Is egg-damaging behavior by great spotted cuckoos an accident or an adaptation?

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Adult great spotted cuckoos *Clamator glandarius* damage the eggs of their magpie *Pica pica* host without removing them from the nest or eating them but by producing the death of the embryo. Observations as well as experiments were used to test several predictions of two different possibilities: great spotted cuckoo egg-damaging behavior is a parasitic tactic resulting from a direct selection process (the adaptation hypothesis), or egg damage is caused by thick-shelled cuckoo eggs which evolved to avoid breakage during rapid laying (the nonadaptation hypothesis). Previously, we provided experimental evidence that egg damage increased the breeding success of cuckoos when they laid late during the laying sequence of the magpie. However, when they laid early, egg-damaging behavior did not increase cuckoo breeding success, contrary to the adaptation hypothesis. In an experimental study, when we simulated laying behavior by the great spotted cuckoo, we found that (1) the number of damaged magpie eggs was significantly lower than in natural parasitism, and (2) whereas in the experimental manipulations the number of damaged eggs did not depend on the number of magpie eggs, in natural parasitism, the number of damaged eggs increased with clutch size of the magpie. These results support the predictions of the adaptation hypothesis, implying that egg damage is not an incidental consequence of rapid egg laying, but an adaptation. Key words: adaptation, brood parasitism, *Clamator glandarius*, egg-damaging behavior, great spotted cuckoo, magpie, *Pica pica*. [Behav Ecol 11:495–501 (2000)]

The females of many avian brood parasites (species that lay their eggs in the nest of other birds) remove or damage at least one host egg shortly before they lay their own egg (review in Soler et al., 1997). The great spotted cuckoo *Clamator glandarius* is an obligate brood parasite, which, in contrast to most other cuckoos, parasitizes large birds, mainly members of the corvid family, and, in Europe, especially the magpie *Pica pica*, with the carrion crow *Corvus corone* as its secondary host (Cramp, 1985). Great spotted cuckoo eggs usually hatch before the magpies’ eggs, but, unlike other cuckoos, the chick does not eject the host’s eggs or young, although many magpie chicks frequently starve in competition for food with the larger cuckoo chick (Cramp, 1985; Soler, 1990; Soler and Soler, 1991). The egg-laying behavior of the great spotted cuckoo has been discussed elsewhere (Soler, 1990; Soler et al., 1997). Generally, cuckoo females lay from the rim of the nest (Arias de Reyna et al., 1982) and frequently damage the eggs of their hosts by either pecking, crushing, or cracking them, always without removing or eating them (Soler, 1990; Soler et al., 1997). These three types of egg damage result in desiccation and death of the embryos in all cases.

Magpies frequently remove the most damaged eggs. Soler (1990) found that removed eggs had larger cracks than those not removed, and later, in an experimental study, we (Soler et al. 1999) found that host response varied significantly according to the type of egg damage. Pecked eggs were removed more frequently than cracked ones, whereas cracked eggs were never removed. However, the egg damage that most readily causes egg removal is albumen leaking from the egg (Soler et al., 1999). In 37.8% of parasitized magpie nests (*n* = 360), there were no damaged eggs (Soler et al., 1997). However, in some cases this could have been due to magpies removing the most damaged eggs. In fact, host clutches in parasitized nests were significantly smaller than those in unparasitized nests (Soler, 1990), and clutches in parasitized nests without damaged eggs were also significantly smaller than those in parasitized nests with damaged eggs (Soler et al., 1997).

Egg-damaging behavior by great spotted cuckoos can be explained by two different hypotheses: (1) the “reduction of nestling competition” hypothesis states that egg-destruction behavior increases the survival of the parasite chick by reducing the number of competing host chicks in the nest, and (2) the “enhancement of hatching success” hypothesis states that egg-damaging behavior may increase the likelihood of late-laid cuckoo egg(s) hatching by destroying eggs that would otherwise hatch earlier than the cuckoo egg(s) and result in terminated incubation for the cuckoo egg(s). Recently, in an experimental study, we demonstrated that the damage is inflicted by the parasite, and we found 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 increasing the likelihood that late-laid cuckoo eggs hatch (Soler et al., 1997).

Brood parasites in general lay eggs with shells thicker than those of their hosts (Brooker and Brooker, 1991; Lack, 1968; Picman, 1997; Spaw and Rohwer, 1987). In *Clamator* species, eggs are particularly strong (thicker and rounder) compared with the eggs of the hosts (Brooker and Brooker, 1991; Gaston, 1976). Pecked eggs bear the only damage directly inflicted by the female great spotted cuckoo; crushed eggs are considered the consequence of impact from the dropping parasitite egg, and cracked eggs are the consequence of host eggs being jostled against one another as the parasite quickly leaves the nest after laying its egg (Soler, 1990, Soler et al., 1997). Thus, it is not clear whether the crushing or cracking of host eggs during the laying of the parasitic egg is an adaptation because this egg-damaging behavior could be the consequence of hurried laying, which incidentally may have led to more frequent destruction of host eggs, but this was not the selective force driving the evolution in the first place (Soler et al., 1997).

In this study we attempted to answer a basic question: is egg damage really a parasitic tactic resulting from a direct selec-
tion process (the adaptation hypothesis)? There is one alternative possibility; namely, that egg damage is incidental, caused by thick-shelled cuckoo eggs which evolved to avoid breakage during rapid laying and which are not driven by natural selection (the nonadaptation hypothesis). Parasitic cowbirds apparently have developed thick shells to resist puncture by hosts (Spaw and Rohwer 1987). However, in great spotted cuckoos thick-shelled eggs have not evolved for the same reason because this species parasitizes large birds that do not need to puncture the parasitic egg because they can easily grasp it.

The aim of this study was to test different predictions of these two hypotheses. First, we present tests of a prediction that fail to support the adaptation hypothesis: (A1) a positive association should exist between the number of damaged eggs and cuckoo reproductive success. Second, we present the results of tests of two predictions that support the nonadaptation hypothesis. (B1) If egg damage is an incidental consequence of parasitic laying, in multiparasitized nests, we predict that as more parasitic eggs are laid per nest, the number of damaged host eggs will also increase. However, if egg destruction is an adaptive behavior, then in multiparasitized nests (three or more cuckoo eggs laid by at least two females), destruction of cuckoo eggs laid previously (the “cuckoo competition hypothesis”) will be expected (a tendency that has been found in the European cuckoo Cuculus canorus; Davies and Brooke, 1988). (B2) The adaptation hypothesis predicts that host-egg damage should be greater with the larger carrion crow than with magpies because larger nestlings pose a greater competitive threat to the cuckoo nestling. In contrast, the nonadaptation hypothesis predicts less egg damage with larger hosts because bigger eggs are more resistant to breakage (Rahn and Paganelli, 1989).

Third, we present the results of an experiment in which we reproduced great spotted cuckoo damage behavior (i.e., laying from the rim of the nest and jostling the host eggs against one another with its feet when the parasite quickly leaves the nest after laying the parasitic egg). This damage experiment would allow us to determine the extent of damage one might expect from (1) the act of laying and (2) the contact of harder- and softer-shelled eggs during manipulation by the parasite, which subsequently would allow us to compare the number of damaged eggs in these experimental manipulations with those provoked by the great spotted cuckoo in naturally parasitized nests. The adaptation hypothesis predicts (C1) that, if the cuckoo purposefully damages host eggs, natural parasitism should damage more magpie eggs than our experimental manipulations reproducing the great spotted cuckoo laying behavior, and (C2) that in naturally parasitized nests the number of damaged eggs should increase as the clutch size of the host increases because as more eggs are laid by the host, the competitive threat to the cuckoo chick is greater; however, in our experimental manipulations, the clutch size of the host does not affect the number of damaged eggs. The nonadaptation hypothesis bears the opposite predictions.

MATERIALS AND METHODS

Field work

Observational data were collected during the breeding seasons of 1990–1995, and the damage experiment was conducted during 1997 in Hoya de Guadix, southern Spain (37°18′ N, 3°11′ W), a high plateau (1000 m) with sparse vegetation, cultivated cereals (especially barley), and many groves of almond trees (Prunus dulcis) and holm oaks (Quercus rotundifolia). Magpies nested in higher density in almond trees but also in oaks, whereas carrion crows showed the opposite tendency (Soler, 1990). During the same period we also found 21 parasitized carrion crow nests which were used to test prediction B2.

During 1990–1994, we found 692 magpie nests, 404 of which (58.4%) were parasitized by the great spotted cuckoo. Magpie nests were located during usually weekly visits to our study plots from the start of the nest-building period. The nests were inspected at least once a week. We recorded the percentage of magpie nests parasitized in each plot, considering a nest parasitized if it contained at least one cuckoo egg. Although we performed several field experiments, we have only included data from nonexperimental nests. We determined the number of damaged eggs by carefully examining all eggs in each nest. During 1997 we monitored 96 magpie nests [40 unparasitized and 56 (58.3%) parasitized by the great spotted cuckoo], and we recorded the number and type of damaged magpie eggs in all parasitized nests. After a careful inspection of damaged eggs, they were classified as pecked, cracked, or crushed. In 11 nests that did not contain cuckoo egg, we found damaged eggs. These nests have not been included in the analyses because presumably they were parasitized by the great spotted cuckoo, but the parasitic eggs had been ejected by the magpies (Soler et al., 1997).

Experimental procedures

The egg-damage experiments were carried out during the 1997 breeding season. We reproduced the two types of damage caused indirectly by the great spotted cuckoo (crushing and cracking) in two different experiments (see below). In both experiments, we used a real magpie nest that was collected after being deserted by the magpies. The magpie eggs were taken from their nests and put in the experimental magpie nest, where all manipulations were made. Sometimes more than one test (between 1 and 4) were made using the same magpie clutch (the eggs that remained without any damage), considering that the number of magpie eggs does not affect the number of damaged eggs (see below). In each test, we recorded the number of magpie eggs and, after careful inspection, the number and type of damaged eggs. Also, by observing carefully, we determined which eggs in the clutch actually received the blow.

Experiment 1

In experiment 1 we determined the extent of damage expected from the act of laying from the rim of the nest (egg-dropping experiment), which in theory crushes host eggs (Soler, 1990). After introducing the magpie clutch into the experimental nest, a strip of cardboard was situated on the top of the magpie nest, and an unincubated cuckoo (or magpie) egg was dropped from the strip of cardboard (i.e., from the rim of the nest).

Three kinds of tests were made: (1) a real cuckoo egg was dropped onto a magpie egg, (2) a real magpie egg was dropped onto a magpie clutch (control), and (3) a real cuckoo egg was dropped onto one or more cuckoo eggs. In all these cases, we recorded number of eggs in the nest, number and type of damaged eggs, and also which egg was damaged, the one dropped or the ones receiving the blow.

Experiment 2

The aim of experiment 2 was to determine the effect of jostling host eggs against one another and/or against the parasitic eggs (egg-jostling experiment) as the parasite supposedly does with its feet when quickly leaving the nest, thereby cracking eggs (Soler, 1990). This second damage experiment would allow us to determine the extent of damage one might expect
from the contact of harder- and softer-shelled eggs during manipulation by the parasite.

The experimental manipulation consisted (after introducing the magpie clutch into the experimental nest) of jostling the eggs with a pen both when one or more cuckoo eggs were together with the magpie clutch (experimental), and when only magpie eggs were included in the experimental nest (control). During preliminary tests, we increased the strength with which we jostled the eggs because no damage occurred. We jostled the eggs strongly to damage some eggs. The strength was such that some of the eggs moved nearly to the rim of the nest. This means that this movement could not be caused incidentally by the cuckoo when it leaves the nest; rather, a movement of this magnitude must be intentional by the cuckoo. Thus, by jostling the eggs as strongly as we did, and considering the results as incidental damage, we have obtained highly conservative results.

Comparison between egg damage in naturally parasitized nests and experimental manipulations
We compared the number of damaged eggs as a consequence of simulated cuckoo egg-laying behavior (that is, incidental egg damage; the results of our experimental manipulations) with those inflicted by the great spotted cuckoo in naturally parasitized nests. For this comparison we used naturally parasitized nests with only one cuckoo egg, and only experimental nests where both types of experimental manipulations (egg dropping and egg ostling) were carried out. We have quantified incidental egg damage by adding eggs crushed and cracked during the two types of experimental manipulations and quantified the damage caused by great spotted cuckoos by adding number of eggs crushed, cracked, and pecked. Considering that we have experimentally demonstrated that most damaged eggs removed by magpies are pecked (Soler et al., 1999), the number of pecked eggs was calculated by adding to the number in the nest the difference between the clutch size of the magpie and the mean clutch size of the magpie in unparasitized nests.

Statistical procedures
We followed the statistical methods of Sokal and Rohlf (1989), and when nonparametric statistics were needed, we used the methods described by Siegel (1988). Residual analyses were used to control for the effects of the number of cuckoo eggs, the number of magpie eggs, and the number of damaged magpie eggs because these three variables can affect the number of egg damaged in the nests and the cuckoo breeding success. The number of damaged eggs (0, 1, 2, or more rarely 3) was normally distributed (Kolmogorov-Smirnov test, p > .1), but this was because of the low power of this test with small sample sizes. So, when analyzing experimental results we have used non-parametric statistic. With our sample sizes, Spearman correlations and Mann-Whitney U tests should be quite powerful. Values given are means ± SEs. All tests are two tailed.

RESULTS
Tests of predictions that fail to support the adaptation hypothesis
Prediction A1
Controlling the effect of number of cuckoo eggs and number of remaining magpie eggs in the nest in a multiple regression, we found that the relationship between the residuals of the number of damaged magpie eggs and variables of cuckoo reproductive success were not significant (partial correlation coefficients: hatching success, R = .05, p = .48, n = 185; fledging success, R = .11, p = .18, n = 162; breeding success, R = .09, p = .24, n = 184). On the other hand, smaller cuckoo nestlings suffered a higher rate of postfledging mortality compared to larger ones (Soler et al., 1994). Therefore, chick mass can be considered a good indicator of cuckoo reproductive success. However, the relationship between the number of damaged eggs and the mass of the cuckoo chicks after controlling for the number of magpie and cuckoo chicks was not significant (partial correlation coefficient R = .12, p = .37, n = 62). Therefore, there is no direct link between number of damaged eggs and cuckoo reproductive success in naturally parasitized nests.

Evidence supporting the nonadaptation hypothesis
The nonadaptation hypothesis states that egg damage is incidental and is caused by the thick-shelled cuckoo eggs which evolved to avoid breakage during rapid laying. We tested two predictions that involve both the adaptation and the nonadaptation hypotheses:

Prediction B1
If egg damage is nonadaptive, in multiparasitized nests, we predict that as more parasitic eggs are laid per nest, the number of damaged host eggs will also increase. As magpies remove damaged eggs, we can test the above prediction by analyzing the relationship between the number of parasite eggs and the number of undamaged host eggs per nest. The prediction was fulfilled because the number of undamaged host eggs decreased with the number of parasite eggs (r = −.27, p < .0001, n = 553). However, this is a nonexclusive test, and the number of damaged host eggs could also increase for adaptive reasons as more parasitic eggs are laid in a nest.

With respect to the alternative possibility (cuckoo competition hypothesis), damaged parasitic eggs in multiparasitized nests (three or more cuckoo eggs laid by at least two females) were found only sporadically [in 3 of 48 (6.3%) multiparasitized magpie nests], and in two of these three cases there were five or more cuckoo eggs laid by three or more different females in the nests with broken cuckoo eggs. This scarcity of damaged parasitic eggs suggests that the cuckoo competition hypothesis is not supported.

Prediction B2
The adaptation hypothesis predicts that host egg damage should be greater for a larger corvid host (carrion crow) than for magpies because larger nestlings pose a greater competitive threat to cuckoo nestlings. On the other hand, the nonadaptation hypothesis predicts less egg damage for larger hosts because they have stronger eggs. The percentage of damaged eggs was significantly lower in carrion crow nests (16.4 ± 6.7, n = 21 nests) than in magpie nests (27.8 ± 1.6, n = 355; Mann-Whitney U test, z = 2.16, p = .03). This is especially strong support for the nonadaptation hypothesis considering that reproductive success of the great spotted cuckoo reached low values when parasitizing the carrion crow (hatching success = 82.2% ± 8.4%, n = 15; fledging success = 62.5% ± 12.5%, n = 14 and breeding success = 50.6% ± 12.5, n = 15) than when parasitizing the magpie (hatching success = 80.8% ± 2.3, n = 213; fledging success = 92.2% ± 1.3, n = 195 and breeding success = 73.2% ± 2.4, n = 213; Mann-Whitney U test, z = 0.26, p = .79; z = 2.89, p = .004 and z = 1.87, p = .06, respectively), which imply that selection pressures for egg destruction are higher when parasitizing carrion crows than when parasitizing magpies.
Experimental egg-damage manipulations: effect of the act of laying

When we dropped one great spotted cuckoo egg onto the magpie clutch to simulate cuckoo laying behavior (laying from the rim of the nest), in most tests only one magpie egg was damaged (85.1%), and 88.5% of the damaged eggs were crushed (Table 1). The albumen leaked out of the egg in only one of the damaged magpie eggs (1.9%), and the cuckoo egg was never damaged; the damaged eggs were invariably those that received the blow (Table 1). There was no significant relationship between the number of magpie eggs used in the test and the number of damaged eggs ($r_s = -0.13, p = .37, n = 47$).

When one fresh magpie egg was dropped onto the magpie clutch in control tests, the results were similar to those found when the egg dropped was that of a cuckoo (Table 1). Similarly, the number of magpie eggs did not significantly affect the number of damaged eggs ($r_s = -0.14, p = .41, n = 97$). The number of damaged magpie eggs (Table 1; multiple log-linear model, $\chi^2 = 5.34, df = 2, p = .07$), the type of damage (Fisher’s Exact test, $p = .75$) and the percentage of eggs with albumen leaking out (Fisher’s Exact test, $p = .56$) were not significantly different for the two groups of tests. However, the dropped egg was more frequently damaged when it was a magpie egg (51.5%) than when it was a cuckoo egg (0%; Table 1; Fisher’s Exact test, $p < .00001$).

When a cuckoo egg was dropped onto one or more cuckoo eggs, only in one out of 12 tests (8.3%) there was any egg damaged (the one receiving the blow).

Experimental egg-damage manipulations: effect of the contact of hard and softer eggs

When we jostled the eggs with a pen to reproduce the supposed behavior of the parasite when quickly leaving the host nest, large differences were found, depending on the content of the nest (Table 2). When there were only magpie eggs in the nest, only a single egg was damaged in one test. However, when there was one or more cuckoo eggs with the magpie clutch, significantly more magpie eggs became damaged (Table 2; multiple log-linear model, $\chi^2 = 16.7, df = 2, p = .002$).

This jostling manipulation provoked a similar percentage of crushed and cracked eggs (Table 2), and similar to that of the egg-dropping manipulation, only sporadically produced egg damage with albumen leaking out of the egg (Table 2). The number of magpie eggs did not significantly affect the number of damaged host eggs ($r_s = -0.13, p = .39, n = 35$). However, as the number of cuckoo eggs in the nest increased (between 0 and 3), the number of magpie eggs that became damaged also increased ($r_s = .60, p = .001, n = 35$).

Egg damage during natural parasitism

During 1997, the same year when the experiment was carried out, damaged magpie eggs were found in 37 (66.1%) parasitized nests, and 55.7% of the nests contained one damaged magpie egg. However, we also found nests with two (21.4%), three (3.6%), and four (5.4%) damaged eggs. We recorded 62 damaged magpie eggs that had been pecked (81% of the damaged eggs), crushed (48.4%), or cracked (43.5%). Pecked, crushed, or cracked eggs were found in 10.8%, 67.6%, and 37.8%, respectively, of the parasitized nests with damaged eggs ($n = 37$). In 19 parasitized nests (33.9%), no damaged eggs were found. As the number of cuckoo eggs per nest increased, the number of magpie eggs decreased ($r_s = -0.28, p = .002, n = 96$), and the number of damaged magpie eggs increased ($r_s = .50, p < .0001, n = 96$).

Comparison between egg damage in naturally parasitized nests and experimental manipulations

Crushed eggs were more common in the experimental manipulations (1.18 ± 0.48, $n = 28$) than in naturally parasitized nests with only one cuckoo egg (0.60 ± 0.65, $n = 25$; Mann-Whitney $U$ test, $U = 182.5, p = .003$). However, the average number of cracked eggs per nest was similar in naturally parasitized nests (with only one cuckoo egg) (0.44 ± 0.82, $n = 25$) and in the experimental manipulations (0.39 ± 0.63, $n = 28$; Mann-Whitney $U$ test, $U = 343, p = .9$).

In agreement with the first prediction of the adaptation hypothesis (C1), we found that natural parasitism by great

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### Table 1

Results of the experimental manipulations during the egg-dropping experiment

<table>
<thead>
<tr>
<th>Experimental manipulation</th>
<th>No. of tests with $n$ damaged eggs</th>
<th>Type of damage</th>
<th>Alburnen leaking</th>
<th>Egg damaged</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 1 2</td>
<td>Crushing</td>
<td>Cracking</td>
<td>Yes No</td>
</tr>
<tr>
<td>Cuckoo egg onto magpie eggs</td>
<td>1 (2.1) 40 (85.1) 6 (12.8)</td>
<td>46 (88.5) 6 (11.5)</td>
<td>1 (1.9) 51 (98.1)</td>
<td>0 (0) 46 (100)</td>
</tr>
<tr>
<td>Magpie egg onto magpie eggs</td>
<td>3 (8.1) 33 (89.2) 1 (2.7)</td>
<td>29 (85.3) 5 (14.7)</td>
<td>2 (5.9) 32 (94.1)</td>
<td>17 (51.5) 16 (48.5)</td>
</tr>
<tr>
<td>Cuckoo egg onto cuckoo eggs</td>
<td>11 (91.7) 1 (8.3) 0 (0)</td>
<td>1 (100) 0 (0)</td>
<td>0 (0) 1 (100)</td>
<td>0 (0) 1 (100)</td>
</tr>
</tbody>
</table>

Figures represent number of tests, and percentages are in parentheses.

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### Table 2

Results of the experimental manipulations during the egg-jostling experiment

<table>
<thead>
<tr>
<th>Experimental manipulation</th>
<th>No. of tests with $n$ damaged eggs</th>
<th>Type of damage</th>
<th>Alburnen leaking</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0 1 2</td>
<td>Crushing</td>
<td>Cracking</td>
</tr>
<tr>
<td>With cuckoo eggs</td>
<td>1 (2.1) 40 (85.1) 6 (12.8)</td>
<td>46 (88.5) 6 (11.5)</td>
<td>1 (1.9) 51 (98.1)</td>
</tr>
<tr>
<td>Without cuckoo eggs</td>
<td>19 (54.3) 15 (42.9) 1 (2.8)</td>
<td>8 (47.1) 9 (52.9)</td>
<td>2 (11.8) 15 (88.2)</td>
</tr>
</tbody>
</table>

Figures represent number of tests, and percentages are in parentheses.
spotted cuckoo damaged more magpie eggs $(2.3 \pm 1.4, n = 25)$ than did our experimental manipulations simulating what could be incidental damage during laying $(1.6 \pm 0.63, n = 28)$; Mann-Whitney $U$ test, $U = 239, p < .05$.

In agreement with the second prediction of the adaptation hypothesis (C2), in our experimental manipulations the clutch size of the host did not significantly affect the number of damaged magpie eggs (egg-dropping experiment: $r = -1.3, p = .37, n = 47$; egg-jostling experiment: $r = -1.5, p = .39, n = 35$, and $r = .006, p = .74, n = 56$, respectively, for tests with and without cuckoo eggs in the nest), but in naturally parasitized nests with only one cuckoo egg, the number of damaged host eggs increased as clutch size of the host increased ($r = .41, p = .031, n = 25$).

**DISCUSSION**

Adaptation is an important concept in evolutionary theory. Adaptations are always the consequence of natural selection. Beneficial consequences that are independent of natural selection are not adaptations, and all known adaptations are in principle explicable by natural selection (Ridley, 1993). However, adaptation has frequently been overestimated; it has sometimes been regarded as the sole influence on evolution, and evolutionary biologists have tended to view natural selection as absolutely dominant on evolutionary mechanisms, assuming that it explains almost any phenotypic difference; however, this assumption is not accurate (Ridley, 1993; Travi-sano et al., 1995).

**Experimental egg-damage manipulations**

Crushed magpie eggs have been considered the consequence of host eggs being struck by the parasite’s egg (Soler, 1990; Soler et al., 1997), as the cuckoo lays from the rim of the host nest (Arias de Reyna et al., 1982). In agreement with this idea, we found that when a cuckoo egg is dropped on a magpie clutch, usually one magpie egg is crushed, although sometimes one magpie egg may be cracked (Table 1). Cracked eggs have been considered the result of the host eggs being struck by the feet of the parasite when quickly leaving the nest (Soler, 1990; Soler et al., 1997). However, in our egg-jostling experiment, we found that this egg manipulation provokes egg cracking as well as egg crushing. Thus, we can conclude that egg dropping usually crushes eggs and may crack some, whereas egg jostling both cracks and crushes eggs.

In the experimental manipulations, crushed eggs were more common than in naturally parasitized nests with only one cuckoo egg. Given that a cuckoo egg dropped onto a magpie clutch almost always damages at least one magpie egg (Table 1), that egg jostling also results in some crushed eggs (Table 1), and that crushed eggs are only rarely removed from the nest by magpies (Soler et al., 1999), we can conclude that cuckoo females lay from the rim of the nest in approximately 50% of the cases (there were magpie eggs crushed in 13 out of 25 magpie nests parasitized with one cuckoo egg).

In the egg-dropping experiment, no cuckoo egg was ever damaged, but when a magpie egg was dropped onto the magpie clutch (control tests), the one dropped was damaged frequently (Table 1). In the egg-jostling experiment, when there was no cuckoo egg in the magpie clutch, usually no magpie eggs were damaged (Table 1), even when the eggs were jostled very strongly (see Methods). This was an expected result because magpie eggs should be adapted to resist natural jostling against each other by the wind. Egg-jostling manipulations caused egg damage when there was at least one cuckoo egg in the magpie clutch, and thus this damage must be the consequence of contact between harder- and softer-shelled eggs; in fact, as more cuckoo eggs were present, more magpie eggs were damaged.

All these results support the idea that the great spotted cuckoo, like other avian brood parasites, lays eggs with shells thicker than those of their hosts (Brooker and Brooker, 1991; Lack, 1968; Spaw and Rohwer, 1987). According to Brooker and Brooker (1991), in *Clamator* species, eggs are thicker and rounder compared with host eggs. This strong shell protects the great spotted cuckoo egg from damage when it collides with the hosts eggs, but it also damages more magpie eggs (egg-jostling experiment). However, this strong shell could also protect the parasitic egg from damage if the nest is multiply parasitized (Brooker and Brooker, 1991). In the egg-jostling experiment, when more than one cuckoo egg was introduced into the magpie clutch, no cuckoo eggs were ever damaged, and in the egg-dropping experiment, when one cuckoo egg was dropped on another cuckoo egg, only in 1 test out of 12 was a cuckoo egg damaged (Table 1). Thus, the strong shell of the great spotted cuckoo egg, besides causing substantial egg damage to the magpie clutch, protects the parasitic egg from damage both when it collides with the host eggs and when other cuckoo eggs are present in multiply parasitized nests.

The strong shell of the cuckoo egg is responsible for part of the egg damage caused by the cuckoo. However, it is unclear whether the damage to host eggs is an adaptation. If cuckoo eggs became more thick shelled as a way of destroying host eggs, it would be an adaptation, but perhaps cuckoos started to lay thick-shelled eggs because they were in a hurry when laying, and females with thick-shelled eggs less often suffered breakage of their own eggs. This incidentally led to more frequent destruction of host eggs, but this was not the selective force driving the evolution in the first place. If this was the case, we would be dealing with an exaptation rather than an adaptation (Gould and Vrba, 1982; but see Skelton, 1992, for problems with terminology).

The basis for the exaptation scenario described above (rapid laying) is a characteristic frequently reported in brood-parasitic females: parasitic eggs are laid quickly, usually in only a few seconds (see review in Sealy et al., 1995). This rapid laying has frequently been suggested to be an adaptation for brood parasitism, as recently shown by Sealy et al. (1995). Rapid laying is adaptive because it allows parasitic females to avoid detection by hosts (Davies and Brooke, 1988; Scott, 1991; Sealy et al., 1995) and thereby provides parasitic females with some important advantages by reducing the chance of (1) host attacks and possible injury (Briskie and Sealy, 1987; Sealy et al., 1995; Soler, 1990), (2) the possibility of attracting other parasitic females or predators (Sealy et al., 1995; Wylie, 1981); and (3) a careful nest examination by the host which would increase the likelihood of parasitic-egg rejection (Davies and Brooke, 1988; Moksnes et al., 1993; Rothstein, 1975; Sealy et al., 1995; but see Soler et al., 1999).

**Evaluation of the adaptation and nonadaptation hypotheses**

A previous experimental study (Soler et al., 1997) demonstrated that egg-damaging behavior in the great spotted cuckoo is advantageous to the chicks of the parasite when the magpie has laid numerous eggs before parasitism. A second experiment revealed that increasing reproductive success of the cuckoo by egg damage is the consequence of both reduction of the number of competing host chicks in the nest and increased probability that late-laid cuckoo eggs will hatch (Soler et al., 1997). This information alone provides strong support for the idea that egg destruction is an adaptive strategy which increases the reproductive success of the great spotted cuckoo (Reeve and Sherman, 1993). However, great spotted cuckoos...
also destroyed magpie eggs when laying early during the breeding cycle of the magpie. Contrary to the prediction of the reduction of nestling competition hypothesis, the breeding success of the great spotted cuckoo was high and similar both in nests parasitized naturally (with host-egg destruction) and experimentally (by us, without host-egg destruction) at the beginning of the laying sequence of the magpie (Soler et al., 1997).

We have some information that suggests that egg-damage behavior could not be maintained by natural selection: the result of the above mentioned experiment, which did not support the prediction of the reduction of nestling competition hypothesis, the prediction A1 (this study), which also failed in this respect, and two other predictions (A2 and A3) that can be tested considering previously published results (Soler et al. 1997).

Under prediction A2, egg destruction could not be considered an incidental behavior if the frequency of pecked eggs is high compared with crushed and cracked eggs (crushed and cracked eggs could be an incidental consequence of a parasite’s visit, but pecked eggs could not). However, pecked eggs accounted only for 14.1% of the damaged eggs (parasite’s visit, but pecked eggs could not). However, these tests are based on comparisons between individuals, and the results are not conclusive. Rather, an experimental approach is needed to draw stronger conclusions. In our experimental manipulations, we found that when we simulated the laying behavior of the great spotted cuckoo the number of damaged magpie eggs was significantly lower than in natural parasitism. In addition, although the number of eggs damaged did not depend on the number of magpie eggs in the experimental manipulations, the number of damaged eggs increased as magpie clutch size increased in natural parasitism. These results support the predictions of the adaptation hypothesis (C1 and C2), implying that egg damage is not an incidental consequence of rapid egg laying, but an adaptation.

Over the history of evolutionary biology, some traits have been described as nonadaptive; however, in all cases after the appropriate analysis it was concluded that the characteristic under study was controlled by natural selection and thus adaptive (Ridley, 1993). This is what has happened in our study concerning great spotted cuckoo egg-damaging behavior: although some tests of predictions did not support the adaptation hypothesis, the behavior turned out to be adaptive after a detailed experimental study.

REFERENCES


