg rejection might influence the egg features that stimulate egg retrieval. Egg rejection evolves in response to the costs of raising foreign offspring. Indiscriminate adoption of eggs could increase these same costs if hosts retrieve parasitic eggs laid near their nests, so we might expect natural selection to favour a more refined egg retrieval behaviour than is shown in species without conspecific brood parasitism.

In this study we examined egg retrieval behaviour in the American coot, *Fulica americana*, a species known to show egg rejection based on egg recognition (Lyon, 2003, 2007), but in which egg retrieval has not previously been studied. Conspecific brood parasitism is common in this species, with up to 40% of nests containing at least one parasitic egg (Lyon, 1993a). Each successful parasitic chick costs the host one chick of its own (Lyon, Hochachka, & Eadie, 2002). Thus, conspecific brood parasitism comes at a significant cost to the host, and this has led to the evolution of host defence mechanisms involving egg recognition, including egg rejection and discriminatory incubation of parasitic eggs (Lyon, 1993b, 2003; Shizuka & Lyon, 2011).

We asked four questions regarding the potential interactions between egg recognition and egg retrieval in American coots. First, do American coots show egg retrieval behaviour? Second, if retrieval occurs, do hosts retrieve their own versus conspecific parasitic eggs at different rates? Finding a difference between the retrieval rates of parasite and host eggs would indicate that brood parasitism has shaped egg retrieval behaviour. Third, what cues predict which objects are retrieved and which objects are left outside the nest bowl? Fourth, do coots make the same acceptance/rejection decisions in different contexts; i.e. do the same cues that

predict which eggs (or objects) are retrieved into the nest also predict which eggs are kept in the nest during incubation? For the last question, we compared retrieval with failure to reject eggs (rather than rejection) because these are analogous behaviours: both behaviours result in eggs being in nests. With similar reasoning, rejecting an egg is analogous with failure to retrieve the egg into the nest.

We studied egg retrieval with a series of egg addition experiments. To determine whether egg retrieval occurs in American coots, we placed eggs or other objects on the sides of coot nests, outside the nest bowl but close enough to it that the egg could be pulled back in to the nest bowl by the incubating bird. We also contrasted egg retrieval with egg rejection, in two ways. First, we compared retrieval rates to rejection rates for brood-parasitic eggs, drawing upon egg rejection rates of natural cases of brood parasitism from an earlier study of the same population (Lyon, 1993b, 2003). Second, we also determined whether the eggs and objects that were retrieved in the present study were subsequently rejected after they had been brought into the nest by the birds.

## METHODS

### Study Area and Study Species

We conducted the experiments on several wetlands in the Riske Creek and Williams Lake areas in British Columbia, Canada in May and June from 2006 to 2008. The wetlands included Jaimeson Meadow wetland near Big Creek, several wetlands near Riske Creek, and the Westwick Lakes along Dog Creek Road close to Williams Lake. Egg rejection rates of parasitic eggs are of naturally occurring cases of brood parasitism from an earlier study conducted on several of these same wetlands in 1987–1990 (Lyon, 2003). In coots, egg rejection is overwhelmingly by burial down into the nest (Lyon, 2003; Lyon, Shizuka, & Eadie, 2015). Although this form of rejection differs from egg ejection shown by most bird species (in which birds remove eggs with their beaks; Davies, 2000), it achieves the same outcome: the parasites do not hatch and compete with host chicks. Coots do show egg ejection, but they eject damaged eggs from the nest, not parasitic eggs (Lyon, 2003). Coots nest over water in patches of hardstem bulrush, *Schoenoplectus acutus*, the dominant emergent plant at all wetlands in our study area. The nests are anchored to the vegetation, and eggs that are displaced over the rim of the nest run the risk of falling into the water. Water levels were stable in these wetlands, which is important because rapid increases in water level affect egg rejection rates in the American coot (Weller, 1971). Additional details about the general study area are provided in Lyon (1993a).

We did not carefully monitor nests to document natural instances of brood parasitism. This is potentially important because coots reject experimental parasitic eggs at a lower rate than actual parasitic eggs (Lyon, 2007); the difference presumably reflects the fact that hosts may use clues like seeing a parasite near their nest to adjust their egg rejection behaviour, a phenomenon that has been shown for some hosts of interspecific brood parasites (Davies & Brooke, 1988). It is unknown, however, whether natural parasitism has any effect on egg retrieval. Regardless, our egg retrieval treatments were haphazardly assigned and treatments would have been random with respect to any instances of natural brood parasitism.

### General Egg Retrieval Experimental Protocol

At our site, the mound-shaped coot nests are invariably constructed from dead bulrush stems, and they have a distinct bowl with rim and sloping sides. At each experimental nest we added a

single egg (or egglike object) to the outside of the nest, in a shallow indentation in the woven stems to prevent the egg from rolling down into the water. We placed the egg or object 3–5 cm down from the rim, rather than on the rim, to ensure that retrieved eggs were actively retrieved and not accidentally knocked back into the nest (Fig. 1). To retrieve eggs or objects, the birds had to pull the eggs up the rim and into the bowl.

Experimental nests were in either the late egg-laying or the incubation stage. We checked most experimental nests 24 h after the egg addition because our preliminary experiments indicated that many eggs were retrieved within 24 h. The vast majority (98%) of retrievals occurred within 24 h (see Results). For the nests where eggs were not retrieved within 24 h, we periodically checked the nest for up to 5 days to assess whether some eggs took longer to retrieve. Eggs that still remained outside the rim on day 5 were scored as not retrieved.

#### *Egg Retrieval Treatments Specific to Our First Three Questions*

We conducted different egg retrieval treatments to address different questions (Table 1, Fig. 1). To ensure independence of each trial, in almost all cases we used each nest only once; the one exception involved five nests that were presented with both their own egg and a conspecific brood parasitic egg from a second nest, as described below.

#### *Do coots retrieve eggs at all?*

To answer this question, we investigated whether birds would retrieve their own eggs ('birds own egg' treatment; Table 1). We

removed a single egg from the nest bowl and placed it outside the nest bowl ( $N = 16$  birds tested; Table 1). Five of these nests were also used to test for retrieval of conspecific parasitic eggs (see next treatment below); in all cases the test for parasitic eggs followed the test with the focal bird's own egg. All statistical tests that involved these two treatments involved the two treatments pooled; we ensured statistical independence by including each of the five duplicated nests only once (i.e. the pooled sample size was 28 nests).

#### *Do coots treat experimental parasitic coot eggs differently from their own eggs?*

In the context of brood parasitism, coots treat parasitic eggs differently from their own eggs and reject about a third of parasitic eggs by burying them down into the nest, while almost never rejecting their own eggs (Lyon, 1993b, 2003). We therefore tested whether coots respond differently to their own eggs and parasitic eggs in the context of retrieval. Our predictions, should egg rejection and retrieval be based on the same recognition system, were (1) that coots should retrieve fewer parasitic eggs than their own eggs and (2) the fraction of parasitic eggs not retrieved should match the fraction of parasitic eggs rejected. At each conspecific brood parasite treatment nest, we placed outside the rim one egg taken from a second coot nest (i.e. an experimental parasite egg; Fig. 1a). To maximize the likelihood that the focal birds would be able to recognize the parasitic egg that we placed at their nest, we chose donor eggs that appeared as different as possible from the focal birds' eggs in terms of background colour and spotting pattern. Given the variation between females available to choose



**Figure 1.** Examples of four experimental treatments used to assess egg retrieval rates. (a) To test response to a parasitic egg, a coot egg from a second nest is placed outside the nest bowl; (b) painted chicken treatment; (c) a wooden cylinder covered with photographic paper of coot egg markings that has been retrieved into the nest; (d) a white wooden cube that has been retrieved into the nest.

**Table 1**

Retrieval rates of different eggs and objects used to test questions about egg retrieval; for a subset of these treatments, the subsequent rejection rate of the retrieved objects is also provided

| Questions and experimental treatments                              | %Retrieval rate | N for retrieval | %Rejection of retrieved eggs <sup>a</sup> | N for rejection <sup>b</sup> |
|--------------------------------------------------------------------|-----------------|-----------------|-------------------------------------------|------------------------------|
| <i>Do birds retrieve eggs at all?</i>                              |                 |                 |                                           |                              |
| Bird's own egg                                                     | 100             | 16              | 0                                         | 16                           |
| <i>Do birds treat conspecific brood-parasite eggs differently?</i> |                 |                 |                                           |                              |
| Conspecific brood parasite                                         | 100             | 17              | 19                                        | 16                           |
| <i>Do egg shape and colour matter?</i>                             |                 |                 |                                           |                              |
| Coot egg painted white                                             | 90              | 19              | 62                                        | 13                           |
| Chicken egg painted white                                          | 47              | 19              | 40                                        | 5                            |
| Unpainted white chicken egg                                        | 86              | 14              | 8                                         | 12                           |
| White chicken egg with UV block                                    | 90              | 10              | 57                                        | 7                            |
| White chicken egg with sham for UV experiment                      | 100             | 8               | 50                                        | 8                            |
| <i>Do birds retrieve non-egg-shaped objects?</i>                   |                 |                 |                                           |                              |
| White cylinder                                                     | 50              | 10              | 20                                        | 5                            |
| Cylinder with coot egg pattern                                     | 40              | 10              | 20                                        | 5                            |
| White cube                                                         | 40              | 10              | 0                                         | 3                            |
| Cube with coot egg pattern                                         | 30              | 10              | 0                                         | 3                            |

<sup>a</sup> Many of these nests were monitored for less than 10 days, so rejection rates are likely to be underestimates.

<sup>b</sup> Sample sizes for subsequent fate of retrieved eggs is smaller than for retrieval because we did not follow the subsequent fates of all retrieved eggs.

from at any point in time, in most cases the difference in appearance between the host and parasite eggs was moderate rather than extreme.

#### *Which features of an object affect its likelihood of being retrieved?*

To investigate the features of an egg or an object that stimulate egg retrieval, we placed objects of varying characteristics (size, shape, colour) outside the nest bowl and determined which, if any, features were correlated with variation in retrieval rates (Table 1). This is the classic approach used by early ethologists (Baerends, 1982; Lorenz & Tinbergen, 1957). While these experiments directly assess factors that stimulate retrieval, an implicit assumption is that any variation in retrieval reflects variation in recognition; specifically, variation in the birds' abilities to distinguish an object from an egg for general retrieval, or from their own eggs in the context of parasitism.

To assess the effect of object size, shape and colour on egg retrieval, we performed nine treatments in addition to the two described above (Table 1). To examine the role of colour we painted real coot eggs white, which changed background colour and removed the spotting pattern, but retained the size and shape of the coot eggs. The painted coot eggs were taken from a different nest than the focal nest and we were often able to use eggs from abandoned and partially depredated nests. The paint used was Beauti-Tone Daylight (Home Hardware Stores Ltd, Burford, ON, Canada), 1 quart Base 75–00 W with the following colours added: B 1.5 shots, C 0.5 shots, U 0.5 shots. To assess the influence of size, shape, paint and ultraviolet (UV) reflection on retrieval, we conducted several treatments with chicken eggs (Table 1). We painted chicken eggs with the same white paint used on the painted coot eggs; comparison of these two treatments should reveal the effect of size and shape on retrieval. To determine whether paint per se affects retrieval rates, we added unpainted white chicken eggs to nests. One specific feature of paint that could be important is that paint typically lacks UV reflectance (our paint did). To assess the specific influence of UV reflectance, we ran two treatments (Table 1): white chicken eggs sprayed with a UV-blocking shellac coating (Krylon Satin Finish spray varnish, Krylon, Cleveland, OH, U.S.A.) and a sham treatment with white chicken eggs sprayed with a coating that did not block UV (Varathane Crystal Clear Diamond TM Wood Finish, Rust-oleum Corp., Vernon Hills, IL, U.S.A.); we checked reflectance with a field spectrometer to ensure that these two sprays did differ in the blocking of UV reflectance when

sprayed on eggs. To ensure that these two treatments did not differ in olfactory cues, eggs in the UV-blocking treatment were given a second coat of the nonblocking spray after their first coat of the blocking spray.

Our motivation for including coot and chicken eggs that were painted white came from our previous egg recognition and rejection studies in Argentina (Lyon & Eadie, 2004) and British Columbia (Lyon et al., 2015). Two species of coots in Argentina are parasitized by a parasitic duck laying immaculate white eggs, and both species show intermediate rejection rates. However, under certain conditions, such as flooding, rejection rates can soar to near 100% (Lyon & Eadie, 2004), which suggests that the coots are always capable of recognizing the ducks eggs even if they fail to always reject them. Egg retrieval experiments provide a way to assess this idea (with the assumption that egg retrieval and rejection are based on the same recognition systems): if coots can always recognize white ducklike eggs as distinct from their own, they should never retrieve them.

Following Baerends (1982), we also investigated whether a general egg shape is necessary for retrieval. We presented birds with two types of objects that deviated from an egg shape: wooden cubes and cylinders. For each of these shapes we had two treatments: painted white or covered with photographic paper containing images of spotting patterns of actual coot eggs, printed so that the size of the spots was similar to real coot egg spots (Fig. 1c and d). We created the photographic images of coot egg patterns by copying photographs of parts of eggs and then duplicating this sample several times to create a larger sheet of the same pattern.

#### *Egg Rejection*

We compared the results of our retrieval experiments to rejection rates of eggs in two ways. First, we compared the retrieval rates of conspecific brood-parasitic eggs with two different estimates of egg rejection for conspecific brood-parasitic eggs from natural cases of parasitism in a previous study (Lyon, 1993b, 2003): (1) the fraction of all hosts that rejected at least one egg and (2) the rejection rate of the subset of nests that received a single parasitic egg. We examined nests with a single parasitic egg because these nests show lower rejection rates than nests with multiple parasitic eggs (Lyon, 1993b); this may be the relevant rate to compare with the present retrieval study because each focal nest received a single egg. Second, we also followed the fates of many of the retrieved

eggs and objects to determine whether any were ever rejected after being brought into the nest. Eggs and objects were considered as rejected if they were at least half buried on our last visit; however, most rejected eggs or other objects were completely buried.

### *Experimental Design and Statistical Approach*

We attempted to spread the treatments between the different wetlands. However, treatments were not allocated evenly between years. The last year of the study (2008) was unplanned, but when new funding permitted an additional field season we added the four cube and cylinder treatments. Uneven representation of treatments across wetlands or years would be problematic if coot responses to eggs vary across time or space. Data from our previous study of egg rejection in this population (Lyon, 2003) allowed us to test whether this is a problem. Using data for 133 parasitized nests spanning 4 years and five major wetland areas, we used a general linear model (GLM), with binomial error and rejection (yes/no) as the dependent variable and year, site and their interaction as independent variables. None of these variables had a significant effect on egg rejection (site\*year:  $P = 0.98$ ; site:  $P = 0.38$ ; year:  $P = 0.65$ ).

All comparisons involve contingency table comparisons of binary results: reject versus accept, retrieve versus not retrieve. We used two-tailed Fisher exact probability tests to compare the results of different treatments or experiments. Multiple comparisons were conducted for three of our main questions, raising the issue of inflated type I error rates. Use of Bonferroni correction, long used for this problem, is now discouraged (Moran, 2003; Nakagawa, 2004). Nevertheless, to provide guidance for readers to be able to interpret for themselves whether multiple comparisons impact our conclusions, we indicate how Bonferroni adjustment would alter our statistical conclusions if applied. One important issue is the lack of a clear standard for what constitutes 'table-wide' error rate (Moran, 2003). We chose each of our three main questions as the appropriate level for  $\alpha$  adjustment: (1) do retrieval and rejection rates of parasitic eggs differ (two comparisons); (2) what factors affect egg retrieval (nine comparisons); and (3) do retrieval rates of objects differ from subsequent rejection of rates of those same objects in the same nest (three comparisons). Bonferroni correction resulted in two changes; two of the six significant contrasts in the second question lose significance, and we identify these contrasts in the results.

### *Ethical Considerations*

This research was conducted under a University of California, Santa Cruz Institutional Animal Care and Use protocol (number 2008044), a banding permit from the Canadian Wildlife Service (number 10516) and a wildlife permit from the provincial branch (British Columbia) of the Canadian Wildlife Service.

All experimental treatments should have had little impact on the reproductive success at the experimental nests. Commercial unfertilized chicken eggs were used for the chicken treatments. A fresh coot egg from a neighbouring nest was used for the parasitic coot egg treatment and these were returned to the source nest when the experiment was completed (all within 4 days). For the white painted coot eggs, we mainly used eggs that we had collected from deserted or partially depredated nests.

## **RESULTS**

### *Coots Retrieve Eggs*

All 16 of the hosts' own eggs that we placed outside the nest bowl were retrieved and all eggs were retrieved within 24 h

(Table 1). Given that coots showed retrieval behaviour, we next explored variation in the objects they retrieved.

### *What Eggs and Objects Do Coots Retrieve?*

All 17 of the experimental parasitic coot eggs were retrieved, a rate that was identical to the retrieval of the hosts' own eggs (Table 1). All eggs had been retrieved by the next nest check (10 nests within 24 h, six nests within 2 days, one nest within 4 days).

Coots also retrieved white painted coot eggs at a high rate (Table 1). This rate did not differ significantly from the retrieval rate of natural coot eggs (both host and parasite treatments combined, Fisher's exact test:  $P = 0.16$ ). The retrieval rate for white painted chicken eggs was considerably lower (Table 1). To examine whether size and/or shape influences retrieval, we compared retrieval rates for white painted coot and chicken eggs because these eggs were the same colour but differed in size and shape. White chicken eggs were retrieved at a lower rate than white coot eggs (Fisher's exact test:  $P = 0.013$ , not significant with Bonferroni correction), indicating that deviation from a coot-shaped or coot-sized egg may stimulate less retrieval.

Unpainted white chicken eggs were retrieved at a high rate (Table 1). This was not significantly different from retrieval rates of natural coot eggs (Fisher's exact test:  $P = 0.084$ , both host and parasite treatments combined), although higher than for painted chicken eggs (Fisher's exact test:  $P = 0.033$ , not significant with Bonferroni correction), suggesting an effect of paint on retrieval. However, the effect of paint was not seen for coot eggs painted white versus natural coot eggs, suggesting that if there was a paint effect, it only appeared when the egg was a different size. UV reflectance did not appear to influence retrieval: the UV-blocked and UV-sham white chicken eggs were both retrieved at similar high rates (Table 1) that did not differ significantly from each other (Fisher's exact test:  $P = 1.00$ ).

Coots retrieved both cubes and cylinders at intermediate rates (Table 1). They retrieved half of the white cylinders, 40% of the white cubes and patterned cylinders and 30% of the cubes with coot spot patterns. Each of these retrieval rates differed significantly from the retrieval rates of real coot eggs (host and parasite pooled: all  $P \leq 0.0005$ ).

### *How Long Does Retrieval Take?*

We checked most nests 1 day after setting up the experiments so we could determine in most cases how quickly eggs were retrieved. Considering only nests that eventually retrieved eggs and that were checked 1 day after the experiment was set up, all but two of these 92 nests (97.9%) retrieved the egg within 24 h.

### *Comparison of Retrieval Rates with Rejection Rates from Separate Rejection Studies*

In an observational study of natural parasitism (in contrast to experimental parasitism), 57 of 133 parasitized hosts (43%) rejected at least one parasitic egg, while 76 hosts (57%) did not reject any parasitic eggs (Lyon, 2003). If the same cues predict rejection and retrieval of parasitic eggs, the retrieval rate of parasitic eggs should mirror the acceptance rate of parasitic eggs. However, the retrieval rate we observed in this study (100%) differs from the acceptance rate observed in our previous study (57%; Fisher's exact test:  $P = 0.0003$ ).

The rejection rate of parasitic eggs varies with the number of parasitic eggs per host nest and is lower for nests receiving a single parasitic egg (Lyon, 1993b), the number of eggs used in our retrieval experiments. Rejection rates are also lower for eggs laid after

incubation (Lyon, 1993b). To ensure that these factors did not confound the above comparison, we determined the rejection rates of the subset of nests parasitized early (host's laying period) and by a single parasitic egg. However, controlling for both of these factors did not change the pattern: the retrieval rate of experimental parasitic eggs (100%) differed from the rejection/acceptance rate of these single, early-laid parasitic eggs: 13 of 21 (62%) were accepted, 8 (38%) were rejected (Fisher's exact test:  $P = 0.0047$ ).

#### *Subsequent Rejection of Objects Birds Retrieved into Their Nest Bowl*

In most but not all treatments, some hosts eventually rejected eggs that they retrieved from the nest rim, and rates of rejection varied across treatments. None of focal birds' own eggs that were retrieved were subsequently rejected from the nest bowl (Table 1). This is as expected since coots very rarely reject their own eggs (Lyon, 2003). However, in the brood-parasite egg treatment, 3 of 16 birds (19%) rejected the egg they had earlier retrieved into their nest ( $N = 16$ ; one nest was depredated before we could assess rejection). At least half of the white coot and the two UV treatment eggs were rejected by the coots (Table 1) while white chicken eggs (painted or unpainted) had relatively low rejection rates (Table 1). In contrast, cubes and cylinders were rejected at very low rates. The sample sizes for the individual cube and cylinder treatments of known rejection fate was small, but when we combined the data from all four treatments, 2 of 16 (12.5%) retrieved cubes and cylinders were subsequently rejected (Table 1).

For some of these treatments, the sample size for the rejection rates of the retrieved eggs was sufficient to statistically compare retrieval and rejection rates for the same eggs. For example, in the white coot egg treatment, 17 of 19 eggs were retrieved, and of the 13 retrieved eggs whose fates were followed, eight were rejected (and hence five were not rejected) (Table 1). The rate of retrieval and acceptance for these eggs differed significantly (Fisher's exact test:  $P = 0.0051$ ). Similarly, retrieval and acceptance rates for the two types of eggs that received a spray shellac combined (the UV-block and UV-sham treatment chicken eggs) also differed: 17 out of 18 of these eggs were retrieved, and of the 15 retrieved eggs whose fates were followed, eight were rejected (Table 1; Fisher's exact test:  $P = 0.0044$ ). For the unpainted chicken eggs, in contrast, retrieval and acceptance rates were not different: 12 of 14 eggs retrieved, 11 of 12 eggs accepted (Table 1; Fisher's exact test:  $P = 1.00$ ).

## DISCUSSION

Our experiments reveal that American coots are prolific egg retrievers: they retrieved all unpainted coot eggs placed outside the nest bowl, including eggs from other conspecific females. Retrieval rates of other eggs and objects varied from high to moderate; none of the treatments completely failed to elicit retrieval. In coots, both sexes incubate the eggs, so we do not know whether both sexes retrieved eggs. This question could be easily addressed in future studies with video cameras.

Egg retrieval has been previously documented in a wide variety of birds: Poulsen's (1953) early compilation included a list of 42 species in 12 avian orders. Moreover, the occurrence of retrieval was invariant within taxonomic orders: if retrieval occurs in one species in an order, then it typically occurs in all that have been tested. This pattern suggests that retrieval is not an evolutionarily labile trait. In addition, Poulsen's (1953) data show that egg retrieval occurs in all of the major clades that are known to be basal groups of extant birds (Hackett et al., 2008): Ratites, Galliformes and Anseriformes. It is therefore feasible that egg retrieval is a trait inherited from a theropod dinosaur ancestor. Some theropods

appear to have been ground-nesting species with egg-brooding or even incubation behaviour (Dong & Currie, 1996; Grellet-Tinner, Chiappe, Norell, & Bottjer, 2006; Varricchio, Jackson, Borkowski, & Horner, 1997), so egg retrieval would have made the same adaptive sense for these animals as it does now for extant ground-nesting birds.

Most of the taxa that show egg retrieval are ground-nesting birds, such as waterfowl and shorebirds; egg retrieval should be fairly easy for birds that nest on the ground (Poulsen, 1953). In contrast, because coots build steep-sided mound nests in marsh vegetation over water, it was unknown whether coots would be able to retrieve eggs. Moreover, to prevent the birds from accidentally displacing our experimental eggs back into the nest with their feet, we placed the eggs down the side of the nest so that the birds had to roll the eggs upslope to retrieve them into their nest bowls. That 100% of the natural (unpainted) coot eggs were retrieved indicates that the nest architecture does not inhibit retrieval in coots. Nest architecture had been shown to affect egg retrieval in one ground-nesting species, the snow goose. Not all eggs were retrieved and the height of the nest rim predicted the retrieval rate: the taller the nest rim, the lower the frequency of eggs retrieved into nests (Lank et al., 1991).

A key result of our study is the observation that coots do not differentiate between parasitic eggs and their own eggs when retrieving eggs. This pattern is a striking contrast to egg rejection, where coots reject a moderate proportion of parasitic eggs but almost never reject their own eggs (33% versus 0.3%; Lyon, 2003). This contrast suggests that brood parasitism has not led to a modification of the cues that stimulate egg retrieval. There are several reasons why brood parasitism might not influence egg retrieval behaviour; most of these make sense in terms of the costs and benefits of egg retrieval.

#### *Costs and Benefits of Egg Retrieval*

Why would coots and other birds retrieve eggs? Egg retrieval comes with both benefits and costs. The main benefit would be the recovery of eggs that a bird accidentally displaces from its own nest (Hořák & Klvaňa, 2009; Lank, et al., 1991). For example, displacement occurs with relatively high frequency in snow geese and retrieval allows these eggs to be returned to the nest (Lank et al., 1991). Coots do occasionally displace eggs from their nest bowls, for example when they are surprised and flush quickly, and our experiments here reveal that these eggs would be readily retrieved back into the nest. The actual fitness benefit of retrieval would depend both on the frequency with which eggs are displaced and on the value of the retrieved egg. For coots, the fitness gains from retrieving a displaced egg may not be quite as high as for other species because posthatching brood reduction due to starvation is very high (Lyon, 1993a; Shizuka & Lyon, 2013).

An amusing corollary to egg retrieval behaviour is the retrieval of inanimate objects into the nest. For example, Conover (1985) found foreign objects, mostly egg-shaped rocks, in up to 10% of ring-billed gull nests at some colonies. Conover (1985) speculated that birds might benefit from adopting rocks because enhanced clutch size serves as a stimulus for longer incubation bouts and birds with smaller clutch sizes were more likely to retrieve rocks. Conover (1985) also considered the possibility that retrieval of rocks might be maladaptive, but that course-grained egg recognition might nevertheless be favoured if the costs of gulls not retrieving their own eggs are greater than the costs of retrieving rocks.

Egg retrieval also comes with costs. In species with brood parasitism, retrieval can result in birds adopting the eggs of other females. In snow geese, for example, parasitic females attempt to

lay eggs in the nests of other females but will lay the eggs beside the nest if the sitting host prevents access to the nest (Lank, Mineau, Rockwell, & Cooke, 1989; Lank et al., 1991). Egg retrieval by the host then results in many of those eggs being incorporated into the host female's clutch. Lank et al. (1991) provided an excellent summary of general hypotheses that could explain why geese and other species with brood parasitism adopt eggs laid by other females. Whether or not egg adoption is costly to the host depends on the costs of adding additional eggs and chicks to the brood. In birds like waterfowl with precocial self-feeding young, it has long been suggested that larger broods enhance fitness through the dilution of per capita predation risk (Andersson, 1984; Eadie & Lumsden, 1985) and this could provide a benefit to adopting eggs of other females. However, in snow geese, brood parasitism is actually costly because it reduces hatching success (Lank, Rockwell, & Cooke, 1990). Interestingly, though, Lank et al. (1991) suggested that geese adopt the eggs to make the best of a bad situation: once an egg is laid near a nest, fitness appears higher for birds that retrieve the eggs than for those that do not. Nest survival data show that nests where eggs are retrieved are more successful than those where they are not, presumably because the conspicuous eggs attract nest predators to the nest (Lank et al., 1991).

For coots, adoption of parasitic eggs would seem to clearly be maladaptive because brood parasitism imposes such a high fitness costs to hosts. Each successful parasitic chick is raised at the expense of a host chick (Lyon et al., 2002). The costs of parasitism could favour the evolution of selective retrieval of host eggs (but not parasitic eggs) using the same recognition mechanisms used for parasitic egg rejection. If the probability of erroneously retrieving parasitic eggs were extremely high, selection could even favour the complete loss of egg retrieval behaviour. Our results indicate that neither of these has occurred. We can suggest three explanations for why coots show egg retrieval despite the potential costs of adopting parasitic eggs. First, egg retrieval may play little role in facilitating parasitism; parasites may be able to access the nest bowls themselves. How parasitic coots get their eggs into host nests is unknown. Interactions between hosts and parasites have been well documented in common moorhens, *Gallinula chloropus*, a relative of the coot, and these behavioural interactions at least suggest the possibility that egg retrieval could be important. Video recordings of parasitic events show that parasitic female moorhens typically lay while the host male is on the nest and covering the nest bowl; the parasite squeezes in close to the sitting male and quickly lays an egg while the male aggressively pecks her (McRae, 1996). It is unclear, however, exactly how the parasitic egg ends up in the nest bowl and whether retrieval by the host is involved. Coots may also maintain indiscriminate egg retrieval in the face of brood parasitism because specific host defences against brood parasitism reduce the costs of parasitism sufficiently to weaken selection against retrieval. Host coots recognize many parasitic eggs and reject them either by burying them or by placing them in inferior incubation positions (Lyon, 2003; Shizuka & Lyon, 2011), and they also recognize and reject parasitic chicks (Shizuka & Lyon, 2010). Poulsen's (1953) observation that egg retrieval appears to be invariant within avian orders may indicate that egg retrieval is an evolutionary constrained trait that is not easily altered by selection. It is therefore possible that retrieving parasitic eggs is maladaptive in coots but impervious to selection.

#### Cues Affecting Retrieval

Early ethologists used egg retrieval studies to determine the egg features that stimulate incubation behaviour, and egg retrieval was also a model system for studying 'releasing mechanisms' (Baerends, 1957). For example, Beer (1962) used retrieval experiments to

determine whether retrieval was tightly connected to incubation behaviours in the black-headed gull, *Larus ridibundus*, and concluded that retrieval and incubation were independent. Baerends and van Rhijn (1975) used retrieval experiments in black-headed gulls to determine whether egg colour affected egg recognition.

Like these early studies, ours examined variation in retrieval rates to determine which egg and object features are important for stimulating retrieval. We recognize that our sample sizes are modest, which is important because conclusions about the lack of importance of cues are based on a lack of significant difference between different treatments. Further study, with larger sample sizes, is needed to fully identify the role that specific cues play in egg retrieval. Egg marking, background colour and size/shape per se do not seem to affect egg retrieval in coots: coot eggs painted a bright white colour and completely lacking any egg markings as well as chicken eggs that were naturally spotless and white were both retrieved at a very high rate that was statistically indistinguishable from retrieval rates for natural coot eggs. However, size/shape does seem to affect retrieval rates when eggs are painted: significantly fewer chicken eggs painted white were retrieved compared to white coot eggs. In addition, paint itself also seems to affect retrieval rates when eggs are larger than typical coot eggs, as chicken eggs painted white were retrieved at a lower rate than unpainted chicken eggs, which are naturally white. This suggests that a combination of difference in egg size/shape and paint (although not colour per se) can reduce egg retrieval in coots.

The potential effect of paint in combination with size/shape makes the interpretation of our cylinder and cube treatments difficult because all four of these treatments involved white paint or a printed coot egg pattern. Thus, lower retrieval rates of these objects could have been the result of a combination of the artificial colour/pattern plus shape rather than object shape per se. Nevertheless, we can still infer that egg shape per se is not essential for retrieval of objects because over 40% of all wooden cylinders and cubes were retrieved in our study. Thompson (1970, cited in Baerends, 1982) presented lesser black-backed gulls, *Larus fuscus*, with cylinders at the edge of their nests and observed that about 40% were retrieved into the nest bowls, a rate very similar to our findings for coots. This may be a general pattern for birds that retrieve. For objects like cylinders that elicit an intermediate retrieval rate, it would be interesting to know whether intermediate retrieval reflects variation between individuals or within individuals. Do some individuals always retrieve the objects while others never do, or are individuals inconsistent across trials with the same objects? This same question has been investigated for egg rejection (Honza, Požgayová, Procházka, & Tkadlec, 2007; Samas, Hauber, Cassey, & Grim, 2011).

#### Different Cues Predict Egg Acceptance and Egg Rejection

Our experiments provide evidence that coots accept eggs at different rates depending on the context (i.e. retrieval of eggs from nest rim and acceptance of eggs inside the nest). For example, retrieval and acceptance rates differed significantly for conspecific parasitic eggs: coots retrieved these eggs from the rim at very high rates (Table 1), but a previous study found that parasitic eggs are often rejected from the nest (Lyon, 1993b, 2003). In addition, for many egg treatments, the birds rejected a moderate proportion of the same eggs they had earlier retrieved (Table 1). We had sufficient sample size to compare retrieval versus rejection rates for the same eggs for three comparisons (white coot egg, unpainted white chicken egg, UV-blocked egg plus its corresponding sham), and in two of these three contrasts, rate of retrieval from the rim was higher than acceptance rate once inside the nest.

In all of these examples, many of the same eggs that stimulated retrieval into the nests then triggered a different response once inside the nest; the eggs were buried down in the nest bowl, the typical response to parasitic eggs. There are a couple of possible explanations for this pattern. First, retrieval and rejection could be based on different recognition cues, and perhaps even involve completely different recognition and response mechanisms. For example, coots could use a general cue for identifying egg-shaped objects, while egg rejection once inside the nest could rely on finer-scaled differences in egg appearance. Alternatively, coots could use the same recognition cue for retrieval and rejection, but the difference in costs of acceptance/rejection mistakes at the two stages could lead to different actions. Central to this 'shifting acceptance threshold' hypothesis is the concept that acceptance/rejection decisions are based not only on the perceived recognition cues but also on the perceived costs associated with errors in acceptance/rejection (Davies, Brooke, & Kacelnik, 1996; Hauber, Moskat, & Ban, 2006; Reeve, 1989). In the context of our study, the perceived cost of rejection error during the egg retrieval stage (i.e. failure to retrieve one's own egg, leading to loss of potential offspring) could have outweighed the potential cost of acceptance error (i.e. retrieving a parasitic egg or foreign object). This is feasible because parasitic eggs or foreign objects in the nest can then be rejected, but failure to retrieve one's own egg would quickly lead to the death of the embryo. The two hypotheses ('different cues' versus 'shifting acceptance thresholds') are not mutually exclusive, as coots could use both different cues and different acceptance thresholds in the retrieval and rejection contexts.

The observation that many birds retrieved eggs from outside their nest bowl only to reject them once they were inside the nest bowl highlights the extreme spatial sensitivity of the two different behavioural responses, retrieval versus rejection. From a cognitive perspective, it is remarkable that a very slight change in an egg's location of a mere few centimetres can trigger two such fundamentally different behavioural responses, both based on egg recognition. This spatial sensitivity may have implications for experimental design in studies of cognitive mechanisms involving egg recognition. For example, in an elegant experiment to determine whether visual or tactile cues influence the number of eggs laid by zebra finches, *Taeniopygia guttata*, Haywood (1993) removed eggs from females as they laid them, glued the eggs together and hung them from the ceiling of the nestbox about 9 cm above the nest bowl. The idea was to provide a visual cue that was not a tactile cue. Similarly, Steen and Parker (1981) presented bantam hens, *Gallus gallus domesticus*, with eggs just beside the nest bowl but covered the eggs with a mesh cage to prevent the laying hen from obtaining tactile cues. If our results about spatial sensitivity are general, specifically that eggs have to be inside the nest bowl to trigger particular sensory responses, then these studies may not have provided the appropriate visual cues that the birds need to make their clutch size decisions. More generally, our study highlights how animals may respond in apparently contradictory ways to the same object, and such experiments allow us to explore the importance of behavioural context in understanding behavioural adaptations.

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