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# Nestling discrimination without recognition: a possible defence mechanism for hosts towards cuckoo parasitism?

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**One of the great evolutionary puzzles is why hosts of parasitic birds discriminate finely against alien eggs, but almost never discriminate against parasitic chicks. A theoretical model has shown that an adaptive host response to alien eggs can be based on learning. However, learned nestling discrimination is too costly to be favoured by selection in hosts of evicting parasites, such as the European cuckoo (*Cuculus canorus*). Indeed, parasitic chick rejection has never been reported for any European cuckoo host species. As learned nestling discrimination is maladaptive, one can expect that a viable alternative for hosts would be to use discrimination mechanisms not involving learning and/or recognition. We suggest that hosts may starve and desert cuckoo chicks that require higher amounts of food than an average host brood at fledging (i.e. feeding rates to a parasite are outside the normal range of host behaviour in unparasitized nests). Our observations of the reed warbler (*Acrocephalus scirpaceus*) at parasitized nests indicate that such behaviour could possibly work in this host species.**

**Keywords:** brood parasitism; *Cuculus canorus*; rejection; coevolution; nestling discrimination; recognition

## 1. INTRODUCTION

Coevolution between brood parasites and their hosts has resulted in some of the best examples of adaptations, for example, egg mimicry in bird parasites (Moksnes & Røskaft 1995) and egg recognition and rejection in their hosts (Davies & Brooke 1989). On the other hand, parasite–host systems provide examples of some behaviours perceived by researchers as clearly maladaptive, for example, discrimination of parasitic nestlings is extremely rare (Nicolai 1974; Fraga 1998; Lichtenstein 2001) despite fine host ability to discriminate against sometimes well-mimetic parasitic eggs (Redondo 1993). Noticeably, in general, all hosts of the European cuckoo show at least some rejection of parasitic eggs, but a host species has never been shown to reject parasitic nestlings (Davies & Brooke 1989).

A simple theoretical model (Lotem 1993) showed that an adaptive host response to parasitic eggs can be based on learning the appearance of eggs in a host's nest. However, learned nestling discrimination is too costly to be favoured by selection when a parasite evicts the host's offspring (e.g. European cuckoo, *Cuculus canorus*) (but see Langmore *et al.* 2003). Thus, it would be logical to expect that a more adaptive alternative for hosts would be to use a discrimination mechanism that does not involve learning and/or recognition. During our research on interactions between the European cuckoo and its most common host, the reed warbler (*Acrocephalus scirpaceus*), we obtained tentative support for the hypothesis that such antiparasitic behaviour could work in this host.

## 2. MATERIAL AND METHODS

We studied interactions between the reed warbler and the cuckoo during the period 1984–2002, in the southeastern region of the Czech Republic (47°40′ N, 16°48′ E). Reed warblers were parasitized by the cuckoo at a relatively high rate (15.0%; Øien *et al.* 1998). Detailed descriptions of the study area and field procedures are presented elsewhere (Øien *et al.* 1998; Kleven *et al.* 1999; Grim & Honza 2001). We investigated parental care by reed warblers in terms of feeding frequencies (number of feedings per hour) and feeding rates (amount of dried food in milligrams delivered per hour). Food samples were collected with a neck-collar (see Grim & Honza 2001). We observed 109 cuckoo nestlings.

## 3. RESULTS

Hosts increased their feeding rates to cuckoo chicks significantly from hatching (day 0) until day 11 post-hatch (11 days is the fledging period of host chicks) (linear regression: $R^2 = 0.66$, $F_{1,24} = 46.22$, $p < 0.0001$). A cuckoo chick at 11 days of age receives 1.4 times more food than an average host brood (3.3 chicks) of the same age (feeding rates (mean ± s.d.) to one chick: reed warbler = 47.8 ± 22.2 mg h$^{-1}$, $n = 14$; cuckoo = 217.1 ± 54.8 mg h$^{-1}$, $n = 11$). Reed warblers did not increase feeding rates from day 12 to day 15 (linear regression: $R^2 = 0.13$, $F_{1,13} = 1.84$, $p = 0.20$). However, at four nests (out of 57) the reed warbler pairs decreased their feeding frequencies to old (more than 12 days old) cuckoo nestlings (nestlings were fed at normal frequencies when 11–12 days old, with 13–26 feedings per hour) and finally stopped feeding them (hereafter defined as desertion) despite a high begging activity in parasitic nestlings. Both parents were always active at the nest (parents were not colour-banded, but we assumed that birds regularly visiting the particular nests are its owners), i.e. starvation could not be caused by the death of one of the parents and insufficient provisioning by the second mate. Moreover, at one of these nests fosterers removed nest material from the parasitized nest and began to build a new nest nearby (*ca.* 2 m away), while the cuckoo chick was still begging. Nestlings died when 14.8 ± 1.0 (mean ± s.d.) days old. Another four cuckoo nestlings died in their nests at the same age (14.3 ± 1.0 days). Nest predation was ruled out as nestlings showed no sign of injuries. All nestlings that were found dead grew normally until day 11 and only later decreased their growth in comparison with successfully fledged chicks (table 1). Moreover, we found one 15-day-old nestling in another nest deserted by its foster parents and two same-age nestlings dead below their nests. In the two latter cases, chicks could simply fall out of the nest because of high activity and are not included in the desertion rate, which was 15.8% (nine out

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Table 1. Mass (g) of cuckoo nestlings that successfully fledged or were deserted by reed warbler hosts.
(Only chicks found within 24 h after hatching (day 0) are included. Growth was measured as (i) mass (g) at a particular age, and (ii) the slope of a regression line of mass (g) against age for each individual nestling. Mean ± s.e. and *p*-values for Mann–Whitney tests are shown.)

| age (days) | fledged ($n = 23$) | deserted ($n = 3$) | $p$ |
|---|---|---|---|
| 0 | 2.9 ± 0.1 | 2.8 ± 0.2 | 0.629 |
| 11 | 53.4 ± 1.0 | 53.7 ± 2.3 | 0.873 |
| 14 | 63.2 ± 1.1 | 48.3 ± 2.7 | 0.007 |
| slope for days 0–11 | 4.7 ± 0.1 | 4.8 ± 0.3 | 0.873 |
| slope from day 12 onwards | 1.9 ± 0.3 | –4.9 ± 0.7 | 0.006 |

of 57 nestlings that survived until fledging or desertion). We did not observe any desertions of unparasitized broods and there were no weight declines in any of the host broods studied ($n = 57$).

## 4. DISCUSSION

We propose that hosts 'discriminated' against parasitic nestlings by not being willing to increase their parental effort above the level designed by selection for the needs of their own nestlings. This is indicated by the fact that cuckoos were fed with increasing amounts of food only until the age of 11 days, which is the time when the host's own young usually fledge. Later, feeding frequencies levelled off (fledged cuckoos) or decreased (deserted cuckoos). Feeding rates to fledged cuckoos in our study were very similar to those reported by Kilner *et al.* (1999).

Cuckoo chicks in reed warbler nests both have a longer nestling period (18 versus 11 days for host chicks) and require more food than an average-sized host brood when 8 days old or older. Both these factors (time and amount of care) could potentially be used as cues by hosts to stop further investment. Moreover, reed warblers feeding a cuckoo chick that overgrew their average-sized brood at fledging reduced their selectivity of foraging behaviour. This was indicated by a decreasing average size of food items delivered to large parasitic nestlings (Grim & Honza 2001). This could result from physiological changes (e.g. exhaustion) serving as proximate cues for restricting parental care to large cuckoo nestlings (Holen *et al.* 2001). The hypothesis that increased parental effort can lead to desertion has been supported experimentally in the puffin (*Fratercula arctica*) (Johnsen *et al.* 1994). Our observations are consistent with a hypothesis suggesting that if a mutant host parent never increases its feeding rate above a fixed threshold, it would effectively starve the super-demanding parasite and at the same time satisfy the needs of its own offspring (Holen *et al.* 2001).

The host desertion behaviour could be a by-product of physiological constraints. However, if there was any genetically determined variation in the individuals' willingness or ability to care for their brood then selection would favour individuals not willing or able to provide care above the level required by an average host brood. This hypothesis predicts that hosts in areas sympatric with the parasite should provide more constrained parental care (length and/or amount of care) than those in allopatry. The same is predicted for among-species differences—regular cuckoo hosts should be less willing to care for broods for prolonged periods than species unsuitable as fosterers.

Observations that host behaviour, under natural conditions, can lead to parasitic chicks' death are very rare—they are reported only for three host–parasite systems (Fraga 1998; Lichtenstein 2001; Langmore *et al.* 2003). All other cases of nestling discrimination in parasitic birds were elicited under unnatural experimental conditions (Redondo 1993; Soler *et al.* 1995), or are indirectly inferred from the similarity between parasitic and host nestlings (reviewed in Redondo 1993). In other cases hosts attacked parasitic fledglings, but these successfully prevented hosts from discrimination by intense begging (see Redondo 1993). Estrildid hosts have an ability to discriminate against their *Vidua* parasites (Nicolai 1974), but under natural conditions, parasites prevent rejection by mimicking host nestlings.

Cuckoo nestlings are unlikely to respond to the selection pressure, resulting from host desertion, increasing their growth and shortening their nestling period. Age at fledging is probably genetically fixed in the cuckoo, as parasitic chicks fledge at the same age in both reed warbler and great reed warbler (*Acrocephalus arundinaceus*) hosts, despite the fact that they grow more slowly and weigh significantly less in nests of the former (Kleven *et al.* 1999). Reed warbler cuckoos are probably growing at the maximum rates allowed by the host's foraging abilities.

Nestling desertion by reed warblers is probably not a result of host nestling recognition ability. Reed warblers readily feed nestlings of several other species introduced into their nests (Davies & Brooke 1988, 1989; Davies *et al.* 1998). Discrimination may work simply because the cuckoo nestling period is much longer than that of the host. Deserting a cuckoo chick before fledging is more costly than egg ejection or desertion at earlier stages of the nesting cycle. However, it is less costly than rearing a parasite until independence. Hosts deserting cuckoo nestlings would gain important advantages: the benefit of potential re-nesting and no costs of prolonged (four extra weeks) care for the parasite. Deserters could also benefit from a better survival in comparison to acceptors (trade-off between current and future reproduction). The fact that a cuckoo nestling is probably unable to respond to this host behaviour by accelerating its growth due to developmental constraints (see above) might potentially also affect the coevolutionary process.

Importantly, our observations indicate that hosts are not forced to accept a cuckoo chick due to its supernormal begging (as previously believed; Redondo 1993) and can respond to cuckoos in a way that releases them from prolonged care for a parasite. Further, reed warbler chick discrimination cannot lead to the evolution of parasitic chick mimicry because discrimination is not based on recognition (similarity of parasitic and host nestlings would not prevent a host from discrimination). Nestling desertion (16%) is relatively rarer than egg rejection (38%; Øien *et al.* 1998) in our study population. This can be due to the relatively low benefits of chick rejection (in comparison to egg rejection), low selection pressure from cuckoos (because of egg rejection by hosts and high predation, less than 5% of hosts experience 11-day-old or older cuckoo chicks) or being an evolutionary novelty. However, we cannot exclude that a similar behaviour is also present or even common in other host species, as virtually no studies have focused on the cuckoo fledging period in any host species so far.

Our observations indicate that more research should focus on host responses to parasitic nestlings during the critical period before fledging (see Redondo 1993). The behaviour of reed warblers towards old cuckoo chicks indicates that some hosts could discriminate against parasitic nestlings even without recognizing them. This gives an interesting impetus for future research on this fascinating issue.

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