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Increase of clutch size triggers clutch destruction behaviour in common moorhens (*Gallinula chloropus*) during the incubation period

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Abstract

Conspecific brood parasitism (CBP) is common in a variety of animal taxa, including birds. In coots (*Fulica* spp.), and the closely related moorhens (*Gallinula* spp.), such parasitism is especially common, and hosts experience considerable costs through increased chick competition soon after hatching. Hence, these birds have evolved egg recognition and rejection abilities, e.g., egg counting, burying the foreign eggs, assigning them suboptimal positions within the mixed clutch, or deserting parasitized clutches. For common moorhens (*Gallinula chloropus*) it has been shown that desertion of parasitized nests pays most at the early egg laying stage. Later on, the costs of desertion exceed the costs of brood parasitism and acceptance is favoured. Here we tested moorhen egg discrimination behaviour during the incubation stage when acceptance of foreign eggs is expected. Four treatments were applied: (1) single added non-mimetic pale blue egg, (2) single added non-mimetic white chicken egg, (3) four foreign conspecific eggs added to the clutch and (4) four foreign conspecific eggs exchanged for four host eggs. Moorhens responded by egg destruction (48%) only to the increased clutch size but not to foreign egg colour and size match. In three nests where egg destruction occurred, all the eggs in the mixed clutch were destroyed by pecking, in two other nests one of the foreign eggs were pecked, while other two were deserted. These results are puzzling since moorhens have been shown to possess refined egg recognition abilities. To our knowledge, such destruction of parasitized clutches by moorhens during incubation has not previ-

ously been reported. We suggest that after clutch completion, moorhens use increase in clutch size as a cue to determine if they have been parasitized, and some individuals choose to reject parasitic eggs by deserting or destroying the whole clutch.

Keywords

Conspecific brood parasitism, egg recognition, nest desertion, clutch size.

1. Introduction

Avian brood parasites and their hosts represent a model system for studying evolutionary aspects of animal cognition because recognition mechanisms are central to host defences against parasitism, and the evolutionary costs and benefits of these mechanisms can be quantified (Rothstein & Robinson, 1998; Davies, 2000; Lyon, 2003). Conspecific brood parasitism (CBP) occurs in diverse taxa, including insects (Tallamy, 2005), fish (Wisenden, 1999), amphibians (Summers & Amos, 1997) and, most prominently, birds (Yom-Tov, 1980, 2001; Lyon & Eadie, 2008).

Some previous studies on American coots (*Fulica americana*) showed that CBP occurs frequently, and induces high costs to the hosts (Lyon, 1993a, b). For instance, a high parasitism rate of 41% was detected in 417 pairs in the population of coots in central British Columbia, Canada (Lyon, 1993a). Parental food supplies were limited, leading to high costs for parasitized coots (Lyon, 2003). As a defence against CBP, coots can not only often distinguish their own eggs from those of a parasite, but — remarkably — can also count their eggs (Lyon, 2003). As methods of foreign egg discrimination, coots bury or move some parasitic eggs to the periphery of the clutch where they are not incubated rather than ejecting them from the nest (Lyon, 2003).

Parasitic female common moorhens (*Gallinula chloropus*) (hereafter moorhens) lay 1–6 eggs in the nests of conspecific neighbours (McRae & Burke, 1996). In a population of moorhens at Peakirk Waterfowl Gardens (Peterborough, UK), at least 27% of nesting females laid one or more eggs in a neighbour's nest and parasitized pairs produced fewer own chicks than their non-parasitized counterparts (McRae, 1998). The occurrence of CBP in tropical populations of the common moorhen in Panama was at least 20% (15 out of 76 nests) (McRae, 2011). Moorhens rejected parasitism by desertion but this was most likely to occur at the early laying stage, more specifically when the first host egg was laid (McRae, 1995, 2011).

In a model, McRae (1995) showed that when hosts are parasitized early in their laying period, it pays to desert and complete their clutch in a new nest, while after the host has laid two or more eggs, it is apparently a better strategy to accept parasitism because the costs of desertion exceed the costs of parasitism. Furthermore, Petrie et al. (2009) showed experimentally that moorhens cease laying and desert their nests significantly more frequently when their first egg is replaced with another female moorhen's egg, but not when it is replaced with their own egg taken from an earlier clutch. Previous experimental studies on moorhen egg recognition have been carried out during the laying period. In order to acquire further insights into the moorhens' egg discrimination behaviour, we experimentally parasitized moorhen nests after clutch completion. We used foreign eggs differing in colour and size and also varied the number of foreign eggs received by host clutches in a moorhen population in south Taiwan, China. Since parasitic eggs laid during the incubation stage would fail to hatch in time, hence pose little costs to the hosts, we predicted no rejection behaviour at this stage, regardless of parasitism contexts.

2. Methods

This study was conducted in Pingtung (31°03'N, 121°04'E), south Taiwan Island, China, from February to May 2011. Common moorhen nests were found by systematically searching all typical and potential nest sites and by monitoring the activities of adults throughout the breeding season. Each nest was assigned to one of the following four experimental groups promptly after the host clutch was complete (see also Table 1): (1) model egg group: for each clutch one blue model egg was added to the host clutch, in which the model egg was made of polymer clay and appeared totally non-mimetic to moorhen eggs but similar in size (ANOVA, $F_{1,66} = 1.74$, $P = 0.19$); (2) chicken egg group: for each clutch one white chicken egg was added to the host clutch, again appearing non-mimetic to host eggs but considerably bigger in size ($F_{1,58} = 886.70$, $P < 0.001$); see also Figure 1 for the appearance of moorhen eggs; (3) conspecific parasitism group (addition): four conspecific eggs from other nests were added to each host clutch (all the four eggs in a trial came from the same foreign clutch); (4) conspecific parasitism group (replacement): four host eggs in the clutch were exchanged with four conspecific eggs from other nests. Egg laying dates and original

Table 1.

Egg rejection frequency and rejection methods of experimentally parasitized common moorhens (*Gallinula chloropus*) in Taiwan.

Treatment group	Acceptance	Rejection			Rejection rate (%)	N
		Ejected	Deserted	Buried		
(1) Model egg	11	0	0	0	0.0	11
(2) Chicken egg	6	0	0	0	0.0	6
(3) Conspecific parasitism (addition)	8	5	2	0	46.7	15
(4) Conspecific parasitism (replacement)	10	0	0	0	0.0	10

clutch size did not differ significantly among the four experimental groups ($F_{3,38} = 2.28$, $P = 0.09$ and $F_{3,38} = 0.32$, $P = 0.81$, respectively).

Groups (1) and (2) allow testing for egg colour and egg size recognition ability of moorhens while groups (3) and (4) allow testing of whether CBP can be detected non-specifically by increased clutch size. Actually group (1)



Figure 1. A unmanipulated common moorhen (*Gallinula chloropus*) clutch from Taiwan. This figure is published in colour in the online edition of this journal, which can be accessed via <http://booksandjournals.brillonline.com/content/1568539x>.

and (2) also increase moorhen clutch size to a small extent. However, such a small change does not trigger any ejection or desertion behaviour in moorhen (Table 1), which means that it has no effect on moorhen's behaviour. The four foreign conspecific eggs were marked by permanent marker pen and added into the centre of the experimental clutch. We chose to add or exchange four eggs since this is the mid-point number of the known range of foreign eggs received by moorhen nests in nature (McRae & Burke, 1996). The mean clutch size at our study site was 7.14 ± 1.55 (3–10, $N = 72$). Thus, the addition of four foreign eggs to a host clutch increases the original clutch size by a factor of ca. 1.6. These experimentally increased clutch sizes are close to the maximum clutch size (10 eggs) recorded in this population; thus, our manipulation did not create abnormally large clutches. For each treatment, experimental parasitism was conducted during the early incubation period (within 2–3 days following clutch completion). Nests were monitored on a daily basis for six days following experimental parasitism in order to record the response, which was classified as acceptance (foreign egg(s) warm and being incubated) or rejection (foreign egg(s) gone, deserted, buried or left cold in the nest) (Moksnes et al., 1991). Egg volume was calculated by using Hoyt's formula (Hoyt, 1979). Data are presented as means \pm SD.

Experimental procedures were in agreement with the local law, and the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal University (CEE-2011-H02).

3. Results

Moorhens accepted all the non-mimetic model and non-mimetic chicken eggs, but showed egg destruction behaviour in 46.7% of the nests in the egg addition conspecific parasitism treatment (Table 1). Destruction rate in that treatment was significantly higher than destruction rate in the conspecific treatment where original clutch size was kept constant by egg exchange (Fisher's exact test, $p = 0.02$). There was no significant difference in egg laying dates of egg destroyers and accepters in the egg addition conspecific treatment ($t_{12,3} = 1.52$, $P = 0.15$). Furthermore, original clutch sizes of accepters were significantly larger than those of destructor within the same treatment (7.88 ± 0.99 vs. 6.14 ± 1.57 , $t_{13} = 2.59$, $P = 0.022$). No destruction was recorded in the latter treatment. In the conspecific egg group involving egg addition, moorhens pecked one of the foreign eggs in two

cases, while they pecked indiscriminately all the eggs (destroying the whole mixed clutch) before deserting the nest in three cases. Two pairs in this treatment deserted the whole clutch without pecking the eggs. In cases where a single foreign egg was ejected, hosts continued to incubate the remaining eggs in the clutch. All the pecked eggs were found in the water around the nests with a pecking hole. The nature of the holes as well as the fact that egg contents were not consumed strongly suggests that these eggs were not predated. Such outcomes were not recorded in any of the other experimental groups.

Furthermore, since the response behaviour of moorhen in our studies is difficult to define, we used the word destruction rather than rejection to describe our results.

4. Discussion

Previous studies on moorhens indicate that egg desertion behaviour is most pronounced during the laying period, when the first host egg is laid (McRae, 1995, 2011). This is adaptive since parasitic eggs would hatch at the same time as host eggs, resulting in competition between host and foreign nestlings. Furthermore, it should be adaptive to accept parasitism once the clutch is complete because the costs of desertion exceed the costs of parasitism (McRae, 1995). Our results for the model and chicken egg treatments are in agreement with this prediction. However, when we added foreign conspecific eggs so that host clutches were increased to 1.6 times the original clutch size, moorhens showed desertion in ca. 50% of the cases. The fact that no desertions were recorded in the conspecific treatment with egg replacement seems to indicate that such egg desertion is probably not based on egg recognition by egg phenotype contrasts per se, but rather that moorhens are sensitive to their clutch size, as has been shown in coots (Lyon, 2003). Although the moorhens correctly ejected one of the added conspecific foreign eggs in two cases, we found no evidence that they distinguish between their own and foreign eggs. The lack of any rejection towards the non-mimetic blue model and white chicken eggs further supports this view. Similarly, McRae (1995) found that moorhens accepted non-mimetic foreign eggs painted red and attributed this to lack of selection for the evolution of egg removal. On the other hand, Petrie et al. (2009) demonstrated conclusively that moorhens do know the appearance of their own eggs and possess refined

cognitive abilities. Hence, egg discrimination may just not be released under some contexts. We conducted our experiments after clutch completion and in our treatments (1) and (2) the nests received only one foreign egg. Thus, it is possible that moorhens recognized these non-mimetic foreign eggs but opted for tolerating them because the costs of parasitism during both incubation (due to extra large clutches) and the early chick stage would be low (McRae, 1995).

Another alternative explanation of the egg destruction behaviour is that it is driven by the costs, or reduced efficiency, of incubating larger clutches. Peer & Bollinger (2000) put forward the incubation efficiency hypothesis and conducted studies to support that the brown-headed cowbird (*Molothrus ater*), a generalized brood parasite, tend to parasitize larger hosts earlier in its evolutionary history, to obtain adequate incubation of its small eggs. There were 8 nests showing acceptance in group (3). Three of these clutches suffered a prolonged incubation period of 21 days, 3–5 days longer than normal clutch size. This indicates that larger clutch size has a negative effect on incubation efficiency in moorhens. Nevertheless, why moorhens destroyed the whole clutch rather than ejected the excessive eggs is still difficult to explain. Additionally, experiments groups (1) and (2) also increased the clutch size by one egg but did not trigger any destruction, which implies that moorhens may have a detection threshold when deciding to reject eggs or not. Furthermore, original clutch sizes of accepters were significantly larger than those of egg destructors in group (3), which indicate that moorhens produce larger clutch sizes are more tolerant to increase of clutch size. One possible explanation is that moorhens with larger clutch sizes have a higher detection threshold. This assumption needs to be tested by investigating the relationship between clutch size and rejection behaviour with a gradual increase in number of eggs.

Some egg destruction by moorhens faced with multiple CBP during the early incubation period might seem to be maladaptive as shown by the three cases in which they pecked indiscriminately all the eggs of the clutch and pushed them out of the nest into the water before deserting. As far as we know, such destruction of parasitized clutches by moorhens during early incubation has not been reported previously. Moorhens in both Britain and Panama destroyed foreign conspecific eggs but only when parasitism occurred before the host started laying; at later stages all rejections were by desertion (McRae, 1995, 2011). On the other hand, there may be costs of

accepting enlarged parasitized clutches which we failed to identify in this study since we did not follow re-nesting attempts and breeding success of the tested birds. Therefore, the decision to reject might have been a better option for some individuals. In addition, since we did not video record the nests, we cannot rule out the possibility that the nests with pecked eggs were deserted by their owners and after having been left unattended, the eggs were destroyed by other conspecifics. In any case, whether pecking and ejection were performed by the nest owners, or not, the only rejections occurred in the conspecific egg addition group. We suggest that after clutch completion, moorhens cue on the increase in clutch size to determine if they have been parasitized, and some individuals choose to reject parasitic eggs by deserting or destroying the whole clutch. Further experiments are needed to better understand this behaviour.

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