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Chick recognition and acceptance: a weakness in magpies exploited by the parasitic great spotted cuckoo

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Abstract Hosts of brood parasites have evolved the ability to discriminate non-mimetic and even mimetic eggs, but not non-mimetic chicks. Here we demonstrate that the great spotted cuckoo *Clamator glandarius* does not provide its magpie *Pica pica* host with a supernormal stimulus that helps to avoid recognition, because single cuckoo chicks introduced into otherwise unparasitized magpie nests are not fed at a higher frequency than single magpie chicks introduced to parasitized magpie nests. Another series of experiments demonstrated that magpies have the ability to discriminate cuckoo chicks, mainly when these are introduced at the end of the nestling period, and especially when the cuckoo chick together with a magpie chick is presented to adult magpies outside the nest. This supports the idea that cuckoos exploit the obligatory reaction of magpies to feed all young that have been hatched in their nests and whose "signatures" they have learnt. Furthermore, the experimental cuckoo chicks in parasitized magpie nests were more likely to be accepted than they were in non-parasitized nests. This supports the hypothesis that magpies may learn to recognise their own nestlings as those present in the nest and may indicate that a comparison between cuckoo and magpie nestlings is the basis of discrimination.

Key words Brood parasitism · *Clamator glandarius* · Chick recognition · *Pica pica* · Supernormal stimulus

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Introduction

The relationship between parasitic cuckoos and their hosts has frequently been described as a coevolutionary arms race, since parasitism usually reduces the reproductive success of the host and therefore results in selection for host defense, which in turn selects for counter-adaptations in the parasite and then for new host defenses (Payne 1977; Mason and Rothstein 1986; Davies and Brooke 1989a, b; Moksnes and Røskaft 1989; Rothstein 1990). Recognition and rejection of parasite eggs by a host and the subsequent evolution of egg mimicry by the brood parasite are thought to be clear examples of such a process (Brooke and Davies 1988; Davies and Brooke 1989a, b; Soler and Møller 1990; Briskie et al. 1992). However, even host species that are capable of accurate discrimination of mimetic eggs appear unable to discriminate a chick that is dramatically different from host chicks (Davies and Brooke 1988; Harvey and Partridge 1988; Rothstein 1990). The absence of nestling discrimination remains an evolutionary enigma that may result from either (1) the hosts of brood parasites not yet having evolved discriminatory responses against the parasite (evolutionary lag hypothesis), or (2) rejection incurring costs greater than acceptance and therefore, parasitism being a stable equilibrium in the cuckoo-host arms race (evolutionary equilibrium hypothesis) (Rothstein 1990).

The lack of chick mimicry in the European cuckoo, *Cuculus canorus*, suggests that hosts cannot discriminate cuckoo chicks, and this is in fact the case in all of the four host species tested (Davies and Brooke 1989a, b) although these same hosts can discriminate cuckoo eggs (Davies and Brooke 1988). However, the European cuckoo chick evicts the host eggs or chicks soon after hatching, thereby reducing the benefits of chick discrimination on the part of the host species (Davies and Brooke 1988). In contrast, the chick of the great spotted cuckoo (*Clamator glandarius*) (1) mimics the young of the host both in appearance (Lack 1968)

(before feathers develop) and in begging calls (Mundy 1973; Redondo and Arias de Reyna 1988), and (2) does not evict the host eggs or chicks. The second point applies even though selection is stronger for host discrimination against cuckoo chicks when host young remain in the nest because of the greater benefits of discrimination to hosts that rear mixed broods of their own and parasitic offpring (Davies and Brooke 1988). This suggests that magpie (*Pica pica*) hosts might be able to discriminate among cuckoo and host chicks, since discrimination by estrildid hosts has selected for chick mimicry in the parasitic viduines (Nicolai 1964).

An elegant model (Lotem 1993) has recently shown that, although learning to recognize eggs is adaptive in the European cuckoo, learning to recognize nestlings might not be so, because the cost of misimprinting (learning to recognize the parasite nestling as the parents' own) may exceed the benefit of correct learning. The same model predicts that if both host and parasite nestlings survive to fledging, learning to recognize nestlings should be adaptive (Lotem 1993). Here we present an experimental test of chick discrimination in a host-parasite relationship where parasite and host nestlings are reared together in order to determine whether hosts really are unable to discriminate against the parasite.

The great spotted cuckoo is a specialist brood parasite which in Europe parasitizes members of the corvid family, particularly the magpie (Cramp 1985). Usually the great spotted cuckoo eggs hatch earlier than those of the magpie host, but the chick does not eject host eggs or nestlings, unlike most other parasitic cuckoos. Rather, the fast-growing great spotted cuckoo chick outcompetes the smaller host nestlings for food and thereby decreases the reproductive success of the host (Cramp 1985; Soler 1990; Soler et al. in press a).

The following hypotheses and predictions were tested:

1. *Hypothesis 1*: magpies should have some ability to discriminate great spotted cuckoo chicks because the chick of the great spotted cuckoo mimics the young of the host, and magpies are able to rear mixed broods of their own and parasitic offspring.

2. *Hypothesis 2*: cuckoos may exploit the host's rule "to feed any chick in the nest". According to this hypothesis we can predict that when magpie and alien young are presented outside the nest, discriminatory abilities of the magpie parents should improve.

3. *Hypothesis 3*: cuckoo nestlings may provide hosts with a supernormal stimulus for parental care, which would help to avoid cuckoo chick recognition (Dawkins and Krebs 1979). If this was the case, we might expect that (a) an alien cuckoo chick should be fed more often than an alien magpie chick presented simultaneously outside an unparasitized host nest (without cuckoos in the nest), and (b) a cuckoo chick cross-fostered in an unparasitized magpie nest should be fed at a higher frequency than a magpie chick fostered in a parasitized magpie nest (containing cuckoo nestlings).

4. *Hypothesis 4*: magpies may learn to recognise their own nestlings as those present in the nest. This hypothesis would be supported if magpies' ability to discriminate cuckoo chicks was better in unparasitized than in parasitized nests.

Materials and methods

Study area

The study site was situated in groves of almond trees (*Prunus dulcis*) located in Hoya de Guadix, southern Spain (37° 18'N, 3° 11'W), a high-altitude plateau approximately 1000 m above sea level, with sparse vegetation, cultivated cereals (especially barley), and many groves of almond trees, the habitat in which magpies are most abundant (Soler 1990). A more detailed description of the study site and the incidence of great spotted cuckoo parasitism of magpie hosts is given in Soler (1990) and Soler et al. (in press a).

Field work

We carried out three series of experiments in 1990–1992, during which a total of 348 magpie nests were found, of which 60.3% were parasitized by the great spotted cuckoo. Parasitized magpie nests were located during regular visits to all magpie nests in our study area from the start of the breeding season.

Both parasitized and unparasitized magpie nests were used in the experiments. A magpie nest was considered parasitized if it contained one or more eggs of the great spotted cuckoo. All nests were visited at least once a week, and parasitized nests were visited more frequently. Frequent monitoring provided detailed information about the stage of the breeding cycle and the number of both parasite and host chicks present in every nest used for carrying out the cross-fostering experiments.

Experimental procedure

Experiment 1

In order to test whether magpies are able to discriminate against the great spotted cuckoo chick (hypothesis 1), cuckoo nestlings were taken from their original nests and placed in a non-parasitized magpie nest. The cuckoo nestling and all host chicks were fitted with neck-collars, and after 3–4 h we checked the nest to record whether the cuckoo and magpie chicks had been fed. The neck-collars were then removed. There is no evidence that the effect of this method differs between cuckoos and magpies; in fact, in another study of food allocation by magpies to parasitic and host nestlings, we found the opposite result to that found here: when both magpie and cuckoo chicks were in a medium developmental stage (open eyes without developed feathers), great spotted cuckoo chicks were fed at a higher rate than were magpie chicks in the same nest (Soler et al. in press b). Thus, neck-collars do not impede one species more than the other from begging properly. If the adult magpies had not delivered any food, the nests were excluded from the analyses. Three different developmental stages of both magpie and great spotted cuckoo chicks were considered: (1) small nestlings with closed eyes, (2) intermediate nestlings with open eyes, but without feathers, and (3) large nestlings with feathers. Each magpie nest was tested only once and the number of magpie chicks in the nest ranged from two to seven for the first development stage, one to six for the second,

and two to six for the third stage. The number of chicks in the nests in the different stages was not related to whether the chick was fed (logistic regression, maximum likelihood method: first developmental stage, $\chi^2 = 1.69$, $n = 12$, $df = 1$, $P = 0.19$; second stage, $\chi^2 = 2.60$, $n = 11$, $df = 1$, $P = 0.11$; third stage, $\chi^2 = 1.67$, $n = 7$, $df = 1$, $P = 0.20$). Therefore, we pooled the data for each developmental stage of magpie chicks. A total of 39 tests were performed.

Three possible magpie responses to the experimental cuckoo chicks were distinguished: (1) fed, (2) not fed, and (3) ejected (or attacked). "Fed" means that the nestling had food in its oesophagus; "not fed" means that there was no food; and "ejected" that the nestling had injuries or had disappeared.

Experiment 2

In this experiment one cuckoo and one magpie chick were presented together outside magpie nests. For non-parasitized magpie nests the alien chick was a cuckoo chick, and for parasitized nests (which only contained cuckoo chicks) a magpie chick. Both chicks were at the end of the third developmental stage (similar size) and both were tethered next to each other on a piece of wood (less than 20 cm apart). This apparatus was then fixed to branches near the nest (distance 1–3 m). The reaction of the magpie hosts was watched from a distance of 75–100 m for 1 h. A total of 28 tests at the same number of nests were carried out. The classification of magpie reactions was the same as those in experiment 1.

Experiment 3

The experimental procedure and assumptions were the same as in experiment 1, except that only experimental chicks and nests of the third developmental stage were used. All tests were performed at least 5 days before chicks left the nest to avoid chicks departing prematurely because of experimental disturbance. A total of 29 tests were conducted (six of the eight parasitized nests had only cuckoo chicks, while the other nests had both magpie and cuckoo chicks). In this experiment we introduced one alien magpie nestling into parasitized nests as a control treatment.

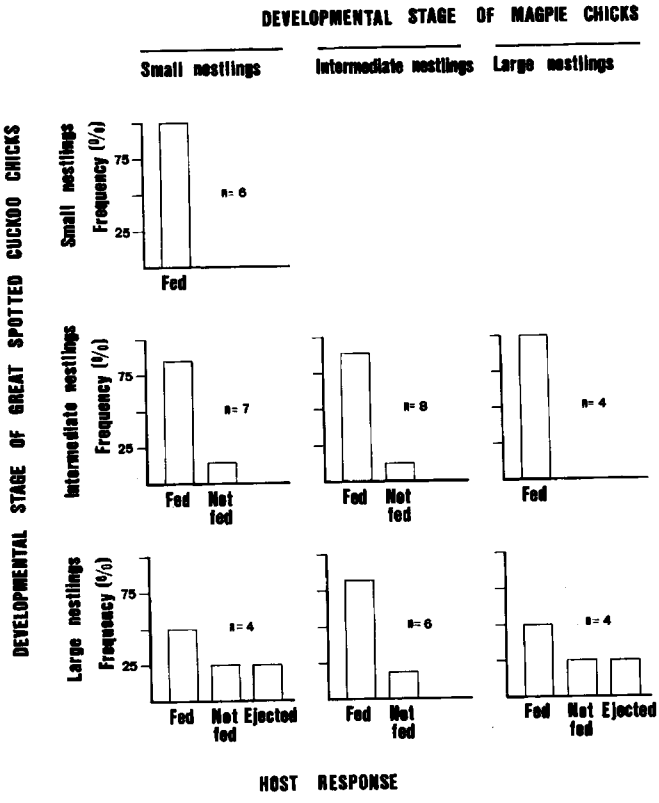

Fig. 1 Response of magpie parents to great spotted cuckoo nestlings introduced into their nests. Three different developmental stages of both magpie and great spotted cuckoo chicks were considered: (1) small nestlings with closed eyes, (2) intermediate nestlings with open eyes, but without feathers, and (3) large nestlings with feathers. Each magpie nest was tested only once and the number of magpie chicks in the nest ranged from two to seven for the first development stage. Three possible magpie responses to the experimental cuckoo chicks were distinguished: (1) fed, (2) not fed, and (3) ejected (or attacked). "Fed" means that the nestling had food in its oesophagus; "not fed" means that there was no food; and "ejected" that the nestling had injuries or had disappeared

Results

Magpies were able to discriminate parasitic chicks to some extent. Most of the cross-fostered cuckoo chicks were fed, but a total of seven (17.9%) were not and two of these were attacked or ejected (Fig. 1). No discriminatory response was exhibited against featherless cuckoo chicks, but discrimination (chicks that were "not fed" and "ejected") increased with the age of the chicks (using only experiments with magpie and cuckoo chicks in the same developmental stage; logistic regression, $r = 0.50$; $n = 18$; maximum likelihood model, $\chi^2 = 4.46$, $n = 18$, $df = 1$, $P = 0.035$). These results support the first hypothesis and demonstrate that magpie hosts have the capacity to discriminate between parasite and host chicks, particularly when large, non-mimetic cuckoo chicks were introduced.

Experimental great spotted cuckoo young were neglected by magpies (not fed, ejected or attacked) significantly more often when presented outside the nest (94%, Fig. 2) than when in the nest (56%, Fig. 3;

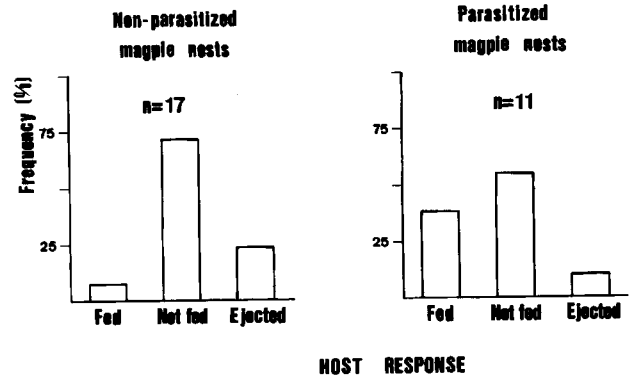

Fig. 2 Response of magpie parents when they were allowed to choose between a cuckoo and a magpie chick presented outside the nest. For non-parasitized magpie nests the alien chick was a cuckoo chick presented outside the nest, and for parasitized nests (which only contained cuckoo chicks) a magpie chick

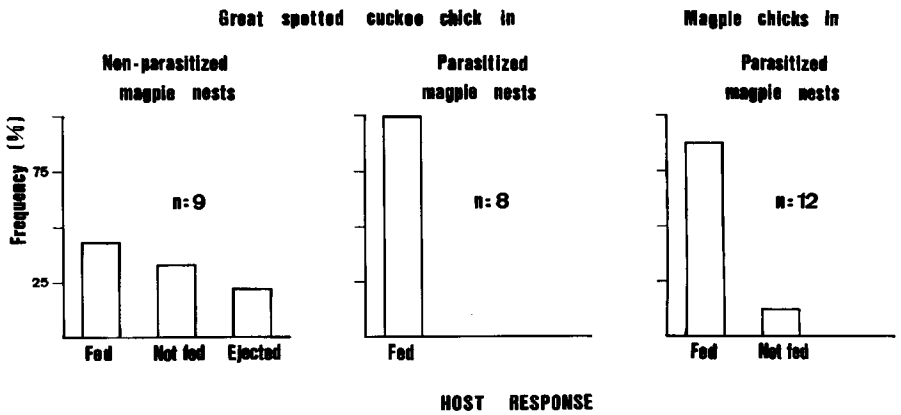

Fig. 3 Response of magpie parents to cross-fostered great spotted cuckoo chicks in unparasitized and parasitized magpie nests, and to alien magpie young in parasitized nests. Magpie responses as in Fig. 1. Only experimental chicks and nests of the third developmental stage (large nestlings with feathers) were used

log-likelihood ratio test, $G^2 = 5.01$, $df = 1$, $P < 0.05$). Experimental magpie chicks were neglected by magpies (not fed, ejected or attacked) in 64% of the tests outside the nest (Fig. 2), but only in 12% of the cases when introduced into the nest (Fig. 3; log-likelihood ratio test, $G^2 = 5.04$, $df = 1$, $P < 0.05$). These results suggest that magpies are more likely to tolerate alien nestlings within than outside the nest (hypothesis 2).

The discriminatory ability of magpie hosts was higher outside the nest when the alien young was a cuckoo chick (94%; Fig. 2) than when it was a magpie chick (64%; Fig. 2; log-likelihood ratio test, $G^2 = 3.82$, $df = 1$, $P = 0.05$). The cross-fostered magpie chick was more likely to be fed (37%) than the cross-fostered great spotted cuckoo chick (6%; Fig. 2; log-likelihood ratio test, $G^2 = 4.09$, $df = 1$, $P < 0.05$). This result is inconsistent with that predicted by the supernormal stimulus hypothesis (hypothesis 3, prediction a). Furthermore, the cross-fostered cuckoo chicks tended also to be fed at a lower frequency in unparasitized magpie nests than the cross-fostered magpie chicks in parasitized nests (44% and 88%, respectively; log-likelihood ratio test, $G^2 = 3.23$, $df = 1$, $P = 0.07$). Thus, magpies are more likely to tolerate alien magpie nestlings over cuckoo nestlings, which is also inconsistent with that predicted by the supernormal stimulus hypothesis (prediction b).

Our cross-fostering experiment (Fig. 3) showed that experimental cuckoo chicks in unparasitized magpie nests were neglected by magpies (not fed, ejected or attacked) (56%) significantly more often than they were in parasitized nests (0%; Fig. 3; log-likelihood ratio test, $G^2 = 6.07$, $df = 1$, $P < 0.05$). This supports hypothesis 4 and may indicate that a comparison between cuckoo and magpie nestlings is the basis of such discrimination (in six of eight cases only cuckoos were present in the nest, thereby preventing comparison of the appearance of magpie and cuckoo chicks). An alternative explanation is that, since magpies were not allocated to the two treatments randomly, the non-parasitized magpie treatment perhaps includes magpies that have already rejected cuckoos by means of better discriminatory abilities. However, given that the ejection of a cuckoo chick under natural conditions has never been recorded (see below), this alternative explanation is quite unlikely.

Discussion

Hosts that feed non-mimetic nestlings appear to behave non-adaptively. However, learning to recognize nestlings may not be adaptive when the cuckoo nestling remains alone in the nest (Lotem 1993). In host-parasite systems in which the parasite is reared along with the host young, nestling discrimination is adaptive (Lotem 1993) and in several cases has been found (Davies and Brooke 1988). Here we have shown experimentally in the magpie and great spotted cuckoo host-parasite system (where the cuckoo chick does not evict host eggs or nestlings) that magpies are able to discriminate against alien great spotted cuckoo chicks.

No discriminatory response was shown against featherless cuckoo chicks, which exhibited the best chick mimicry. However, magpies do not recognize featherless chicks of other species either, even if mimicry does not occur (Alvarez et al. 1976). Therefore, this cuckoo chick mimicry is not a response to magpie discrimination. The reason for cuckoo chick mimicry could be that originally the cuckoo chick was similar in appearance to magpie chicks.

The lack of discrimination against featherless cuckoo chicks could be because discrimination against unlike chicks usually (in the absence of parasitism) has no value while young are still in the nest. If hosts follow the rule "feed any chick in the nest", they behave adaptively, because it does not give rise to errors in chick recognition.

The results of our experiments were not consistent with those predicted by the supernormal stimulus hypothesis. The absence of feeding of cuckoos could simply result from the smaller parasite chick being unable to compete against its larger host nest-mates. However, this is not the case; in a previous study (Soler et al. in press b), we have shown experimentally that the cuckoo chicks operate as a supernormal stimulus.

The cuckoo chicks provide stronger stimuli for parental care, and they receive most of the food brought to the nest by the foster parents even though they may be smaller. However, in this study we have found that cuckoo chicks, when cross-fostered in unparasitized magpie nests were neglected by magpies at a higher frequency than magpie chicks fostered in parasitized magpie nests. Therefore, we conclude that the great spotted cuckoo does not provide a supernormal stimulus to its hosts in order to avoid recognition. There is also no evidence for a supernormal stimulus effect in European cuckoos (Davies and Brooke 1988, 1989a, b).

The discriminatory ability of magpies against cuckoo chicks is better in unparasitized than in parasitized nests (Fig. 3). This result supports the hypothesis that magpies learn to recognise their own nestlings as those present in the nest, and that this comparison is the basis for discrimination. Parents evidently learn the "signatures" of the chicks present in the nest and do not always accept an alien chick if it is different from those already present in the nest. The ability of magpies to discriminate against alien cuckoo chicks was higher when (1) a well-developed cuckoo chick was introduced into a magpie nest containing featherless chicks, and (2) when both the cross-fostered cuckoo and the magpie chick were well developed (Fig. 1). In the first case, discrimination may simply be due to the fact that the magpie is able to compare its very small young with a very big chick suddenly appearing in its nest. In the second case, the discrimination rate might have been higher because, as many cross-fostering experiments have shown, parents learn the features of their young at the end of the nestling period, usually shortly before fledging (Beecher et al. 1981; Beecher 1988; Lessells et al. 1991; Medvin et al. 1993). The important question is whether the magpie's discriminatory ability has evolved as a response to cuckoo parasitism. Recognition of chicks by their parents develops in species in which parents are likely to confuse the identity of their offspring (Stoddard and Beecher 1983; Medvin and Beecher 1986). In the magpie, a solitary and territorial species in which fledglings are cared for by the parents in a large territory (Birkhead 1991), the most important selection pressure for recognition appears to be parasitism by the great spotted cuckoo. This conclusion is also supported by the fact that the ability of magpies to discriminate against alien cuckoo chicks was always higher than against alien magpie chicks (Figs. 2 and 3).

Under natural conditions we have never recorded the ejection of a healthy cuckoo chick ($n = 327$ parasitized nests; data from 1982–1993). Only starved chicks disappear from a magpie's nests, and cuckoo nestlings starved only in magpie nests suffering from multiple parasitism (Soler 1990; Soler et al. in press a). This absence of discrimination in nature perhaps occurs because magpies learn the signatures of all the young present in the nest. Alternatively, magpie hosts might be able to recognize cuckoo chicks, but accept parasitic chicks because of enforced parasitism by the cuckoos (this "mafia" hypothesis suggests that, if the host ejects the parasite egg, the parasite will prey upon the host nestlings; Zahavi 1979). Great spotted cuckoos appear to enforce parasitism on magpie hosts in our study area (Soler et al. in press c). Enforced parasitism could thus increase the cost of chick discrimination. The great spotted cuckoo is therefore one step ahead in the coevolutionary arms race because of the ready acceptance of cuckoo chicks. This step is very difficult for hosts to counter.

In cases where parasite and host nestlings are reared together, two very important factors prevent the evolution of discrimination. First the time taken for discrimination to spread through the host population will decrease as the parasitism rate increases because selection presures are stronger. Second, the frequency at which host nestlings survive to fledging prevents the evolution of discrimination because the costs of misimprinting may outweigh the benefits of correct learning when host nestlings fail to survive at a high frequency (Lotem 1993). In our host-parasite system, an average of 0.35 magpie chicks fledged in parasitized nests (Soler 1990; Soler et al. in press a). The chick survival rate is not sufficiently high to suggest that magpie discrimination against cuckoo chicks will soon appear, even considering that the parasitism rate is more than 50% (Soler et al. in press a). The reasons why magpies do not discriminate against cuckoo chicks are that (1) the mafia mechanism of enforced parasitism is working (Soler et al. in press c), and (2) nestling discrimination is mainly found in host-parasite systems where parasitism causes little or no mortality among host young (Rothstein 1990; Lotem 1993).

If cuckoos and their hosts are involved in a continuing arms race, it would be expected that discrimination against parasite chicks at the beginning of the nestling period would evolve since the cost of misimprinting is higher during later stages. The discriminatory capacity of hosts may also be related to the level of mimicry by the cuckoo chicks, which may have evolved due to host recognition (see above). The degree of mimicry by great spotted cuckoo chicks decreased with increasing age (Lack 1968; personal observations). If we prevented the learning of offspring phenotypes by magpies (experiments 1 and 2), we found that the recognition of alien cuckoo chicks increased with their age. In a number of cases in previous years we have placed alien magpie nestlings in both parasitized and unparasitized magpie nests containing nestlings in a similar developmental stage. None of these ($n = 35$) nestlings were ever ejected by the nest owners. Therefore, cuckoos were exploiting the effects of learning of chick phenotypes by magpie hosts, and the mafia mechanism could simultaneously delay the evolution of chick ejection. This might explain why we have never recorded natural cases of chick ejection.

In summary, our results show that the great spotted cuckoo chick does not provide a supernormal stimulus to magpies to avoid chick recognition, and that magpies are able to discriminate cuckoo chicks introduced into their nests. Cuckoos exploit the obligatory reaction of magpies to feed all young that have been hatched in their nests and whose signatures they have learnt.

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