

The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare?

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ABSTRACT

Question: Why do hosts of parasitic birds defend against parasitic eggs but not nestlings?

Data incorporated: Reported cases of parasitic chick discrimination or mimicry and all previously published explanations for the rarity of these phenomena.

Method of analysis: Contrasting the predictions of previous hypotheses and fitting available data from both parasitic and non-parasitic birds to assess the relative validity of each explanation.

Results: None of the previously suggested hypotheses appears to provide a general explanation for the scarcity of chick discrimination. Various cognitive and behavioural traits potentially usable for discrimination of parasitic chicks are present in virtually all avian taxa, including host lineages, yet these traits are not used to reject parasites. Thus, low selection pressure imposed by rare parasites is the most likely general explanation for the absence of these adaptations in the context of brood parasitism. Based on this, I predict that nestling discrimination and mimicry should predominantly evolve in hosts that are forced to accept parasite eggs because of the close match between parasitic and host eggs. This is likely to occur due to egg mimicry or phylogenetic and physical constraints. I demonstrate that available evidence is in line with this rare parasite hypothesis.

Conclusion: A host's own behaviour may play a crucial role in retarding the escalation of the arms-race to the nestling stage.

Keywords: arms-race, brood parasitism, co-evolution, discrimination, evolutionary equilibrium, evolutionary lag, recognition.

INTRODUCTION

The apparent absence of adaptations in response to strong selection pressures is puzzling. One widely discussed example is the lack of nestling discrimination by most hosts of parasitic birds – both scientists and laypersons wonder at the picture of a miniature passerine feeding a huge cuckoo chick (Rothstein and Robinson, 1998; Davies, 2000). On the one hand, many hosts of parasitic birds evolved very fine discrimination against parasite adults

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(Sealy *et al.*, 1998) and eggs (Davies, 2000). On the other hand, parasitic nestling discrimination has been documented only a few times (Soler *et al.*, 1995a; Fraga, 1998; Lichtenstein, 2001a; Payne *et al.*, 2001; Grim *et al.*, 2003; Langmore *et al.*, 2003). This rarity of nestling discrimination is even more enigmatic because other phenotypic changes and behavioural traits involved in arms-races (Dawkins and Krebs, 1979) between brood parasites and their hosts provide textbook examples of adaptations and co-evolution [e.g. egg mimicry by cuckoo host races (Alcock, 1998; Futuyma, 1998)].

In this review, I summarize current evidence for nestling discrimination by host parents and discuss all proposed explanations for the ‘rarity of chick discrimination’ enigma. I will argue that the previous explanations are applicable only under limited circumstances and will propose a general hypothesis that applies to all host–brood parasite systems.

AVAILABLE EVIDENCE FOR CHICK DISCRIMINATION

By ‘recognition’ I mean the internal process that can [but need not (see Sherman *et al.*, 1997; Soler *et al.*, 1999; Mateo, 2002)] lead to behavioural discrimination. By ‘discrimination’ and ‘rejection’ I mean the behavioural acts of differential response to two stimuli (Beecher, 1991). Furthermore, I differentiate between ‘nestling rejection’, which always results in nestling death (e.g. nest desertion or chick removal), and ‘nestling discrimination’, which does not (e.g. differential parental allocation of food within a parasitized brood). While nestling rejection is a specific co-evolved response to parasitism, nestling discrimination may also result from an inability of parasitic chicks to communicate their state of hunger effectively to fosterers.

Clear-cut cases of chick rejection are scarce (Table 1). Langmore *et al.* (2003) reported that Australian superb fairy-wrens *Malurus cyaneus* deserted 40% of nests with Horsfield’s bronze cuckoo *Chrysococcyx basalis* and all nests with the shining bronze cuckoo *Ch. lucidus*. This host behaviour selected for nestling vocal mimicry in Horsfield’s bronze cuckoos (Langmore *et al.*, 2003). African estrildids are parasitized by mimetic *Vidua* finches and discriminate against alien nestlings other than those of their particular mimetic parasite (Nicolai, 1964; Payne *et al.*, 2001; Schuetz, 2005).

South American bay-winged cowbirds *Agelaioides badius* discriminate fledglings of the generalist parasite the shiny cowbird *Molothrus bonariensis*, but rear chicks of the specialist parasite the screaming cowbird *M. rufoaxillaris* (Fraga, 1998; Lichtenstein, 2001b). Shiny cowbird chicks grow normally in the nests of this host but are provisioned very poorly after fledging and usually do not survive more than 24 h outside host nests. In contrast, screaming cowbird fledglings are provisioned fully and appear very similar to host bay-wing fledglings. This indicates that similarity of bay-winged and screaming cowbird chicks is mimetic (Grim, 2005). The low success of shiny cowbird chicks – almost 70% of chicks starve to death – in nests of rufous-bellied thrushes *Turdus rufiventris* also involves active parental discrimination to favour own versus parasitic chicks (Lichtenstein, 2001a).

Levaillant’s cuckoo *Clamator levaillantii* has a begging call resembling the vocalizations of host young, the arrow-marked babbler *Turdoides jardineii* (Mundy, 1973). Fosterers sometimes attack the cuckoo but not host young in fledged broods; however, when the cuckoo begins to beg, the hosts stop the attacks and start to feed the parasite (Redondo, 1993; Payne, 2005 and references therein). These behavioural interactions clearly indicate that the babbler host is able to discriminate against the parasite and the Levaillant’s cuckoo chick is able to effectively counter the discrimination with calls mimicking those of the host’s own young.

Reed warblers *Acrocephalus scirpaceus* deserted 15% of older common cuckoo *Cuculus canorus* chicks in a study area in the Czech Republic (Grim *et al.*, 2003). Reed warblers

Table 1. Overview of host–parasite systems with reported cases of chick rejection/discrimination or mimicry

Host	Parasite	Natural egg rejection rate (%)	Evictor parasite	References
<i>Malurus cyaneus</i>	<i>Chrysococcyx basalis</i> , <i>Ch. lucidus</i>	0	+	Langmore <i>et al.</i> (2003)
Estrilidae spp.	Viduae spp. ^a	0	–	Nicolai (1964, 1974), Payne <i>et al.</i> (2001)
<i>Agelaioides (Molothrus) badius</i>	<i>Molothrus rufoaxillaris</i> , <i>M. bonariensis</i>	0	–	Fraga (1998), Lichtenstein (2001b)
<i>Turdus rufiventris</i>	<i>Molothrus bonariensis</i>	0	–	Lichtenstein (1998, 2001a)
<i>Turdoides jardineii</i>	<i>Clamator levaillantii</i>	0 (?) ^b	–	Mundy (1973), Steyn (1973)
<i>Acrocephalus scirpaceus</i>	<i>Cuculus canorus</i>	38	+	Grim <i>et al.</i> (2003)
<i>Prunella modularis</i>	<i>Cuculus canorus</i> ^c	0	+	Davies and Brooke (1989)
<i>Gerygone igata</i>	<i>Chrysococcyx lucidus</i>	0	+	McLean and Waas (1987), Gill (1998), McLean and Maloney (1998)
<i>Corvus splendens</i>	<i>Eudynamys scolopacea</i>	0	– (India)	Dewar (1907)
Ploceidae spp.	<i>Chrysococcyx caprius</i>	0 (?) ^b	+	Reed (1968)
<i>Molhoua</i> spp.	<i>Urodynamis taitensis</i>	0 (?)	+	McLean and Waas (1987)
<i>Turdoides</i> spp. (India)	<i>Clamator jacobinus</i>	0 (?) ^b	–	Jourdain (1925), Lack (1968), Gaston (1976)
<i>Psarocolius</i> spp., <i>Cacicus</i> spp.	<i>Scaphidura (Molothrus) oryzivora</i>	^d	–	Smith (1968), Webster (1994), Ortega (1998), Cunningham and Lewis (2005)

Note: Systems are listed according to quality of evidence from direct to circumstantial. ‘0 (?)’ = the available evidence suggests that hosts are either pure acceptors or reject natural parasitic eggs only very weakly. See text for details.

^a Includes approximately 15 host–parasite species pairs where mimicry evolved independently (Davies, 2000).

^b Parasitic eggs are reported to be a very good match for host eggs (Davies, 2000; Payne, 2005), thus rendering egg rejection unlikely.

^c Cross-fostering study with *Fringilla coelebs* chicks (see text for details).

^d Giant cowbird hosts’ responses to parasite eggs are strongly specific for a particular host-breeding colony (Smith, 1968) and the parasite evolved highly mimetic eggs (see Figure 1 in Smith, 1968; but for detailed discussion, see Ortega, 1998, pp. 108–113).

discriminate parasitic cuckoo chicks by restricting their parental care at the nest to about 14 days, which is enough time to rear their own nestlings (which fledge when 10–11 days old) but not enough time to rear the cuckoo nestlings (which fledge when 18–21 days old). In this system, discrimination does not involve chick recognition (Grim *et al.*, 2003) and the cue triggering this ‘discrimination without recognition’ behaviour is the duration of parental care (T. Grim, unpublished data). Neither the intensity of this care nor the presence of a single chick in the nest could explain desertions (T. Grim, unpublished data).

Davies and Brooke (1989) cross-fostered chaffinch *Fringilla coelebs* chicks to dunnoek *Prunella modularis* nests. Chicks either disappeared or grew subnormally, while host young survived well. This may indicate some sort of parental discrimination against alien chicks (see later for discussion).

Indirect but suggestive evidence for parasitic chick discrimination and chick mimicry was found for host grey warblers *Gerygone igata* versus parasitic shining bronze cuckoos (McLean and Waas, 1987; Gill, 1998), and host house crows *Corvus splendens* versus parasitic koel *Eudynamis scolopacea* (Dewar, 1907; Payne, 2005 and references therein). Parasitic chick appearance and begging varies geographically with the appearance of host nestlings in these systems. Additionally, the begging calls of the diederik cuckoo *Chrysococcyx caprius* covary with begging calls of its various hosts (Reed, 1968), suggesting a response to host discrimination. McLean and Waas (1987) also described noticeable similarity of begging calls of host *Mohoua* spp. versus the parasitic long-tailed cuckoo *Urodynamis taitensis* chicks.

Jourdain (1925) and Lack (1968) made a case for chick mimicry in the Jacobin cuckoo *Clamator jacobinus* and the great spotted cuckoo *Clamator glandarius* (see also Mundy, 1973). Accordingly, in the Jacobin cuckoo Gaston (1976) reported that host ‘babblers began to lose interest in the young cuckoo in the last few days before it left the nest’ (p. 334) and mentioned cases when a cuckoo fledgling was ignored by its fosterers. For the great spotted cuckoo, Redondo (1993) and Soler *et al.* (1995a) reported experimentally induced rejection of parasitic chicks by magpie *Pica pica* hosts. However, discrimination of foreign chicks does not occur under natural conditions and therefore cannot select for any chick mimicry (for a discussion, see Grim, 2005).

Giant cowbird *Scaphidura (Molothrus) oryzivora* nestlings are similar to nestlings of their oropendola (*Psarocolius* spp.) and cacique (*Cacicus* spp.) hosts but the morphological similarity disappears after parasite chicks gain independence from fosterers, which is suggestive of mimicry (Redondo, 1993). Unfortunately, hosts’ responses to parasite chicks are unknown.

Geographical variation in rictal flange colour of brown-headed cowbird *Molothrus ater* nestlings was hypothesized to reflect chick rejection and/or discrimination by hosts (Rothstein, 1978). However, there is no evidence that any hosts of that parasite adjust their provisioning rates according to rictal flange colour (Ortega, 1998). Thus, the geographical variation among subspecies of the brown-headed cowbird more likely resulted from non-adaptive evolutionary processes, namely founder effects or random drift.

Davies and Brooke (1988, table XVI) included the cuckoo finch *Anomalospiza imberbis* in their list of mimetic parasites. However, there is no resemblance between the parasitic cuckoo finch young and host cisticola (*Cisticola* spp.) and prinia (*Prinia* spp.) offspring (Davies, 2000, p. 23). [For more details on chick discrimination and mimicry in general, see Redondo (1993) and Grim (2005).]

In general, host behaviour towards parasitic chicks has received limited attention in observational or experimental studies. The absence of evidence is not evidence of absence,

thus it is possible that chick discrimination and rejection are more common than available evidence indicates. However, there are theoretical reasons to expect host defences against alien nestlings to be rarer than adaptations against alien eggs. I will discuss these reasons in the framework of evolutionary lag, proximate constraints, host exploitation, and evolutionary equilibrium hypotheses (Table 2).

THE EVOLUTIONARY LAG HYPOTHESIS

The evolutionary lag hypothesis suggests that no rejecter mutations are present in the host gene pool or that such mutations have not yet spread (Rothstein, 1982; Hosoi and Rothstein, 2000).

Failure to respond to selection

Mutations are by definition random with respect to possible adaptive improvement (Futuyma, 1998, p. 282). In general, natural selection requires heritable variation correlated with fitness variation, and there is no guarantee that such variation exists. The absence of such variation may even lead to extinction (Futuyma, 1998, p. 713).

Table 2. Overview of hypotheses on nestling discrimination in hosts of parasitic birds

Hypothesis	References
The evolutionary lag hypothesis	
Failure to respond to selection	Rothstein (1975, 1982), Kemal and Rothstein (1988)
Lack of pre-adaptations	Redondo (1993)
The proximate constraints hypothesis	
Physical insufficiency	This study (cf. Rohwer and Spaw, 1988)
Cost of misimprinting	Lotem (1993), Lawes and Marthews (2003)
Variability of chick appearance	Davies and Brooke (1989), McLean and Maloney (1998)
Instability of chick appearance	Davies and Brooke (1989)
Absence of comparative material	Davies and Brooke (1989)
The host exploitation hypothesis	
Exploitation of pre-existing adaptive behaviour	Redondo (1993)
Supernormal stimulus	Dawkins and Krebs (1979), Soler <i>et al.</i> (1995a), Grim and Honza (2001)
The evolutionary equilibrium hypothesis	
Mafia	Soler <i>et al.</i> (1995b), Soler and Soler (1999)
Beneficial parasitism	Smith (1968), Webster (1994)
Handicap principle	Zahavi and Zahavi (1997)
Low benefits after eviction of host brood	Davies and Brooke (1989), Lotem (1993)
Low parasitism rate	This study
Parasitic egg rejection by a host	This study

Note: Selected papers on the particular hypothesis in the References column include also those arguing against particular hypotheses. See text for details.

Some acceptor hosts of the brown-headed cowbird have been in contact with the parasite for a long time and show various pre-adaptations (large nests, large bills, eggs dissimilar to those of cowbirds) known to facilitate the evolution of egg rejection. Yet, phylogenetically close species have evolved egg rejection (Peer and Sealy, 2004). In the absence of any apparent constraints (but see Hauber *et al.*, 2004) on the evolution of egg rejection, we are left with only one explanation: chance plays an important role in evolution (Rothstein, 1975, 1982). Kemal and Rothstein (1988) supported this idea by showing that acceptors are able to differentiate between broken and intact eggs and to eject broken eggs, but they are unable to use this behaviour in the context of brood parasitism even when heavily parasitized (Hauber, 2003). Similarly, dunnocks are able to remove dead chicks from their nests but accept both cuckoo eggs and nestlings (Davies and Brooke, 1989; but see later). What is probably lacking is a mutational change in their decision-making mechanisms (see also Sherman *et al.*, 1997; Hauber and Sherman, 2001).

Lack of pre-adaptations

The lack of any adaptation may in principle be explained by a lack of suitable pre-adaptations. A quantitative change in an existing behaviour is more probable than the emergence of a qualitatively new behavioural pattern (Dawkins, 1982; Hosoi and Rothstein, 2000). For example, nest desertion in response to brood parasitism is easy to evolve because it requires only a small change in triggering of pre-existing desertion behaviour that evolved in response to various nest intruders and predators (Hosoi and Rothstein, 2000). Similarly, the evolution of egg ejection is a logical extension of nest sanitation behaviour (Rothstein, 1975, Moskát *et al.*, 2003).

In contrast, Redondo (1993, p. 248) argued that nestling rejection could not be expected to evolve from sanitation behaviour because parents only remove dead nestlings from their nest – ejection of living nestlings would be strongly selected against when signs indicate that chicks are healthy. However, the ejection of living eggs must also be strongly selected against when there are signs that eggs are ‘healthy’ (unbroken). There is no reason to assume that parents can remove eggs if they carry new stimuli (cracks when they are broken or different colour when they are parasitic) and simultaneously claim that they cannot do the same with nestlings. In fact, removal of living nestlings in passerines has been observed (Robertson and Stutchbury, 1988; Møller, 1992). Thus, in addition to nest sanitation behaviour (*contra* Redondo, 1993), brood reduction (Clotfelter *et al.*, 2000), offspring desertion (Székely *et al.*, 1996), and infanticide (Crook and Shields, 1985; Møller, 1992) could provide behavioural pre-adaptations for an adaptive response to parasite nestlings.

Most importantly, currently there are no methods available to test whether there has been insufficient time or frequency of beneficial mutations to improve host pre-adaptations. Thus, the evolutionary lag hypothesis can be considered as an explanation of the last resort (Davies, 2000; Hosoi and Rothstein, 2000). Therefore, I pay more attention to other, testable explanations.

THE PROXIMATE CONSTRAINTS HYPOTHESIS

Various physical and cognitive constraints may affect evolution of chick discrimination (Table 2). For other constraints that apply to both egg and chick rejection, see Grim (2002, table 1).

Physical constraints

Theoretically, a host might reject a parasitic egg but accept a parasitic chick because the chick is much heavier than an egg to eject [for physical constraints on egg rejection, see Rohwer and Spaw (1988), Røskoft *et al.* (1993)]. Such a behaviour may be adaptive in hosts of non-evicting parasites where at least some host chicks survive to fledging despite the competition for food with a parasitic chick (Davies, 2000). However, even small birds can remove both relatively large (e.g. Davies and Brooke, 1989) and living (e.g. Robertson and Stutchbury, 1988; Møller, 1992) nestlings of other pairs from their nests. Some fosterers may refuse to feed experimentally cross-fostered nestlings and even peck them to death (Holcomb, 1979; Redondo, 1993; Soler *et al.*, 1995a).

One could argue that chick ejection by hosts of the common cuckoo would provide little benefit, as cuckoo chicks evict host eggs and nestlings. However, a substantial delay between hatching and the start of eviction of the host's eggs/nestlings by the cuckoo chick [mean 20.5 h in the nests of the reed warbler (M. Honza and K. Voslajerova, unpublished data)] allows enough time to recognize and eject a parasitic chick. Thus, the main problem for a host is presumably not the physical removal of the parasitic chick *per se*, but the recognition of parasitic nestlings.

Learning constraints

Egg recognition in some bird species may be learned by an imprinting-like process (Lotem *et al.*, 1992, 1995; see also Victoria, 1972; Rothstein, 1974). Such behaviour would be adaptive even when the host is parasitized during its first breeding attempt (Lotem, 1993). In contrast, imprinting on nestling appearance is not adaptive in hosts of evicting parasites because the only object for the host to imprint on would be the parasite (Lotem, 1993) [but it may be adaptive in hosts of non-evicting parasites (see Lawes and Marthews, 2003)].

Nevertheless, in various birds first-year naive breeders are already able to reject alien eggs, which indicates that imprinting is not a universal basis for egg recognition (Davies and Brooke, 1988; Stokke *et al.*, 1999; Marchetti, 2000; Soler *et al.*, 2000, 2004; Amundsen *et al.*, 2002; see also Mark and Stutchbury, 1994, for recognition of adult parasites by first-time breeding females). Thus, Lotem's hypothesis can be viewed as an argument about cognitive constraints in a few host species where parents learn chick appearance.

Redondo (1993, p. 240) stated that in species that reject alien eggs there are no obvious reasons why hosts should not use 'an already existing set of egg recognition mechanisms' to reject parasite chicks. However, the validity of this argument is limited for two reasons.

First, in hosts where discrimination is learned naive breeders tend to accept more parasitic eggs than old breeders who tend to reject alien eggs (Lotem *et al.*, 1992, 1995). Therefore, old hosts that have 'an already existing set of egg recognition mechanisms' (Redondo, 1993) would have only a poor chance of facing the young cuckoo because the parasite was probably destroyed at the egg stage. In contrast, naive breeders that perform poorly in egg discrimination should also perform poorly in nestling discrimination [based on the assumption that egg and nestling discrimination mechanisms are similar (Redondo, 1993)]. Thus, situations when the parasitic nestling could potentially be rejected should be very rare – both in naive and experienced breeders. Consequently, the selection for chick mimicry would be very weak despite the existence of host egg discrimination abilities. To make things worse for the host species, there are good reasons to expect that young naive breeders may be parasitized more frequently than old experienced individuals (Brooker and Brooker, 1996; Grim, 2002).

Second, in hosts with innate discrimination (i.e. independent of experience), different sensory modalities may serve recognition of eggs versus nestlings. Eggs may be recognized by visual or tactile cues (Langmore *et al.*, 2005), while nestling discrimination is more likely based on vocal cues (Langmore *et al.*, 2003). Thus, ‘an already existing set of egg recognition mechanisms’ (Redondo, 1993) would be again unavailable for chick discrimination. If both egg and chick discrimination were based on the same cues (e.g. visual), then even a naive host would have a poor chance of facing the parasite chick due to the temporal order of its innate defences (i.e. the parasite would be killed at the egg stage, thus leaving nothing to be discriminated at the chick stage).

Chick variability constraint

McLean and Maloney (1998) suggested that low interspecific variability of physical appearance of altricial nestlings would lead to unacceptably high recognition costs in chick rejecters. However, birds are capable of well-developed discrimination of individual conspecifics [e.g. their offspring (Beecher *et al.*, 1981)] based on intraspecific variation, not to speak of interspecific discrimination. Even when such discrimination takes place at a later developmental stage (fledging), differences between two host offspring at *any* stage are surely much smaller than differences between parasitic and host young [one exception – chicks of *Vidua* parasites are well within the intraspecific variability of the host species chicks’ traits – is the result of previous host selection that led to excellent mimicry (Sorenson and Payne, 2001)]. It is highly unlikely that birds are capable of cognitive feats enabling discrimination of conspecifics, but not heterospecifics.

Appearance stability constraint

Davies and Brooke (1988) argued that eggs look the same throughout incubation, whereas nestlings’ phenotypes change during growth making chick discrimination hard. However, at least in some species eggs may change their appearance during laying and incubation – they get soiled and become less transparent [e.g. *Turdus* spp. (personal observations; see also Figure 1 in Mason and Rothstein, 1986)]. Parents’ cognitive ability to respond to minor differences in continually changing nestling morphology and vocalizations when allocating food within a brood (Wright and Leonard, 2002) also casts doubt on the ‘changing chick appearance’ argument.

Simultaneous comparison constraint

The idea that discrimination is easier if there is a model present for comparison (Dawkins, 1982) was supported by the finding that host nestling discrimination was observed mainly in non-evicting parasites (Davies, 2000) (but see Table 1), where hosts can compare their own nestlings with the alien nestlings. However, to discriminate effectively, birds do not need any comparative material: hosts of both evicting and non-evicting parasitic birds are able to reject the entire parasite clutch (exchanged by experimenters for an original one) even without any of their own eggs present (e.g. Victoria, 1972; Rothstein, 1974; Lotem *et al.*, 1995; Lahti and Lahti, 2002). More importantly, estrildids (hosts of non-evicting *Vidua* finches) can discriminate against a whole brood of another species with no conspecific young for comparison (Payne *et al.*, 2001).

In addition, there are cognitive systems that could well work in the context of parasitic chick discrimination without any of the host’s own nestlings present for comparison:

1. Discrimination can be innate [parent–offspring recognition (Sherman *et al.*, 1997; Langmore *et al.*, 2003); mate recognition (Slagsvold *et al.*, 2002); predator recognition (Mark and Stutchbury, 1994; Veen *et al.*, 2000)].
2. Discrimination can be based on individuals' own phenotype [self-referent phenotype matching (Hauber and Sherman, 2001; Mateo, 2002)].
3. A host could theoretically learn begging vocalizations of its nest-mates when it is nestling itself. Later, when it starts to breed on his or her own, the host could compare this learned template (Sherman *et al.*, 1997) with chick vocalizations and reject any chick(s) with mis-matching begging calls.
4. Increasing evidence shows that songbirds use olfaction in fine-scale discrimination (e.g. Petit *et al.*, 2002) and thus a host could also imprint on its nest-mates' scent as a recognition cue.
5. A future host can also learn from the appearance of its nest-mates (Soler and Soler, 1999) but only after its eyes open several days after hatching. Because appearances of the hatchlings and chicks may change quickly over several days in some species, it is questionable whether such a mechanism could be used against newly hatched parasitic nestlings. However, discrimination based on the learning of nest-mates' appearance could work against older parasitic chicks.
6. Both hosts of evicting and non-evicting parasites may employ password-recognition (Hauber *et al.*, 2001). Here, innate predisposition to recognize a specific cue ('password') triggers learning of other traits of the password-giver's phenotype. According to this scenario, even host nestlings that are reared alongside parasite nestling(s) will be able to identify and learn about conspecific traits without mistakenly incorporating parasite-specific traits into their recognition template (see hypotheses 3–5 above).

Most importantly, observations of naive first-time breeders rejecting alien eggs (see above) strongly point to the possibility that the recognition of a host's progeny can be experience-independent, supporting hypothesis (1). This is in line with increasing awareness of the importance of non-imprinting recognition mechanisms in studies of recognition in birds (Göth and Hauber, 2004).

In summary, neither behavioural nor cognitive constraints can provide any general explanation for the paucity of chick discrimination.

THE HOST EXPLOITATION HYPOTHESIS

According to the host exploitation hypothesis, the main problem for hosts is that they recognize their offspring based on the very same traits that signal offspring food requirements (Redondo, 1993). Signals provided by parasitic nestlings are misinterpreted by hosts as signals of high-quality offspring (Redondo, 1993). Discrimination of alien nestlings would require marked change of a host's cognitive system to make a food allocation system ('this nestling is hungrier') different from a nestling discrimination system ('this nestling is mine').

The validity of the host exploitation hypothesis has been questioned by data on magpies raising great spotted cuckoos. Magpies recognize their own nestlings as those present in the nest (Soler *et al.*, 1995a), but are also able to discriminate against cuckoo nestlings introduced to non-parasitized broods at the end of the nestling period. This clearly shows that magpies can discriminate among nestlings according to both their hunger level and their appearance – they can ignore alien nestlings despite their intense begging. These observations indicate

that 'food allocation' and 'nestling recognition' are two separate decision-making mechanisms. Thus, both Redondo's host exploitation model and Lotem's imprinting model (see above) are essentially arguments about cognitive constraints. As cognitive constraints are easily modified by selection (Sherman *et al.*, 1997), these models have only limited applicability for evolutionary hypotheses.

Similar to the host exploitation hypothesis, the supernormal stimulus hypothesis (Dawkins and Krebs, 1979) suggested that cuckoo intense begging manipulates host behaviour so that 'the host can no more resist the supernormal manipulative power of the cuckoo nestling than the junkie can resist his fix' (Dawkins and Krebs, 1979, p. 496). While a cuckoo chick provides hosts with the supernormal stimulus (Grim and Honza, 2001), this supernormal behaviour is not an adaptation against host discrimination but serves to compensate for the subnormal visual component of the begging signal (Kilner *et al.*, 1999).

THE EVOLUTIONARY EQUILIBRIUM HYPOTHESIS

The evolutionary equilibrium hypothesis states that rejection costs outweigh or balance parasitism costs, resulting in a stable equilibrium maintained by stabilizing selection (Rohwer and Spaw, 1988; Lotem *et al.*, 1992, 1995; Brooker and Brooker, 1996; Lawes and Marthews, 2003). Hosts can accept parasitism when parasites punish rejecters (Soler *et al.*, 1995b; Soler and Soler, 1999) or when parasitism provides benefits [e.g. parasitic chicks may remove ectoparasites from host chicks (Smith, 1968)]. Raising a parasitic chick may also be a handicap indicating parental qualities of parasitized individuals (Zahavi and Zahavi, 1997). The handicap idea could hardly work in cuckoo or cowbird hosts as these have typically short life-spans and the costs of raising a parasitic chick are too high, but tests of this hypothesis are not yet available. More realistic scenarios under the evolutionary equilibrium hypothesis are asymmetry in benefits of egg versus chick discrimination and a low selection for anti-parasitic adaptations at the chick stage.

Asymmetry of benefits of egg versus chick discrimination

Selection for host anti-parasitic adaptations is stronger at the egg stage than at the nestling stage because egg rejection provides greater benefits (Davies and Brooke, 1988). After a cuckoo chick hatches, it may be too late in the breeding season for re-nesting (Dawkins and Krebs, 1979; Davies and Brooke, 1988). This may hold for some species breeding only during a short time window of northern summer (Moksnes *et al.*, 1993). However, the time delay between egg rejection and potential hatchling rejection by desertion (which is the most costly alternative) would be only about 10 days in reed warblers. This would probably have a minimal effect on differences in overall breeding success of egg versus nestling rejecters in the reed warbler. Costs of breeding later in the season [average loss of 0.20 eggs and 0.38 young for 10 days delay in breeding due to declining breeding success during the season (Øien *et al.*, 1998)] would be offset by a strongly declining probability of nest predation at warbler nests (see Figure 1 in Davies and Brooke, 1988). Even no re-nesting would provide benefits for deserters: no costs of prolonged care for the parasite and increased probability of survival due to lack of breeding (Nur, 1984). Therefore, selection should favour anti-parasitic behaviour even after host offspring were evicted by the parasite. If costly nest desertion at the egg stage frequently evolved as a response to parasitism (Davies and Brooke, 1989; Hosoi and Rothstein, 2000), there is no reason why nest desertion at the nestling stage should not be favoured as well. Thus, asymmetry of benefits between egg and nestling stages is unlikely on its own to explain the absence of nestling rejection in cuckoo hosts.

The rarer enemy hypothesis: rare eggs versus rarer chicks

In general, intensity of selection is manifested in the cost of not responding to a selection pressure and the probability of facing this pressure. Even the most deleterious event for an animal provides negligible selection if it is sufficiently rare. This might provide the clue for understanding the rarity of parasite nestling discrimination.

As egg discrimination provides greater benefits and is less costly (in terms of cognitive costs and costs of recognition errors) compared with nestling discrimination (Davies and Brooke, 1988), it should be selected more strongly and spread more quickly after a naive host starts to be exploited by the parasite (however, this alone cannot explain the rarity of chick rejection; see above). Thus, the egg discrimination threshold [i.e. the frequency of encountering a parasite at the egg stage needed for positive selection of host defences against eggs (see also Sherman *et al.*, 1997)] is clearly lower than the chick discrimination threshold (i.e. the frequency of encountering a parasite at the chick stage needed for positive selection of host defences against chicks) (Fig. 1).

After the parasite starts to exploit a particular host (Fig. 1a), the parasitism rate must reach some level (Fig. 1b) to select for host defences – that is, the benefits of anti-parasitic response must exceed the costs of defence. An increase in host defences decreases fitness of the parasite. This could lead to parasitism rates sufficiently low to select against host defences (Fig. 1c) (Soler *et al.*, 1998; Takasu, 1998). This in turn lowers selection pressure on the parasite and parasitism rates increase (Fig. 1d) (Brooker *et al.*, 1990).

However, the selection pressure is always stronger on the evolution of parasite adaptations than on host counter-adaptations (Dawkins and Krebs, 1979; Servedio and Lande, 2003). Therefore, the parasite can win the battle against the host at the egg stage in the long term by evolving ‘perfect’ mimicry – that is, when similarity of parasite and host eggs does not leave any signature cues (Beecher, 1991) available for recognition. Now parasitism rate – unconstrained by host defences – should increase (Fig. 1e). Only then may the parasitism rate overcome the chick discrimination threshold and the evolution of nestling discrimination is expected (Fig. 1f).

If mutation is random, then even novel hosts may defend against parasitism not with egg rejection but with nestling rejection. If egg rejection arises later, it will spread more quickly than nestling rejection. This may decrease the effective parasitism rate at the chick stage

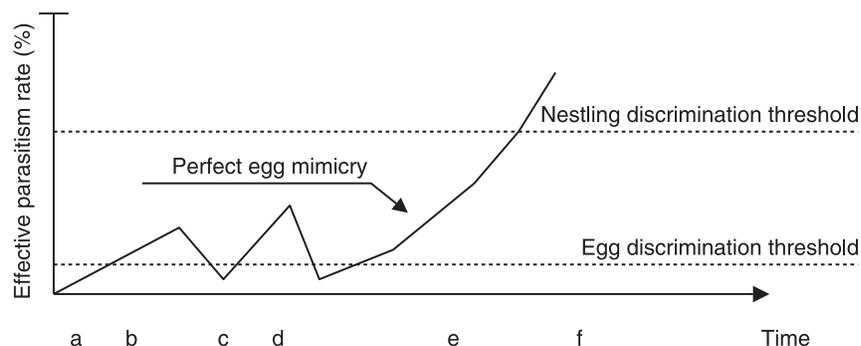


Fig. 1. Hypothetical changes in the effective parasitism rates with respect to two thresholds that selection pressure must overcome in order to select for egg- or nestling-related adaptations in a host. For details, see the section entitled ‘The rarer enemy hypothesis’ in the text.

below the chick discrimination threshold. Importantly, the evolution of egg rejection is not prohibited by the increasing frequency of nestling rejection – that is, egg rejection constrains nestling rejection both at the individual and population levels but *not* vice versa. Selection acting on nestling discrimination in an egg rejecter is frequency-dependent on the rate of egg rejection.

Parasite egg rejection renders few opportunities that favour nestling recognition over egg recognition. Cuckoo eggs are ‘rare enemies’ (Dawkins and Krebs, 1979). However, cuckoo nestlings are even ‘rarer enemies’. Some parasitic eggs are rejected by hosts (e.g. reed warblers, 38%), some accepted eggs are depredated with the host clutch (23%) or ejected by another cuckoo (4%), and some are infertile, laid too late in the breeding cycle of the host, or do not hatch for some other reason (2%) (Øien *et al.*, 1998; I.J. Øien *et al.*, personal communication). All these processes cumulatively relax selection on the evolution of nestling discrimination. Even egg acceptors face fewer chicks than eggs due to egg predation.

The rarer enemy hypothesis predicts that unless a host stops rejecting parasite eggs, it is unlikely that selection pressure at the nestling stage will reach a level necessary for positive selection of costly anti-nestling adaptations. In strong rejecters, such as *Phylloscopus* warblers (Moksnes and Røskoft, 1992), there is virtually no selection for nestling discrimination. In contrast, almost all hosts listed in Table 1 are probably 100% acceptors of natural parasitic eggs, which supports the hypothesis.

The only egg rejecter reported to discriminate parasitic chicks is the reed warbler (Table 1). Reed warblers from the population where chick discrimination was reported reject about 40% of naturally laid parasitic eggs (Øien *et al.*, 1998), but the high parasitism rates in this particular population (~15%) suggest the defence is not very effective. However, the warbler adopts a strategy of delayed chick discrimination, probably to ensure itself that it has a cuckoo in the nest. No costs of recognition errors were found so far: reed warblers were reported never to desert one-warbler-nestling broods (Davies, 2000, Grim and Honza, 2001). The advantage of error-free defence bears the cost of long care for the parasite before desertion, which should slow down the spread of chick rejection. Furthermore, this study population is most likely parasitized by cuckoos only for a short time (Honza *et al.*, 2004), which may also explain the co-existence of two anti-parasitic strategies (see Planqué *et al.*, 2002).

The dunnock is a 100% acceptor of cuckoo eggs. In turn, three of seven chaffinch chicks transferred to dunnock nests by Davies and Brooke (1989) disappeared within 3 days and even surviving chicks grew subnormally. In contrast, the reed bunting *Emberiza schoeniclus* accepts 0% of parasitic eggs and reed warbler chicks transferred to two reed bunting nests grew well (Davies and Brooke, 1989). These differences are expected under the rarer enemy effect. Because of the small sample sizes, the dunnock clearly warrants more detailed study of its responses to alien nestlings.

Chicks of all bronze cuckoos (Table 1) evict host offspring, which casts doubt on the traditional view that simultaneous comparison of own and alien nestling is necessary for discrimination (Davies, 2000). Some authors (e.g. Redondo, 1993; Gill, 1998) considered discrimination against foreign nestlings in a species that accepts foreign eggs to be puzzling. However, as egg rejection keeps effective parasitism rates at the nestling stage at levels that might not allow positive selection for nestling discrimination, there are good reasons to expect exactly this pattern.

At a general level, almost all hosts of the common cuckoo show a relatively high rejection rate of parasitic eggs (Davies and Brooke, 1989), which could – together with extremely low parasitism rates – explain the absence of nestling discrimination in these hosts. Hosts of the

brown-headed cowbird are either close to 100% egg rejecters (selection for nestling rejection is then nil) or they accept almost all parasite eggs, which is probably a result of a recent colonization by the parasite (Rothstein and Robinson, 1998), so we cannot expect to observe nestling rejection either.

A recent mathematical model (Planqué *et al.*, 2002) is in line with the rarer enemy effect (see also Britton *et al.*, in press). The authors assume that a host defensive strategy is an innate trait (see also May and Robinson, 1985; Takasu, 1998; Servedio and Lande, 2003). Planqué *et al.* (2002) showed that a chick rejection strategy cannot invade a host population where individuals eject parasitic eggs. These conclusions represent mathematical support for the verbal model presented in the present paper. Furthermore, egg rejection is more likely to spread as a first defence in the host gene pool. Finally, the model also indicates that a seemingly beneficial mixed strategy of rejection of both eggs and nestlings is less likely to establish itself in competition with pure egg rejection than with a strategy of pure chick rejection (Planqué *et al.*, 2002). I stress that the verbal rarer enemy model (this study) and the mathematical model of Planqué *et al.* (2002) are not identical to each other. Most importantly, Planqué *et al.* (2002) did not explicitly predict that chick discrimination should evolve mainly in egg acceptors, or discuss any empirical evidence in favour of their hypothesis.

I emphasize that the importance of egg rejection is a major constraint on the evolution of chick rejection because this constraint may work in any hosts of cuckoos, cowbirds, and other brood parasites without any limitations. Most importantly, both behavioural (e.g. food allocation rules, nest sanitation, infanticide, brood reduction) and cognitive (e.g. innate mate recognition, self-referent phenotype matching) adaptations potentially useful for discrimination of parasitic chicks evolved in virtually all birds. Theoretically, there is no reason to expect that only species exploited by brood parasites are 'special and unlucky' to be devoid of these pre-adaptations. Empirically, various such pre-adaptations (e.g. food allocation rules) are in fact found in host species that accept parasite nestlings (see also Rothstein, 1982; Kemal and Rothstein, 1988).

THE ARMS-RACE HYPOTHESIS REVISITED

Davies and Brooke (1989) described an arms-race between the cuckoo and its host as a sequence of evolutionary events. Parasitism of naive host selects for rejection of non-mimetic eggs, which selects for mimicry in parasite's eggs, and the process can result in host extinction, host switching by the parasite, or parasite extinction. If the host is freed from parasitism and egg recognition is costly, the host can revert to become an egg acceptor (Davies and Brooke, 1989). However, when egg rejection has insignificant costs, it may be retained for long evolutionary periods (Rothstein, 2001).

Additional stages should be added. Where the parasite has successfully evolved perfect egg mimicry, effective selection for nestling discrimination by a host can start, because this selection is no longer inhibited by egg rejection. Evolution of nestling discrimination by a host can be followed by evolution of chick mimicry, or the parasite can go extinct or switch hosts. If a parasite evolves perfect chick mimicry, it could drive its host extinct.

Some of the parasite–host systems from Table 1 fit a slightly different scenario. The evolution of egg discrimination in some hosts is physically constrained by the dark interiors of their nests (Fraga, 1998; Gill, 1998) or by a close similarity of parasite and host eggs due to the phylogenetic constraints (Sorenson and Payne, 2001). However, these constraints would affect the evolution of nestling discrimination in the same way as parasitic egg mimicry.

FUTURE DIRECTIONS

More experimental cross-fostering studies are urgently needed to shed more light on the prevalence of chick discrimination and rejection among hosts of parasitic birds. The rarer enemy hypothesis suggests that acceptors of natural parasitic eggs should be tested first (Table 1). It is predicted that these hosts should feed less, refuse to feed, or even desert alien chicks that differ phenotypically (e.g. in mouth markings, begging calls, and behaviour) from their own nestlings. In these cross-fostering experiments, I recommend that: (1) Naturally non-parasitic species should be used as potential objects of discrimination by hosts because natural parasites may already be mimetic and thus avoid being discriminated against (Schuetz, 2005), and (2) these species should feed similar types and amounts of food to nestlings and be of similar body size to the host species. (3) Cross-fostering of these 'parasitic' chicks to nests of their own conspecifics would control for possible confounding effects of the cross-fostering process itself.

Parasites of discriminating hosts may have already evolved chick mimicry. Therefore, traits of chicks of obligate brood parasites should be manipulated experimentally to reveal host discriminating abilities (Redondo, 1993; Schuetz, 2005). The host discrimination hypothesis would be supported if significant differences in host parental care to own and alien nestlings [and/or growth performance of these (Grim, in press)] were found. The parasitic chick mimicry hypothesis would be supported if the host discriminated against alien experimental chicks but discriminated less or not at all against chicks of its natural parasite.

Furthermore, comparative methods may show whether hosts of brood parasites evolved more restrictive feeding regimes than closely related non-parasitized species. I predict that egg-accepting hosts of brood parasites (which are under stronger selection for chick discrimination than egg-rejecting hosts, under otherwise equal conditions) should be less responsive to begging strategies that deviate from those of their own chicks than egg-rejecting hosts or non-hosts.

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