Great spotted cuckoos improve their reproductive success by damaging magpie host eggs

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Abstract. Adult great spotted cuckoos, *Clamator glandarius*, damage the eggs of their magpie, *Pica pica*, host without removing or eating them. The number of damaged magpie eggs was recorded in 360 parasitized nests of which 62.2% contained between one and eight damaged magpie eggs. Egg-destroying behaviour may be adaptive if it reduces nestling competition and/or enhances the hatching success of the cuckoo. To clarify the role of egg destruction for the reproductive success of great spotted cuckoos, unparasitized magpie nests were experimentally parasitized (without egg damage) by introducing cuckoo eggs or chicks. Egg damage was common in parasitized nests but the eggs were not damaged by the hosts. Egg damage increased the breeding success of the cuckoos, by both reducing the number of competing host chicks in the nest and increasing the likelihood that late-laid cuckoo eggs would hatch.

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Avian brood parasites lay eggs in the nests of other birds. Many of them remove or damage at least one host egg; the female parasite usually does this shortly before she lays her own egg (Friedman 1968; Payne 1977; Sealy 1992). Removal or destruction of a host egg has been reported in the European cuckoo, *Cuculus canorus* (Gärtner 1981; Wyllie 1981; Davies & Brooke 1988) and in almost all other species of the genera *Cuculus* (Friedman 1968; Jensen & Clinning 1974; Moksnes & Røskaft 1987; Brooker & Brooker 1989a), *Chrysococcyx* (Jensen & Clinning 1974; Gill 1983; Brooker et al. 1988; Brooker & Brooker 1989b) and *Clamator* (Mountfort & Ferguson-Lees 1961; Valverde 1971; Soler 1990), as well as in less well known cuckoos such as *Eudynamis* and *Scythrops* (Brooker & Brooker 1989a). Similarly, cowbirds, *Molothrus* spp. (Mason 1980; Carter 1986; Wolf 1987; Sealy 1992) and most species of honey guides, Indicatoridae, cuckoo-weavers, *Anomalospiza*, and widow-birds, Viduinae, also remove host eggs during parasitic laying (Friedman 1960; Lack 1968).

Brood-parasitic females can damage, remove or eat host eggs. It is usually inferred that the

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parasite removes a host egg at laying because parasitized nests contain significantly fewer eggs than unparasitized nests (e.g. Post & Wiley 1977; Zimmerman 1983; Brooker & Brooker 1989a), and that the host egg is eaten by the parasite (Hoy & Ottow 1964; Scott et al. 1992). However, as has been shown previously (Soler 1990), a significantly smaller clutch in parasitized than unparasitized nests may result from the removal of damaged eggs by the host, given that many birds eject their own cracked eggs (Kemal & Rothstein 1988; Soler 1990).

The great spotted cuckoo, *Clamator glandarius*, is an obligate brood parasite, which parasitizes mainly magpies, *Pica pica*, in Europe, the carrion crow, *Corvus corone*, being its secondary host (Cramp 1985). Nestlings of the great spotted cuckoo do not eject the eggs or young of the host, but the eggs generally hatch several days before the magpie's eggs, and magpie chicks frequently starve in competition for food with the larger cuckoo chick (Cramp 1985; Soler 1990; Soler & Soler 1991). Mountford & Ferguson-Lees (1961) showed that great spotted cuckoo females remove one or two host eggs at laying. However, in other studies, egg removal was never observed, although damaged eggs in parasitized nests were frequent (Valverde 1971; Soler 1990). Parasites destroying host eggs without removing or eating them has

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also been recorded in different *Molothrus* species (Hoy & Ottow 1964; Post & Wiley 1977; Mason 1980; Carter 1986).

Egg-damaging behaviour by great spotted cuckoos may reduce nestling competition or enhance the hatching success of the cuckoo. The 'reduction of nestling competition' hypothesis states that egg-destruction behaviour increases survival of the parasite chick by reducing the number of competing host chicks in the nest. The 'enhancement of hatching success' hypothesis states that egg-damaging behaviour increases the likelihood that late-laid cuckoo egg(s) will hatch because of the destruction of host eggs that would otherwise hatch earlier than those of the cuckoo and would cause the host to cease incubation before the cuckoo egg had hatched.

We mention only adaptive hypotheses; however, it is not clear whether the crushing of host eggs during the laying of parasite eggs is an adaptation. Cuckoo eggs may have become thick-shelled to prevent breakage during the hurried laying. This may have 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 were the case we would really be dealing with an exaptation rather than an adaptation (Gould & Vrba 1982; but see Skelton 1992 for problems with terminology).

Our aims in this paper are to describe the egg-damaging behaviour of great spotted cuckoos, provide evidence that eggs are not damaged by the host and test experimentally both the reduction of nestling competition and the enhancement of hatching success hypotheses.

MATERIALS AND METHODS

Field Work

We carried out the field work during the breeding seasons of 1990–1995 (although some observations were conducted in 1982–1983 and 1986–1988) 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 nest at high density in almond trees but also nest in oaks (Soler 1990).

We inspected nests usually twice weekly. During 1990–1994 we found 692 magpie nests, 404 of

which (58.4%) were parasitized. We weighed great spotted cuckoo chicks in 1992 and 1993 with a 300 g Pesola spring balance 1–2 days before they left the nest. Although in these years we performed several field experiments, we have included data only from non-experimental nests. We determined the number of damaged eggs by carefully examining all eggs in each nest. We recorded breeding parameters such as laying date, clutch size, number of eggs hatched and number of fledglings from nearly all nests.

Experimental Procedures

To clarify the role of egg destruction for the breeding success of great spotted cuckoos we experimentally parasitized (without egg damage) unparasitized magpie nests by introducing real cuckoo eggs or chicks in three experiments. Since the success of cuckoos depends on the timing of laying relative to the laying sequence of the magpie (see below), we simulated parasitism early and late during the laying sequence. Each experiment was performed in a different year. The controls were, in each case, from the same year as the experiment.

Experiment 1

To test the adaptation hypothesis for egg damage by great spotted cuckoo females laying late (after clutch completion), we experimentally introduced one cuckoo chick recently hatched (0–1 days old) into each of 15 unparasitized magpie nests, where the oldest magpie chick was between 1 and 7 days old. Three experimentally parasitized nests that were depredated were not considered. In experimentally parasitized nests the cuckoo chick was 5.3 ± 0.61 ($\bar{X} \pm$ SE, $N=12$) days younger than the oldest magpie chick, while in naturally parasitized nests the cuckoo chick was 3.6 ± 1.94 ($N=5$) days older than the oldest magpie chick. This difference was statistically significant (Mann–Whitney *U*-test: $z=2.8$, $P<0.01$). We used as controls 13 naturally parasitized nests with only one cuckoo egg matched with respect to laying date and area with experimental nests.

Experiment 2

We introduced one cuckoo egg into 11 unparasitized magpie nests again simulating late-laying

of the cuckoo egg. In two of these nests, the cuckoo egg hatched simultaneously with the magpie eggs, and we have not considered these further. The eggs used in the experiment were laid between 3 and 6 days later than the last magpie egg in the experimental nest ($\bar{X} \pm$ SE $= 4.4 \pm 0.37$, $N=9$). As controls we used seven naturally parasitized nests with only one cuckoo egg matched to experimental nests with respect to laying date and area.

Experiment 3

To see whether the reduction of nestling competition hypothesis also applies when cuckoos lay early in the breeding cycle of the host, we simulated early laying of the cuckoo egg by experimentally parasitizing 17 unparasitized magpie nests with one great spotted cuckoo egg that had been laid between 1 and 4 days later than the first magpie egg of the experimental nest. Four experimentally parasitized nests that were depredated, and four others that were naturally parasitized later by great spotted cuckoos, were not considered. We used as controls 16 naturally parasitized nests with one cuckoo egg matched with respect to laying date and area. Differences in hatching dates between magpie and great spotted cuckoo chicks were not significantly different between naturally and experimentally parasitized nests (Mann–Whitney U-test: $U=36$, $N_1=14$, $N_2=6$, NS).

Statistical Procedures

We followed the statistical methods of Sokal & Rohlf (1989), and when non-parametric statistics were needed we used the methods described by Siegel (1988). Values given are $\bar{X} \pm$ SE. All tests are two-tailed.

Ethical Note

We obtained the majority of cuckoo eggs and chicks from multi-parasitized magpie nests (between five and 10 cuckoo eggs per nest) where usually no more than three cuckoo fledglings are produced (Soler et al., in press). Thus, experimental treatment improved the cuckoo's breeding success because we redistributed a number of cuckoo eggs or chicks from multi-parasitized to unparasitized magpie nests (only one per nest). Our experimental treatment imposed a high

starvation rate on experimentally parasitized magpie chicks (magpie breeding success in experimentally parasitized nests $= 50.6 \pm 4.80\%$ in experiment 1, $27.0 \pm 8.55\%$ in experiment 2 and $32.7 \pm 5.37\%$ in experiment 3). However, the magpie is a brood-reduction strategist and competition among chicks is usually strong and chick starvation frequent (magpie breeding success in unparasitized nests $= 50.5 \pm 1.89\%$, $N=122$, Soler et al., in press). Thus, only experiments 2 and 3 produced a higher starvation rate than that naturally occurring in unparasitized nests. The effect of natural parasitism was usually stronger than that of experimental parasitism (magpie breeding success in naturally parasitized nests $= 8.9 \pm 4.11\%$ in experiment 1, $17.3 \pm 6.15\%$ in experiment 2 and $14.0 \pm 5.19\%$ in experiment 3). Sample sizes were as small as possible in order to reduce the impact of our experimental manipulations on the welfare of magpie chicks.

RESULTS

Laying Behaviour

We first consider whether egg damage was really inflicted by cuckoos, or was incidentally caused by hosts. We can reject egg damage by hosts because (1) in none of 337 unparasitized magpie nests did we find damaged eggs, and (2) in the 29 naturally parasitized magpie nests (control group in experiments 1 and 3) 52 of 207 magpie eggs suffered damage, while in the 21 experimentally parasitized nests (experiments 1 and 3) only two of 94 magpie eggs were damaged ($\chi_1^2 = 23.2$, $P<0.0001$). Considering nests as independent data, in 36 naturally parasitized nests (with only one cuckoo egg, control) we found 15 nests with broken eggs whereas in the 34 experimentally parasitized nests only two suffered egg damage ($\chi_1^2 = 21.81$, $P<0.00001$). Thus, we can conclude that the damage is inflicted by the parasite because experimental parasitism did not cause egg damage.

During 1982–1983 and 1986–1994, we monitored 430 parasitized magpie nests and observed the act of parasitism on 10 occasions, but we never saw a great spotted cuckoo carry away host eggs. We recorded the number of damaged magpie eggs in 360 parasitized nests. Damaged magpie eggs were found in 224 (62.2%) of these parasitized nests, but none in unparasitized ones. In

Table I. Breeding success of great spotted cuckoos in relation to time of parasitism during the breeding cycle of the magpie host

Time of parasitism	Eggs laid	Eggs hatched *N* (%)	Chicks fledged *N* (%)
Magpie laying period	57	45 (78.9)	42 (73.7)
Clutch completed	27	12 (44.4)	10 (37.0)

Only nests that received one parasitic egg in only one period of the breeding cycle were considered.

36.2% of the nests ($N=224$), we recorded one damaged magpie egg, but we also found nests with two (55), three (41), four (27), five (11), six (5) or more (4) damaged eggs. In 136 parasitized nests (37.8%), there were no damaged eggs, but in some cases this could have been due to magpies removing their most damaged eggs (Soler 1990). For this reason, host clutches in parasitized nests were smaller than those in unparasitized nests (Soler 1990). In the present study, clutches of parasitized nests without damaged eggs were also significantly smaller ($\bar{X} \pm$ SE $= 4.8 \pm 0.21$, $N=131$) than those of parasitized nests with damaged eggs (5.6 ± 0.10, $N=223$; Mann–Whitney *U*-test: $z= -2.58$, $P<0.01$).

The damaged eggs of the magpie were pecked, crushed or cracked (Soler 1990). Pecked eggs represented 14.1% of the damaged eggs ($N=241$) and were found in 18.5% of the parasitized nests ($N=157$). Crushed and cracked eggs represented 55.2 and 30.7% of the damaged eggs ($N=241$), respectively, appearing in 60.5% and 31.2% of the nests with damaged eggs ($N=157$). Pecked eggs usually had very small holes, which did not allow the albumen to leak. The size (length × width) of cracks in 11 recently damaged eggs was 0.33 ± 0.05 mm². Thus, the damage to eggs was not readily visible.

Parasite eggs were usually deposited during the laying period of the magpie (71.3%, $N=314$). In nests with more than one parasitic egg, second and third eggs were laid during the last days of the host's laying period, or when clutches were completed. Of 84 great spotted cuckoo eggs for which we know the laying time, 29 (34.5%) were laid early in the host's breeding cycle (one to three eggs already laid by the host), 28 (33.3%) were laid late in the host breeding cycle (four to seven eggs already laid by the host), and the rest after clutch completion (Table I).

Reduction of Nestling Competition Hypothesis

Observational evidence

The stage in the breeding cycle at which parasitism occurred significantly affected the reproductive success of the parasite (Table I). Of 15 nests parasitized before magpies started laying, 10 were deserted. Hatching and fledging success of the great spotted cuckoo were significantly greater when the parasitic eggs were laid before rather than after the clutch was completed by the magpies (Table I; Fisher's exact test: $P<0.01$ for eggs hatched and chicks fledged). However, if we consider breeding success (percentage of chicks fledged with respect to eggs laid) there was no significant difference between the two groups (Table I; Fisher's exact test: NS). Thus, the effect is due solely to the difference in hatching success.

The number of magpie eggs destroyed by the great spotted cuckoo increased as the number of eggs already laid by the magpies increased (Fig. 1).

Experimental evidence

In experimentally parasitized nests without host-egg destruction, the breeding success of the parasite was lower than in nests naturally parasitized (experiment 1, Table II).

In experiment 2, the proportions of both eggs hatched and chicks fledged were significantly lower in nests to which we added cuckoo eggs than in naturally parasitized nests (Table II, experiment 2). Five out of nine experimental eggs failed to hatch because magpies ceased incubation before the cuckoo egg had hatched, and three out of four chicks did not fledge because they starved.

When we simulated laying of a parasite egg early in the breeding cycle of the host, the reproductive success of the cuckoo was similar in
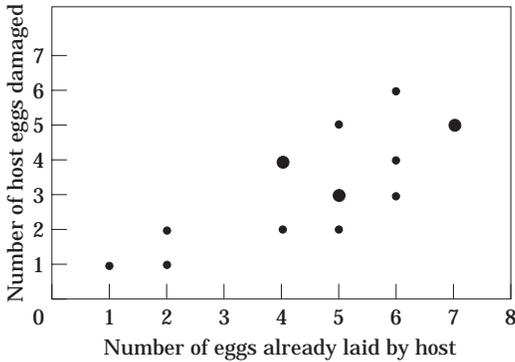
Figure 1. Relationship between the number of eggs already laid by magpies and the number of eggs damaged by great spotted cuckoos. Only nests with one parasite egg were considered. Small points represent one datum, large points represent two data. $r_s = 0.74$, $N = 15$, $P < 0.01$.

naturally and experimentally parasitized nests (Table II, experiment 3).

DISCUSSION

Laying Behaviour

Host-egg destruction or removal has been explained by four adaptive hypotheses (see review in Sealy 1992), but only one (reduction of nestling competition hypothesis) is plausible for great spotted cuckoos because (1) they damage host eggs without removing them, and (2) their nestlings do not eject host eggs or young, and egg destruction would therefore be advantageous by reducing the number of competing host nestlings.

Our results clearly show that great spotted cuckoos do not remove host eggs, a conclusion consistent with previous reports (Soler 1990; Soler et al., in press). More than 62% of the parasitized nests had damaged host eggs. Thus, damaging eggs by inflicting small cracks is a frequent behaviour of this parasite. As a general rule, when brood parasites puncture the host's eggs, they do so without breaking them (Hoy & Ottow 1964; Post & Wiley 1977; Carter 1986). We suggest that this sort of damage confers two advantages to the parasite. (1) The host may not detect the subtle damage, and hence not examine the nest carefully enough immediately to detect and reject the parasite egg. If the host discovers the damaged egg later, the parasite egg may go undetected because the host will be accustomed to seeing it in the nest. (2) Small cracks will decrease the risk of attracting insects and bacteria because the damaged egg can be ejected without the rest of the yolk or the egg white remaining in the nest.

Great spotted cuckoo eggs laid after clutch completion produced significantly fewer chicks than those laid early during the laying sequence (Table I). This result has two explanations. (1) Magpies often cease incubating eggs about 5–8 days after the first chicks hatch (personal observation), and this could occur before the egg of the cuckoo hatches, if laid very late. (2) Great spotted cuckoo eggs need a shorter incubation period than magpie eggs (Alvarez & Arias de Reyna 1974), which favours the earlier hatching of the parasite, providing a clear advantage for great spotted cuckoo chicks (Soler et al. 1994a) and for brood parasites in general (Payne 1977; Briskie & Sealy 1990). However, if the parasitic egg is laid after

Table II. Breeding success of the great spotted cuckoo in naturally and experimentally parasitized nests

	Natural parasitism	Experimental parasitism	Fisher's exact test, P
Experiment 1			
Eggs hatched	13/13	—	
Chicks fledged	13/13	7/12	0.01
Experiment 2			
Eggs hatched	7/7	4/9	<0.05
Chicks fledged	7/7	1/4	<0.05
Experiment 3			
Eggs hatched	14/16	8/8	NS
Chicks fledged	13/14	6/8	NS

clutch completion and the short incubation period is insufficient to assure an earlier hatching, the cuckoo chicks miss their advantage and may starve in competition with the chicks of the host.

Reduction of Nestling Competition Hypothesis

Observational evidence

Because survival rate of the cuckoo chicks decreased the later the eggs were laid in the host breeding cycle (Table I), the reduction of nestling competition hypothesis predicts that as the number of eggs already laid by the magpies increases, the number of magpie eggs destroyed by the great spotted cuckoo should also increase. This was in fact the case (Fig. 1). This is not an artefact of the fact that parasites that lay in nests at the beginning of the magpie laying period have few eggs that they can damage, since adult great spotted cuckoos revisit previously parasitized nests (Soler et al. 1995), and have the same opportunities to damage eggs in every nest.

Experimental evidence

The reduction of nestling competition hypothesis, which states that egg-destruction behaviour increases survival of the parasite chick, was supported because experiment 1 (Table II) demonstrated that egg-damaging behaviour in the great spotted cuckoo is advantageous to its chicks when the magpie has laid numerous eggs prior to parasitism. This result, however, may be due to two different mechanisms. (1) Egg destruction may increase survival of the parasite chick by reducing the number of competing host chicks in the nest or (2) it may increase the likelihood of late-laid cuckoo egg(s) hatching by destroying eggs that would otherwise hatch earlier than, and result in terminated incubation for, the cuckoo egg(s), as suggested by observational data (Table I). Hatching success appears to be the best predictor of cuckoo reproductive success, as there was very little mortality after hatching (Table I). Because experiment 1 cannot be used to distinguish between these two possible mechanisms, we performed experiment 2, again simulating late parasite-laying but adding cuckoo eggs instead of chicks. This second experiment (Table II) revealed that egg damage increases the cuckoo's reproductive success by reducing the number of competing host chicks in the nest and increasing the likelihood that late-laid cuckoo eggs will hatch.

These results support the idea that egg destruction is an adaptive strategy which increases the reproductive success of the great spotted cuckoo. However, the cuckoo's breeding success was high and very similar in nests parasitized both naturally (with host-egg destruction) and experimentally (by us, without host-egg destruction) at the beginning of the laying sequence of the magpie (Table II, experiment 3), which suggests that great spotted cuckoo nestlings, which hatch before magpie nestlings, successfully elicit parental care from the magpie and do not need the help of their parasitic parents to reduce the number of future competing host nestlings. Why then do adult cuckoos unnecessarily destroy magpie eggs when they lay early in the magpie's laying sequence? We suggest three possible reasons. (1) By reducing the number of magpie eggs in the nest the parasite increases the cost of egg ejection (Davies & Brooke 1988) because with fewer magpie eggs in the nest, each is more valuable and a mistake in egg ejection by the magpie becomes more costly. (2) Great spotted cuckoo nestlings reared alone weigh significantly more than those reared together with other cuckoo or magpie chicks (Soler et al. 1994a). (3) Great spotted cuckoos that die after fledging weigh significantly less than those that live until migration in August (Soler et al. 1994b). Great spotted cuckoo fledglings could therefore improve their chance of survival by monopolizing the parental care of the magpie.

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