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Equal rights for chick brood parasites

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Evolutionary interactions between brood parasites (e.g. cuckoos) and their hosts (e.g. small songbirds) became an important model for the study of coevolution, recognition and other subjects central to evolutionary biology. I argue that both primary literature and textbooks provide an unequal picture of brood parasite–host relationships: they make an impression that hosts can defend against parasite only at the egg stage but not at the nestling stage. However, the general impression that chick discrimination is either very rare or even non-existent does not follow from available data — it is studies of chick-related host adaptations which are rare. Using quantitative data on publication and citation rates of egg *vs*. chick studies I show that there is a strong inequality in favour of egg studies and against chick studies in respect to both research effort (number of studies, number of model host species, studies sample sizes) and citation rates. This bias is apparent in both observational and experimental studies. I argue that current poor knowledge of chick discrimination and mimicry can hardly be explained by logistic obstacles. Both theoretical frameworks and experimental designs were developed and successfully used in several studies of parasite chicks. I suggest that chick discrimination and mimicry should become a priority issue in brood parasitism research in the future to reach a more balanced view of host–parasite interactions.

Introduction

Coevolution is one of the major issues embraced by evolutionary biology (Thompson 1994). A widely known example of coevolution is brood parasitism, i.e. evolutionary interaction between avian parasites (e.g. cuckoos) and hosts (e.g. small songbirds) that lose fitness by raising parasitic progeny. General textbooks on evolutionary biology (e.g. Futuyma 1998), ecology (e.g. Begon *et al*. 1996) and behavioural ecology (e.g. Krebs & Davies 1993, Manning & Dawkins 1998, Alcock 2005) include brood parasitism among premier examples for coevolution and host–parasite interactions especially those based on recognition by hosts of their parasites (*see* also *Annales Zoologici Fennici* 41(6)).

All these textbooks focus primarily on host defences against parasitism and parasite counter-defences. However, only egg discrimination and egg mimicry are discussed in detail while chick discrimination and chick mimicry are sparsely mentioned (Alcock 2005). This is not surprising because studies of host responses to parasitic chicks seem to be uncommon (reviewed in Redondo [1993] and Grim [2006a], *see* also Grim [2005a] and Payne [2005a]). Moreover, a reading of most brood parasitism papers gives

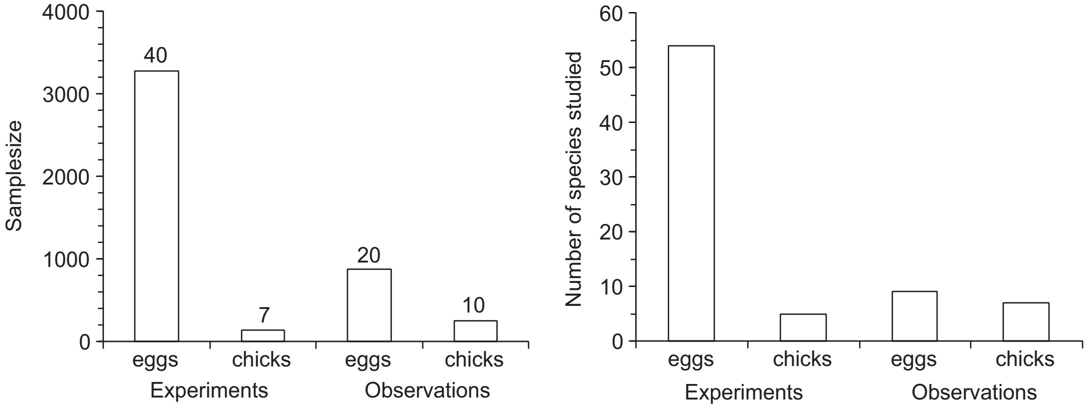

Fig. 1. Research effort devoted to eggs and nestlings in studies of the cuckoo and its hosts. (**a**) Total number of nests with eggs *vs*. nestlings observed or experimentally manipulated, superscripts show number of studies. Experiments refer to egg rejection experiments and studies based on cross-fostering or any manipulation of parasitic and hosts chicks to test hypotheses on brood parasitism and parent–offspring interactions. Observations refer to studies of natural parasitism rates and studies reporting growth or fledging success of parasitic chicks. (**b**) Total numbers of studied host species. Data are from 73 studies published from 1985 until October 2005 (source: Web of Science; search parameters: "brood parasitism or cuckoo"). Only studies based on field research were included.

the impression that hosts may defend against parasitism solely by egg rejection (for supporting data *see* below). However, hosts defend against parasitism at several stages: by nest defence (Grim 2005b), egg rejection (Davies & Brooke 1989) and chick rejection (Langmore *et al*. 2003). I believe that a more balanced view of co-evolutionary arms races is desirable and future papers dealing with brood parasitism should mention all three possible host defence strategies.

A quick look at brood parasitism studies reveals that we know a lot about parasitic eggs and very little about parasitic chicks (Rothstein & Robinson 1998, Davies 2000, Payne 2005b). There are both research and citation aspects of this unequal treatment of eggs *vs*. chicks. Paying attention to research, publication and citation biases is an important part of scientific work (e.g. Windsor 1997, Møller & Jennions 2002, Leimu & Koricheva 2005, Wong & Kokko 2005) and the study of brood parasitism should be no exception. Although the unequal proportion of studies on eggs *vs*. chicks exists in the study of all avian brood parasite–host systems, I will deal with the issue using the studies of the well known brood parasite, the common cuckoo (*Cuculus canorus*; hereafter "cuckoo"), to illustrate the magnitude of the issue.

Research: number and sample sizes of egg *vs*. chick studies

An overview of brood parasitism papers on the cuckoo included in the Web of Science (papers published from 1985 to 2005, search phrase: "brood parasitism or cuckoo") showed that only a minority of studies of hosts of the cuckoo paid any attention to parasitic chicks (Fig. 1a). Further, there is a large difference in cumulative sample sizes of the egg *vs*. chick studies (Fig. 1a). Finally, ten times more cuckoo host species were experimentally tested for their responses to parasitic eggs than to parasitic chicks (Fig. 1b). I did not include studies based on museum collections (which would greatly increase sample size for egg studies). Noticeably, almost all the studies of parasitic eggs within the analysed 1985–2005 period were designed to test for host discrimination abilities while only two (out of total of 16) studies of parasitic chicks were designed to test for chick discrimination.

The extent of this research inequality is unlikely to be explained by a lower availability of chicks than eggs for experiments. Although predation continually decreases sample sizes for chicks until fledging, it probably does not do so 20 times which would be necessary to explain the huge sample size differences (Fig. 1). It could also be argued that some brood parasites have very low breeding densities (Davies 2000) thus decreasing the amount of data obtained per a unit of effort. But one does not need parasitic chicks themselves to study host discrimination abilities (*see* Grim [2005] and [2006a] for discussions and Grim [2007] for an example). In fact cross-fostering of chicks of other non-parasitic species is *essential* to understand both initial stages of interspecific parasitism (Slagsvold 1998) and evolved host responses (Davies & Brooke 1988, 1989, Grim 2007). This method should be generally applicable unless the mechanism of identifying of nestlings in the nest is dependent in any way on watching them hatch (for a detailed discussion of chick recognition mechanisms *see* Grim [2006a]). Also cross-fostering of host own chicks shed a light on the proximate mechanism of chick discrimination in a cuckoo host (*see* Grim 2007).

Further, a large amount of work has been done on chicks of open-nesting passerines, many of which suffer high predation and serve as hosts for interspecific brood parasites in studies of parent–offspring interactions (reviewed in Wright & Leonard 2002). Here chick availability for research (i.e. sample size) seems not to be a constraint. In addition, some studies of brood parasitic chicks achieved strong conclusive results despite being based on very limited sample sizes (e.g. Dearborn [1998] $n = 6$ in some analyses; Tanaka & Ueda [2005] $n = 6$; Grim [2006b] $n = 6$ per some host species). This directly rejects the hypothesis that low research effort on host discrimination of parasitic chicks can be explained by sample size limitations.

Nevertheless, any chick experiments are less easily done than any egg experiments. First, to test for host egg-related responses (ejection, desertion, etc.) it is convenient to use artificial models and experimenters are not dependent on the supply of natural parasitic eggs (which are very rare as a rule in cuckoo hosts nests, Davies [2000]). In contrast, it is probably impossible to employ artificial models of nestlings because chick movements are critical for eliciting parental (or fosterer) care (*see* Wright & Leonard 2002). Second, any egg traits potentially relevant for recognition and discrimination by hosts (egg size, shape, background colour, spotting, etc.) are easily manipulated experimentally (Davies & Brooke 1989). Although it is possible to manipulate some chick traits as well (*see* e.g. Schuetz 2005b) chicks are generally less amenable to experimental manipulation both due to ethical and logistic reasons. Third, hosts respond to eggs usually within a time window of several days or even hours (Davies 2000) whereas parasitic chicks may be discriminated against after much longer periods (e.g. two weeks from hatching, Grim *et al.* [2003], Grim [2007]). Thus, from a logistic point of view the egg studies are less costly and provide more data per unit of effort than the chick studies. Nevertheless, this certainly does not mean that research on chicks is impossible or unrewarding (*see* Grim 2006a).

To sum up, there are no severe theoretical or logistic obstacles for the study of chick discrimination – both theoretical frameworks (Lotem 1993, Planqué *et al.* 2002, Grim 2006a, Britton *et al.* 2007), comparative approaches (Payne 2005a) and experimental designs (Langmore *et al.* 2003, Schuetz 2005b, Grim 2007) were already developed and successfully employed for the study of chick recognition and discrimination.

Citations: representation of eggs *vs.* chicks in references

Superimposed on the so far discussed research inequality is the uneven citation index of egg *vs.* chick papers (citation frequency is generally accepted as an important measure of research interest, *see* e.g. Leimu & Koricheva [2005]). The citation inequality is seemingly not apparent when one compares citation rate of egg *vs.* chick papers (2.6 *vs.* 2.5 citations per year on average). However, this comparison is more obscuring than revealing. In fact, papers that experimentally tested for host-chick discrimination (Davies & Brooke 1988, 1989) also tested for egg discrimination and are as a rule cited as sources for information on egg discrimination but not on chick discrimination. Additionally, other studies on chicks are concerned with begging behaviours (Kilner et *al.* 1999) and growth (Grim 2006b) and were not intended to study host chick discrimination.

Therefore I searched for terms "chick", "nestling", "discrimination" and "rejection" in the text of PDF files of recent (last 5 years, up to October 2005) field studies of the cuckoo. The studies dealing with parasitic chicks cite papers on parasitic eggs without exception (16 out of 16 in the cuckoo literature). In a striking contrast, the studies dealing with parasitic eggs do not cite any papers on parasitic chicks — only one out of 30 field studies on parasitic eggs in the cuckoo published during the last five years cited a paper on chick discrimination. Most papers on parasitic eggs in general do not mention even a possibility that host defences could extend beyond the egg stage — thus, they overlook not only *Cuculus canorus* papers but also those on other host–parasite systems (e.g. Nicolai 1964, Redondo 1993, Fraga 1998, Lichtenstein 2001). This citing inequality may give an impression that chick discrimination is even non-existent (*see* e.g. Winfree 1999). This is, of course, not so (Grim 2006a).

Clearly, I do not claim that this inequality reflects some deliberate intent to squelch chick discrimination studies. Possibly this reflects a natural feedback between number of already published studies on some issue and number of new research projects on the very same issue. This commentary, of course, is not meant to devalue egg discrimination studies in any way. However, appreciation of the chick discrimination issue would perhaps lead to a more balanced view of host–parasite coevolution (*see* also Windsor 1997).

Rarity of chick discrimination and mimicry: reality or myth?

The supposed rarity (e.g. Johnsgard 1997) or even non-existence (e.g. Winfree 1999) of parasitic-chick discrimination and mimicry reported in literature did not follow from available data even at the time of publishing of the above mentioned reviews (*see* Redondo 1993, and Grim 2006a: table 1). In general, hosts of parasitic birds do reject natural or experimental parasitic chicks by nest desertion (Langmore *et al.* 2003, Grim *et al.* 2003, Grim 2007), non-willingness to feed them (Lichtenstein 2001, Payne *et al.* 2001) or by direct physical attacks, thus killing and/or ejecting them from the nest (Redondo 1993, Soler *et al.* 1995). Unfortunately, the proximate mechanisms underlying host's chick discrimination responses under natural conditions are generally poorly known. Superb fairy-wrens (*Malurus cyaneus*) in Australia seem to recognize parasitic bronze-cuckoos (*Chrysococcyx* spp.) according to the structure of begging calls (Langmore *et al.* 2003). Unexpectedly, European reed warblers (*Acrocephalus scirpaceus*) are able to reject (desert) old cuckoo chicks even when this host does not specifically recognize them (Grim 2007). Proximate mechanism of this host discrimination response seems to be a time-limited pre-programmed parental care independent of the nest content (for details *see* Grim [2007]).

In fact, it is studies of chick discrimination which were and still are rare (Fig. 1). As for chick discrimination itself we simply do not know whether it is rare or relatively common as only five cuckoo host species were studied in this respect — in contrast to 54 host species tested with parasitic eggs — and sample sizes of these chick studies are very limited indeed (Fig. 1a). To my best knowledge, this research inequality was invoked never before as a potential confounding factor that may lead to general conviction of the rarity of chick discrimination.

The most telling observation in support of this argument is that the very first groundbreaking studies of host responses to cuckoo eggs (Davies & Brooke 1988, 1989) also tested host responses to cross-fostered alien chicks with the results suggestive of parasitic chick discrimination by some hosts (*see* discussion in Grim [2006a]). Strikingly, a plethora of egg discrimination experimental studies followed during next two decades but very few chick discrimination studies were conducted. One study that paid attention to entire nestling period up to fledging in the cuckoo (Grim *et al.* 2003) found that hosts (reed warblers) in fact show chick discrimination. There is now experimental evidence that the behaviour of reed warblers is indeed defence against parasitism by cuckoos (Grim 2007).

Additional factors may increase general impression of rarity of chick discrimination and mimicry. For example, chick mimicry is usually judged from similarity in appearance of parasitic and host chicks and host discrimination is inferred when a similarity in parasitic and host chick phenotypes is found (for reviews *see* Redondo [1993] and Grim [2005a]). However, visually mimetic parasitic chicks can be rejected while visually non-mimetic parasitic chicks can be accepted by hosts as mimicry may be limited to vocal signals only (Langmore *et al*. 2003). Implications of this observation are discussed elsewhere (Grim 2005a).

In my opinion, one of the major problems in the study of brood parasitism currently is the ruling paradigm that chick discrimination is a rare escalation of the arms-race which according to theory is not expected to evolve (e.g. Lotem 1993; but *see* Langmore *et al*. 2003). The current research focus on the egg stage in parasite–host interactions provides an information feedback that again and again strengthens our impression that host defend against parasitism only when faced with alien eggs (for an exception *see* Stokke *et al*. [2005]). As Amotz Zahavi noted in a similar context "*A major disadvantage of a dominant theory that is accepted by everyone around you is that observers in the field have a strong tendency to overlook findings that do not fit in with the theory.* [...] *exceptions either go unreported, or, if reported, are not considered important in discussions of the findings*." (Zahavi 2003: p. 862).

Research priorities

The minority of brood parasitism studies that investigated host responses to chicks of several species of brood parasites (for review *see* Grim [2006a], for case studies e.g. Redondo [1993], Fraga [1998], Lichtenstein [2001], Payne *et al*. [2001], Langmore *et al*. [2003], Grim *et al*. [2003], Schuetz [2005a], [2005b], Grim [2007]) are typically not considered in descriptions of host–parasite arms races (for an exception *see* Stokke *et al*. [2005]). This is unfortunate as it might discourage students of brood parasitism to invest their research effort in the study of host responses to chicks.

Why should the study of host responses to parasitic chicks be rewarding? Chick rejection is an additional line of host defences against parasitism which can take place when egg discrimination does not work (Langmore *et al*. 2003) or cannot work — e.g. when perfect egg mimicry or similarity of parasitic and host eggs resulting from phylogenetic constraints prevents evolution of egg discrimination (Grim 2005a, 2006a). There are good theoretical reasons — and suggestive empirical evidence — to expect that we should find chick discrimination mainly in egg acceptors (Planqué *et al*. 2002, Grim 2006a, Britton *et al*. 2007). Clearly, if chick discrimination was find to be more prevalent in such hosts it would profoundly change our view of coevolutionary dynamics between brood parasites and their hosts. Additionally, interactions between parasitic chicks and their hosts already proved to be important model systems for the study of more general evolutionary issues, e.g. communication of chick hunger and parental feeding rules (Kilner *et al*. 1999, Hauber & Montenegro 2002), altruism directed to unrelated individuals (Kilner *et al*. 2004) and virulence in general (Kilner 2005, 2006, Grim 2006c).

Our poor understanding of host responses to parasitic chicks also impairs our knowledge of both hosts' and parasites' reproductive success and, thus, their population dynamics (May & Robinson 1985). For a brood parasite to be successful a host has to either (1) lack both egg and chick recognition and discrimination abilities, or (2) has to make recognition errors when confronted with alien propagules (Fig. 2). Under (2) the costs of recognition errors and discrimination mechanisms may even outweigh the benefits of the rejection process forcing the host to be an acceptor (Lotem 1993). Recognition errors may happen at four temporal stages, i.e. when a host faces female adult parasite during its egg laying, then incubation period, care for chicks at the nest and finally post-fledging care (Fig. 2). First, observing an adult parasite near the nest increases the probability of correct recognition of alien eggs by hosts (e.g. Moksnes *et al*. 1993). Here, both general nest attentiveness (Mermoz & Fernandéz 1999) and specific host recognition of the parasite (Grim 2005b) play essential roles. Both low nest attentiveness (Grim & Honza 2001) and errors in differentiating adult parasite and innocuous intruders near the nest (Grim 2005b) increase the probability of

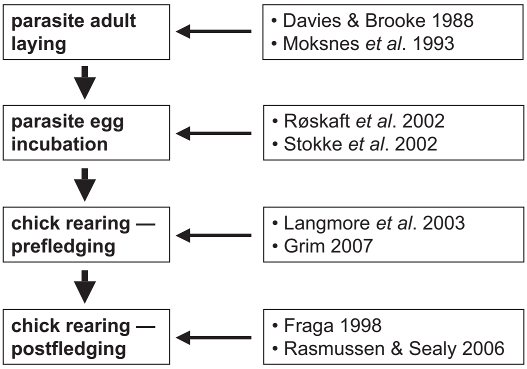

Fig. 2. Stages where recognition errors by hosts (i.e. *acceptance errors* in the presence of brood parasitism and *rejection errors* in the absence of brood parasitism) are necessary for brood parasitism to be successful. Recognition errors at each stage cumulatively increase the reproductive success of the parasite. *See* section "Research priorities" for detailed explanation.

successful parasite reproduction. Second, once the parasite successfully laid into a host nest the host can commit egg acceptance errors (Røskaft *et al*. 2002, Stokke *et al*. 2002), thus, again increasing parasite success. Third, after hatching the host may wrongly accept an alien parasite nestling (Langmore *et al*. 2003) or incorrectly reject own chick(s) under experimental conditions (Grim 2007). Fourth, some hosts may delay their chick rejection response until post-fledging period (Fraga 1998) and there is a window for recognition errors also at this final stage by preferentially feeding parasitic offspring (Rasmussen & Sealy 2006). To sum up, the knowledge of recognition errors at various stages of host–parasite interaction (Fig. 2) would greatly enhance our view of brood parasite–host coevolution dynamics and may serve as a good model for working of multiple recognition mechanisms as well (*see* also Mateo 2004).

In my view research on host behaviour to parasitic chicks should become a priority in the study of brood parasitism in the years to come. This should not occur at the expense of studies of egg discrimination mechanisms but instead lead to a broadening of the current research focus. This would hopefully allow for a more balanced understanding of host–parasite interactions in particular and coevolution in general.

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