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Manuel Soler · Juan José Soler · Tomás Pérez-Contreras

The cost of host egg damage caused by a brood parasite: experiments on great spotted cuckoos (*Clamator glandarius*) and magpies (*Pica pica*)

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Abstract Adult great spotted cuckoos, *Clamator glandarius*, frequently damage one or more eggs of their magpie host, *Pica pica*, without removing or eating them. The presence of damaged host eggs could signal parasitism thereby increasing the probability that the parasitic egg is ejected. This hypothesis was tested by experimentally introducing a model cuckoo egg with or without damaged host eggs. Magpie responses to experimental parasitism did not differ significantly between treatments implying that damaged host eggs are not used by magpies to assess parasitism. We followed the fate of magpie eggs naturally damaged by the great spotted cuckoo or experimentally damaged by us. Host response was very similar for naturally or experimentally damaged host eggs, but varied significantly according to the type of egg damage, eggs being removed more frequently when pecked than crushed, while cracked eggs were never removed. However, the egg damage that most readily causes egg removal is albumen leakage.

Key words Brood parasitism · *Clamator glandarius* · Coevolution · Egg-damaging behaviour · *Pica pica*

Introduction

Avian brood-parasitic females frequently remove or damage one or more host eggs when laying their eggs (reviewed in Soler et al. 1997). Some brood-parasitic species, mainly of the genera *Clamator* and *Molothrus*, damage host eggs without eating or removing them (Hoy and Ottow 1964; Valverde 1971; Post and Wiley

1977; Mason 1980; Carter 1986; Soler 1990; Soler et al. 1997).

The great spotted cuckoo (*Clamator glandarius*) is an obligate brood parasite, which in Europe mainly parasitizes the magpie (*Pica pica*). In this parasitic species, the male and female frequently cooperate in laying, and cuckoo females usually lay from the rim of the nest, depositing the egg in less than 3 s (Arias de Reyna et al. 1982).

The great spotted cuckoo does not remove host eggs, but damages some while laying (Valverde 1971; Soler 1990; Soler et al. 1997). Damaged magpie eggs have not been found in unparasitized nests although they are frequent in parasitized nests (Soler et al. 1997), and damaged eggs were either pecked, crushed or cracked (Soler et al. 1997).

Magpies frequently remove the most damaged host eggs. Soler (1990) found that removed eggs had larger cracks than those not removed. In 37.8% of parasitized magpie nests ($n=360$), there were no damaged eggs (Soler et al. 1997), although the magpies could have removed the most damaged eggs before the nests were inspected. Clutch size in parasitized nests was significantly smaller than that of unparasitized nests (Soler 1990), and clutch size of parasitized nests without damaged eggs was smaller than that of parasitized nests with damaged eggs (Soler et al. 1997).

Egg-damaging behaviour by great spotted cuckoos has been hypothesized to be adaptive because (1) egg destruction increases the survival of the parasitic chick by reducing the number of competing host chicks in the nest (“reduction of nestling competition hypothesis”), or (2) egg-damaging behaviour may increase the hatching probability of a late-laid cuckoo egg by destroying eggs that would otherwise hatch earlier than, and result in terminated incubation for the cuckoo egg(s) (“enhancement of hatching success hypothesis”). We recently demonstrated that egg damage is inflicted by the parasite, and that egg damage increases the breeding success of the great spotted cuckoo both by reducing the number of competing host chicks in the nest and by

M. Soler (✉) · J.J. Soler · T. Pérez-Contreras
Departamento de Biología Animal y Ecología
Facultad de Ciencias, Universidad de Granada
E-18071 Granada, Spain
e-mail: msoler@goliat.ugr.es
Fax: +34-58-243238

increasing the likelihood that late-laid cuckoo eggs hatch (Soler et al. 1997).

Egg rejection behaviour may incur rejection costs (Davies et al. 1996), thus selection acts against intense scrutiny of eggs, unless there is a good likelihood that parasitism has occurred, then this risk may not be worth incurring. Since female parasites usually cause damage shortly before they lay their own eggs (Payne 1977; Sealy 1992), it could be argued that the presence of damaged host eggs in the nest could be used as a sign of parasitism by the host, thereby increasing the probability of the parasitic egg being recognized and ejected. The prediction of this hypothesis is that the rejection rate of parasite model eggs should be higher in nests with damaged eggs than in nests without such eggs. The first aim of this work was to test this hypothesis experimentally. Another possibility is that the presence of damaged eggs may be the result of predation rather than parasitism, in which case the rejection rate in the presence of damaged eggs would be predicted not to differ from that in nests without such eggs. However, partial predation is very uncommon in magpie nests, and so the initial prediction may hold even if some egg damage is due to predators.

Our second aim was to determine the fate of damaged host eggs. We have previously shown that magpies remove the most damaged eggs (Soler 1990). However, these observations could not be considered conclusive because eggs damaged in a certain way (pecked, crushed or cracked) may be ejected more frequently and quickly than others. Therefore, we followed the fate of damaged eggs after introducing a model cuckoo egg into magpie nests in an experimental approach to determine the magpie response to damaged eggs.

Methods

Field work

Field work was conducted during the breeding season of 1997 in Hoya de Guadix, southern Spain (37°18' N, 3°11' W), a cereal-producing plain at 900–1000 m above sea level with sparse vegetation and cultivated cereals (especially barley). In some areas, there are holm oaks, *Quercus rotundifolia*, which provide nesting sites for magpies, although this species mainly nests in the abundant groves of almond trees, *Prunus dulcis*, reaching a high nesting density (Soler 1990).

At the beginning of May, we started searching for magpie nests and most were found during the nest-building or laying period. In this study, we have considered a nest as parasitized when there were one or more cuckoo egg at the time we made the experimental manipulation (some unparasitized nests were parasitized later). We usually inspected nests twice a week and determined the number of naturally (and experimentally) damaged eggs, as well as the type of damage by carefully examining all eggs in each nest. Damage was categorized as: (1) pecked, (2) crushed (probably a consequence of being struck by the parasite's egg, since the cuckoo lays from the rim of the nest) or (3) cracked (probably the result of the host eggs hitting one another after being struck by the feet of the parasite when she quickly leaves the nest). Two eggs were both pecked and crushed and we included them in the group of pecked eggs because this is the most easily determined kind of egg breakage. We measured the length and width of the hole of pecked eggs and the dent

of the crushed eggs (in both naturally and experimentally damaged eggs) with a digital caliper to the nearest 0.01 mm. In the case of cracks, only length was measured but in order to calculate the surface we considered breadth to equal 0.5 mm.

Experimental procedures

In the egg recognition experiment, model eggs resembling those of the great spotted cuckoo were introduced into magpie nests. In some randomly chosen nests (experimental group), when the model egg was introduced, one or more magpie eggs were damaged, mimicking that caused by a cuckoo (pecked, by making a small puncture using the tip of a pen; crushed, by dropping a real cuckoo egg on the magpie clutch; cracked, by jostling the eggs with a pen); in others (control group), the cuckoo egg model was introduced without harming any magpie egg.

Cuckoo model eggs were made of plaster of Paris, and were painted with acrylic paints to mimic real great spotted cuckoo eggs, which have a light blue-green ground colour with abundant spots. These model eggs also resembled real cuckoo eggs in size and mass (Soler and Møller 1990). The model egg was considered to have been accepted by magpies if it remained in the nest, being incubated, after 7 days. The model eggs were considered ejected if after 7 days they were absent from the nest when this had not been deserted or depredated. In two cases, the nest was deserted after the experimental introduction of the cuckoo model egg; as we cannot be sure that this was a response to the experimental manipulation, these two nests were not included in the analyses.

In the experimental group, we followed the fate of each damaged magpie egg (damaged-egg rejection experiment) after introducing the cuckoo model egg into the magpie nests (see above). As with our assessments of responses to model eggs, we considered the damaged egg to have been accepted when it remained in the nest after 7 days; otherwise, we recorded it as removed. We used the term "removed" instead of "ejected" because we do not know whether the damaged eggs were ejected or eaten.

We used log-linear analysis techniques for multiway cross-tabulations, using Delta = 0.5. Delta is a constant that is added to all frequencies in the observed table before it is submitted to the actual analysis. This is a recommended procedure when the table contains several cells with low frequencies (e.g. less than 10); it is a correction analogous to the Yates correction for two-way tables, and this correction does not affect the results unless the table contains low frequencies (Everitt 1992). Values given are the mean \pm SE. All tests are two-tailed.

Results

Egg-recognition experiment

A total of 69 tests were made, 55 in unparasitized magpie nests and 14 in parasitized ones. A cuckoo egg model was introduced into 36 nests while damaging one or more of the magpie eggs, and into 33 without egg damage. Magpie responses to experimental parasitism did not differ significantly between treatments. The ejection rate of mimetic model eggs did not change with treatment nor with the status of the nest (parasitized or unparasitized) (Fig. 1a; multiple log-linear analysis, $\chi^2 = 3.81$, $df = 3$, $P = 0.28$).

The number of damaged eggs per magpie nest did not affect the magpie response (Fig. 1b; multiple log-linear analysis, $\chi^2 = 4.21$, $df = 3$, $P = 0.24$). If we consider nests where at least one damaged egg was removed and nests where none of the damaged eggs was removed,

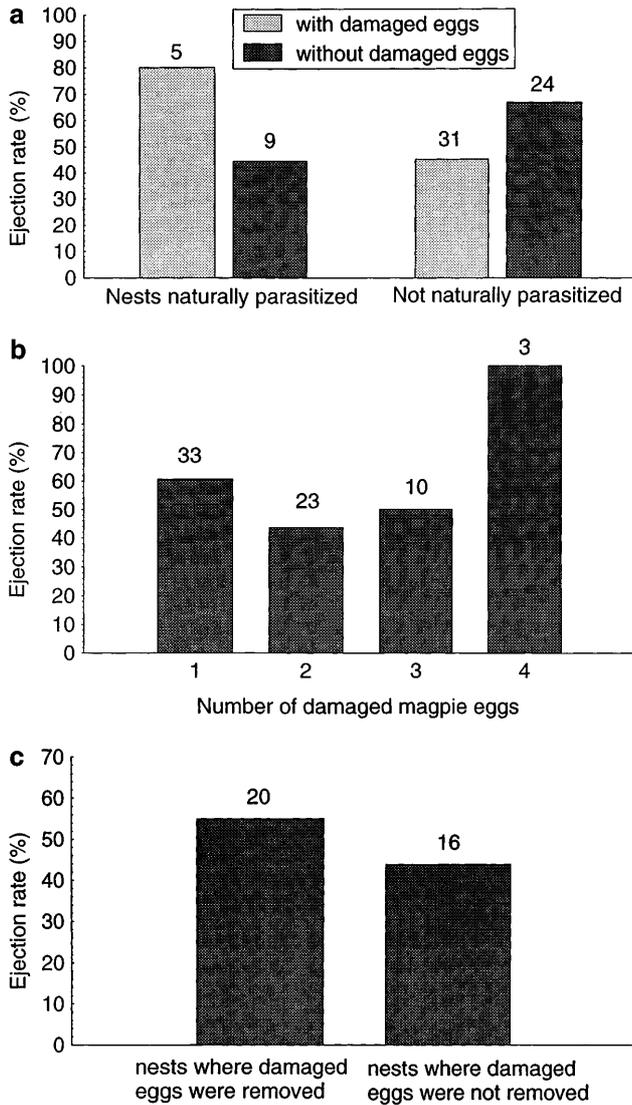


Fig. 1 Ejection rate of the model cuckoo eggs resembling those of the great spotted cuckoo. **a** In nests naturally parasitized and not naturally parasitized according to the treatment: with damaged eggs (experimental group) and without damaged eggs (control group). **b** In experimentally parasitized nests according to the number of damaged magpie eggs. **c** In experimentally parasitized nests where damaged eggs were removed by magpies and where damaged eggs were not removed by magpies

there was no significant difference in ejection rates for the two groups (Fig. 1c; Fisher exact test, $P=0.50$).

The fate of damaged host eggs

Natural evidence

The fate of naturally damaged eggs was determined for 46 of the 52 damaged magpie eggs (Fig. 2). These damaged eggs were pecked (9.6%), crushed (38.5%) or cracked (51.9%) ($n=52$). Magpie responses varied significantly with the type of egg damage, removal being

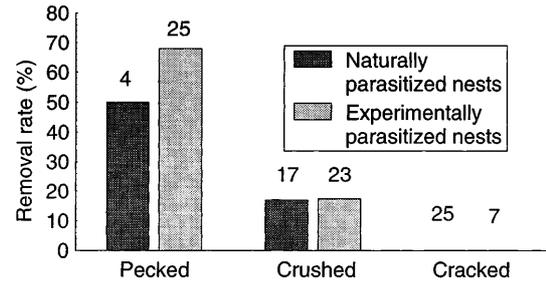


Fig. 2 Removal rate of damaged magpie eggs according to the type of egg damage in both naturally and experimentally parasitized nests

more frequent for those pecked than those crushed, while those cracked were never removed (Fig. 2; multiple log-linear analysis, $\chi^2=9.37$, $df=2$, $P=0.009$). However, the removal rate of pecked, crushed and cracked eggs was very similar for naturally and experimentally damaged eggs (Fisher exact test, $P > 0.5$ in all cases).

Removed eggs had significantly larger damaged areas ($128.9 \pm 38.6 \text{ mm}^2$, $n=5$) than those not removed ($71.2 \pm 77.7 \text{ mm}^2$, $n=40$; Mann-Whitney U -test, $U=39.0$, $P=0.027$). However, this was only true when shell fragments were lost, since larger dent size did not increase removal (dent size of removed eggs: $133.0 \pm 47.2 \text{ mm}^2$, $n=3$; dent size of non-removed eggs: $138.4 \pm 77.6 \text{ mm}^2$, $n=14$; Mann-Whitney U -test, $U=19.0$, $P=0.80$). Perhaps the evidence of damage that most prompts egg removal is albumen leaking from the egg. We found that 2 out of 2 eggs with albumen leakage were ejected, while only 2 out of 18 (11.1%) with no albumen leakage were ejected, the difference being statistically significant (Fisher exact test, $P=0.03$).

Experimental evidence

We damaged one egg in 29 nests and more than one in 12 nests (two in 9, and three in 3). With these latter 12 tests, we sought to determine whether the response of magpies depended on the type of damage. When more than one egg was damaged per nest, each type of damage was inflicted only once. We found that in 7 of the 12 nests, the response of the magpies was different, some eggs being accepted and others removed according to egg damage. However, the number of damaged eggs per nest did not affect the removal rate (multiple log-linear analysis, $\chi^2=2.17$, $df=2$, $P=0.34$). Thus, we can consider eggs, rather than nests, as independent data points.

The type of damage significantly affected the response of the magpies against damaged eggs. As in naturally parasitized nests, cracked eggs were not removed, crushed eggs were removed at a low rate, and pecked eggs at a high rate (Fig. 2; multiple log-linear analysis, $\chi^2=11.35$, $df=2$, $P=0.003$).

Removed pecked eggs had significantly larger holes ($27.6 \pm 9.8 \text{ mm}^2$, $n=15$) than those not removed ($15.9 \pm 4.4 \text{ mm}^2$, $n=8$; Mann-Whitney U -test, $U=23.0$,

$P=0.017$). As with naturally damaged eggs, larger dent size did not increase the probability of removal (dent size of removed eggs: $14.3 \pm 25.8 \text{ mm}^2$, $n=4$; dent size of non-removed eggs: $112.4 \pm 61.5 \text{ mm}^2$, $n=18$; Mann-Whitney U -test, $U=31.0$, $P=0.67$).

Most of the damaged eggs leaking albumen were removed (15 out of 17, 88.2%). However, when no albumen was leaking, only 21.9% (7 out of 32) of the damaged eggs were removed, the difference being statistically highly significant (Fisher exact test, $P < 0.00001$).

Pecked eggs with albumen leakage had significantly larger holes ($27.9 \pm 9.9 \text{ mm}^2$, $n=13$) than those with no albumen leaking ($18.5 \pm 7.1 \text{ mm}^2$, $n=11$; Mann-Whitney U -test, $U=34.0$, $p=0.030$). However, larger dent size did not increase the probability of albumen leaking (dent size of crushed eggs with albumen leaking: $88.4 \pm 59.1 \text{ mm}^2$, $n=3$; dent size of crushed eggs with no albumen leaking: $116.7 \pm 65.1 \text{ mm}^2$, $n=22$; Mann-Whitney U -test, $U=27.0$, $P=0.62$).

Discussion

Egg recognition experiment

Females of some avian brood parasites damage host eggs while laying their own (reviewed in Soler et al. 1997). This means that the females of these avian brood parasites (mainly from the genera *Molothrus* and *Clamator*), by leaving damaged eggs in parasitized nests perhaps provide the host with a sign that may increase the probability of the parasite egg being ejected. This possibility has never been tested before. Here we experimentally demonstrated that the presence of damaged eggs in the nest does not increase the probability of parasite egg ejection (Fig. 1). Even in nests where at least one damaged egg was removed, the parasite egg was not ejected more frequently than in nests where damaged eggs were not removed. Thus, the presence of damaged host eggs in the nest is not used by magpies as an indication of parasitism by the great spotted cuckoo.

Why then does the presence of damaged eggs in parasitized nests not increase the ejection rate of parasitic eggs? Damaged eggs are frequent in naturally parasitized nests, so the evolution of such a behaviour might be expected. One possibility is evolutionary lag, i.e. it would be adaptive for magpies to increase the rejection rate of cuckoo eggs when there are damaged eggs in the nest, but do not do so because this behaviour has not yet evolved.

A conceptually similar hypothesis has been tested for the hosts of the common cuckoo *Cuculus canorus*. In this case, the indicator of parasitism was the presence of an adult cuckoo, and a model female cuckoo increases the likelihood that hosts reject the cuckoo egg (Davies and Brooke 1988; Moksnes and Røskoft 1989; Moksnes

et al. 1993; Davies et al. 1996). However, this is not always the case for hosts of brood parasites: the presence of a model female brown-headed cowbird, *Molothrus ater*, near the nest plus a cowbird egg in the nest did not influence the rejection behaviour of cowbird hosts (Hill and Sealy 1994; Sealy 1995). Furthermore, in the magpie, the presence of an adult great spotted cuckoo near the nest also did not increase the ejection rate (M. Soler, J.J. Soler, A.P. Møller, unpublished data). Thus, the presence of a female brood parasite near the host nest may be another sign of parasitism, but the hosts do not always respond to it.

What happens to damaged host eggs?

An experimental approach was needed to determine the frequency and the fate of each type of damaged magpie egg, given that those found under naturally occurring conditions are those that have not yet been ejected by magpies (thus pecked eggs and eggs with albumen leakage are more common than recorded).

The magpie response, under both natural and experimental conditions, varied significantly with the type of egg damage, pecked eggs being removed more frequently than crushed ones, while cracked ones were never removed (Fig. 2). However, the removal rate of pecked, crushed and cracked eggs was very similar in natural and experimental nests. This suggests that our experimental egg damage was similar to that made by the cuckoo.

Carey (1986) showed that small triangular holes found in eggs of parasitized nests of three different host species of the brown-headed cowbird increased both eggshell water vapour conductance and daily water loss, provoking death of the embryo. This effect on pecked eggs must also apply to crushed and cracked eggs because just a small crack produced at the beginning of the incubation period is sufficient to increase the rate of water loss beyond limits tolerated by the embryo. Thus, damaged eggs have no chance of hatching successfully. Furthermore, damaged eggs could attract insects and bacteria increasing the risk of chicks becoming infected. This may explain why it is adaptive to eject own damaged eggs in a nest, as many bird species do (Kemal and Rothstein 1988).

Pecked eggs are damaged directly by the female cuckoo (see below for crushed and cracked eggs). A high percentage of pecked eggs were removed by magpies and those removed were the most damaged and those with leaking albumen. Thus, pecked eggs found by us in naturally parasitized nests had smaller holes from which albumen was not leaking, and the most damaged eggs had probably been removed prior to our observations. Given that crushed and cracked eggs were removed only sporadically (17% and 0%, respectively), removal of pecked eggs accounts for the significantly smaller host clutch size in parasitized than in unparasitized nests (Soler 1990). Thus, the frequency of pecked eggs in

naturally parasitized nests is likely to be much higher than actually recorded.

Host eggs become crushed when the parasite egg falls as the cuckoo lays from the rim of the nest (Arias de Reyna et al. 1982). This is indirect egg-damaging behaviour, and should result in selection for cuckoo egg shells stronger than those of host eggs. In fact, *Clamator* species lay eggs with shells that are thicker and more rounded than those of their hosts (Lack 1968; Gaston 1976; Brooker and Brooker 1991), and this is also the case for *Molothrus* species (Hoy and Ottow 1964; Spaw and Rohwer 1987; Rahn et al. 1988; Picman 1989, 1997; Brooker and Brooker 1991). Parasitic species of the subfamily Icterinae have, on average, a 40% thicker and 30% heavier shell than non-parasitic species (Rahn et al. 1988), and a 40% increase in shell thickness would double the force required to break the shell (Ar et al. 1979). Brooker and Brooker (1991) suggested that a stronger egg shell in *Clamator* and *Molothrus* species is adaptive because it protects the parasite's egg from damage if the nest is multiply parasitized. However, another non-exclusive possibility is that the advantage of a strong egg shell in both genera (both damage host eggs without removing or eating them, although *Molothrus* species also remove host eggs) could be to allow the female to lay very quickly (from the rim of the nest, at least in the case of the great spotted cuckoo). Alternatively, it could be to crush one or more host eggs (egg-damaging behaviour has been shown to be adaptive; Soler et al. 1997).

Cracking occurs when host eggs are jostled against one another as the parasite quickly leaves the nest after laying the parasitic egg. This is also indirect egg-damaging behaviour, though doubt has arisen whether such egg damage is accidental or deliberate in the brown-headed cowbird parasitizing the red-winged blackbird, *Agelaius phoeniceus*. Blankespoor et al. (1982) recorded that blackbird eggs were more frequently cracked than cowbird eggs. However, in a subsequent paper, Carey (1986) suggested that perhaps the phenomenon documented by Blankespoor et al. (1982) resulted from differences in thickness and strength of parasite and host eggs rather than from behavioural attempts by cowbirds to crack host eggs. However, in the case of the great spotted cuckoo-magpie system, it is clear that cracked eggs are the result of a deliberate attempt to destroy host eggs. First, because cracked eggs are very common (51.8% of damaged eggs in 46.7% of parasitized nests with damaged eggs; this study). Second, because damaged eggs were common in naturally parasitized nests, and experimental parasitism did not cause egg damage (Soler et al. 1997). And third, because we had to jostle the eggs very vigorously to damage some of them, movement which could not be caused incidentally by the cuckoo when it leaves the nest. In the present study, cracked eggs represented the most frequent type of egg damage, may be because these eggs are never removed by magpies, this type of egg damage not being easily discerned.

The great spotted cuckoo and other brood-parasitic species damage host eggs without breaking them (Hoy and Ottow 1964; Post and Wiley 1977; Carter 1986). We have suggested that this subtle damage could confer an advantage to the parasite by decreasing the probability that magpies detect the cuckoo egg (Soler et al. 1997). The failure of the host to detect this kind of damage will lower the risk that it will examine the nest carefully. The presence of damaged host eggs does not increase the ejection rate of parasitic model eggs (this study). When the damage is subtle, the host may not recognize the presence of even many damaged eggs which might provoke nest desertion, as occurs in the yellow-winged blackbird *A. thilius* when parasitized by the shiny cowbird *M. bonariensis* (Massoni and Reboresda 1998). Thus cuckoos both reduce future nestling competition, because some host embryos will die from the egg damage, and reduce the probability that magpies will abandon their nest due to detection of partial depredation.

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