# Host Defences Against Brood Parasite Nestlings: Theoretical Expectations and Empirical Evidence

# 29

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**Abstract**

In the past, chick discrimination was assumed to be non-existent without virtually any research invested to check the reality. Models of brood parasitism considered the benefits of chick rejection small and costs too high; consequently, the nestling stage was long ignored in studies of host–parasite coevolution. Remarkably, the majority of recent studies that addressed parasite chick biology did find evidence for host behaviours that alleviate the costs of parasitism during nestling stage. Most of the hosts that (apparently) discriminate against parasite chicks are acceptors of natural parasite eggs; this pattern is in line with the rarer enemy model. The main impetus for future work is therefore not naively assuming but empirically checking the (non)-existence of chick discrimination to show how common is chick discrimination in reality. This will allow to elucidate mechanisms of chick discrimination, both those that specifically evolved as a response to past parasitism pressure and those stemming from non-specific general host life history traits, and factors that facilitate or constrain their evolution.

## 29.1 Introduction

Life cycles of both brood parasites and hosts develop through a series of stages, from egg laying, through incubation, hatching, nestling and fledgling periods to independence during non-breeding periods. At each stage the interactions involve costs and benefits for both parties and, consequently, affect overall population and evolutionary dynamics of both parasites and hosts (Dawkins and Krebs 1979). Despite the large and increasing research effort into brood parasite–host systems, we are still far

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from a coherent understanding of the complete host–parasite life cycles. This is because of an imbalance in research efforts across all life stages: a great majority of studies have addressed, and still addresses, the incubation stage (egg rejection and mimicry); few studies have focused on the egg laying and hatching processes and nestling and fledgling periods.

Here, I focus on the nestling period (Soler 2009), which has been typically neglected in comparison with the egg stage (Grim 2007a). Recent advances in this tiny field of study suggest that host–parasite interactions during the nestling stage may have fundamental effects on parasite–host coevolution.

## 29.2 Theoretical Explanations

Most historical discussions of chick discrimination, i.e. differential behavioural response of hosts towards own vs. foreign chicks (e.g. Langmore et al. 2003; Grim 2007b; Shizuka and Lyon 2010), tried to explain its absence (or, at best, rarity), taking the lack of such host adaptation for granted. Today, all previous explanations for the absence are invalid because good empirical evidence for various modes of chick discrimination has accumulated during the last ca. 15 years (Table 29.1). All previous explanations for the rarity of chick discrimination were reviewed and refuted with theoretical arguments or empirical evidence (Grim 2006). To avoid unnecessary duplication, I am not going to repeat the arguments here. If anything, post-2006 empirical data provide additional support for rejecting traditional explanations. Here I give just one example.

It has been argued that evicting parasites, like common cuckoos (*Cuculus canorus*), eliminate comparative material (host own chicks) which prevents host chick recognition; this hypothesis was in line (at the time of publication) with chick discrimination being reported mainly from non-evicting parasite–host systems. However, there are at least six different cognitive systems that might be employed as a basis for chick discrimination without material for comparison (see section “Simultaneous Comparison Constraint” in Grim 2006). All those cognitive mechanisms are known in birds and work in other social and behavioural contexts; this rejects the notion that discrimination is impaired by the lack of comparative cues. I see no theoretical reason why chick discrimination should be an exception. Indeed, empirical data support this view: the best evidence for chick discrimination comes from hosts of evicting parasites (Langmore et al. 2003; Fig. 29.1a). In fact, it was even more often reported from evicting than from non-evicting parasites (Table 29.1).

The “material for comparison” idea stemmed from findings of early egg discrimination studies—but there is ample evidence that even foreign egg discrimination is not limited by the absence of own eggs for comparison (Bán et al. 2013). The hypothesis of missing comparative material probably reflected a notion that cuckoos evict immediately after hatching; this notion is wrong because cuckoos start to evict only when they are 1 or 2 days old (Honza et al. 2007; Grim et al. 2009b). Therefore hosts do have material for comparison, either eggs (why should a host not assess a contrast between, e.g. own egg colour and parasite egg skin colour?) or their own

**Table 29.1** Overview of host–parasite systems with reported cases of (apparent) chick discrimination or mimicry

| Host | Parasite | Natural egg rejection rate (%) | Evictor parasite | References |
|---|---|---|---|---|
| **Anecdotal observations** | | | | |
| *Acrocephalus arundinaceus* | *Cuculus canorus* | 57[a] | + | Honza et al. (2010) |
| *Alauda arvensis* | *Cuculus canorus* | 0[b] | + | Hegemann and Voesten (2011) |
| *Phoenicurus phoenicurus* | *Cuculus canorus* | 0 | + | Grim and Rutila (Chap. 16) |
| *Turdoides* spp. | *Clamator jacobinus* | 0[c] | – | Jourdain (1925) and Gaston (1976) |
| **Phenotypic similarity** | | | | |
| *Acanthiza chrysorrhoa* | *Chalcites lucidus* | 0[d] | + | Langmore et al. (2011) |
| *Corvus splendens* | *Eudynamys scolopacea* | 0 | – | Dewar (1907) |
| Estrildidae spp. | Viduinae spp. | 0[e] | – | Nicolai (1964, 1974), Payne et al. (2001) and Schuetz (2005a, b) |
| *Gerygone igata* | *Chalcites lucidus* | 0 | + | McLean and Waas (1987), McLean and Rhodes (1991), Gill (1998), McLean and Maloney (1998) and Thorogood et al. (2017) |
| *Malurus coronatus* | *Chalcites basalis* | 0[f] | + | Langmore et al. (2011) |
| *Mohoua* spp. | *Urodynamis taitensis* | 67[g] | + | McLean and Waas (1987) |
| Ploceidae spp. | *Chrysococcyx caprius* | 0[c] | + | Reed (1968) |

(continued)

**Table 29.1** (continued)

| Host | Parasite | Natural egg rejection rate (%) | Evictor parasite | References |
|---|---|---|---|---|
| *Turdoides jardineii* | *Clamator levaillantii* | 0[c] | – | Mundy (1973) and Steyn (1973) |
| Tyrannidae spp. | *Dromococcyx pavoninus* | 0[h] | +[h] | Sánchez-Martínez et al. (2017) |
| **Direct evidence** | | | | |
| *Acrocephalus scirpaceus* | *Cuculus canorus* | 38 | + | Grim et al. (2003) and Grim (2007b) |
| *Agelaioides badius* | *Molothrus rufoaxillaris* | 0 | – | Fraga (1998) and De Mársico et al. (2012) |
| *Anumbius annumbi* | *Molothrus bonariensis* | 0[i] | – | Delhey et al. (2011) |
| *Estrilda astrild* | *Vidua macroura* | 0[j] | – | Schuetz (2005a,b) |
| *Eumyias thalassinus* | *Cuculus canorus* | 0 | + | Yang et al. (2013) |
| *Gerygone flavolateralis* | *Chalcites lucidus* | 0[k] | + | Sato et al. (2015) |
| *Gerygone laevigaster* | *Chalcites minutillus* | 0 | + | Tokue and Ueda (2010) |
| *Gerygone magnirostris* | *Chalcites minutillus* | 0 | + | Sato et al. (2010b) |
| *Hirundo daurica* | *Chrysococcyx maculatus* | 0 | + | Yang et al. (2015) |
| *Malurus cyaneus* | *Chalcites basalis* | 0 | + | Langmore et al. (2003, 2008, 2009, 2011) and Colombelli-Négrel et al. (2012, 2014) |

| | | | | |
|---|---|---|---|---|
| *Passer cinnamomeus* | Various cuckoo spp. (potentially) | 0 | + | Huo et al. (2018) |
| *Pica pica* | *Clamator glandarius* | 5[l] | – | Redondo (1993), Soler et al. (1995), Soler and De Neve (2012), Roldán et al. (2013) and Soler et al. (2013a, 2017) |
| *Prunella modularis* | *Cuculus canorus* | 0 | + | Davies and Brooke (1989) |
| *Turdus merula* | *Cuculus canorus* | ?[m] | + | Grim et al. (2011) |
| *Turdus rufiventris* | *Molothrus bonariensis* | 0 | – | Lichtenstein (2001) |

Also cases based on mere similarity (cf. Grim 2005, 2013) are included to highlight any promising study systems for future research. If rejection rates of natural egg parasitism were not reported or cited in the study given in “References” column, I retrieved data from another sources (see footnotes). If only results from experimental parasitism with model eggs were known, I assumed that acceptance of dissimilar non-mimetic models implies acceptance of more similar natural parasite eggs (Grim 2005). I have excluded *Psarocolius* and *Cacicus* spp. vs *Scaphidura oryzivora* system (Table 1 in Grim 2006) because subsequent studies did not verify original findings (see Davies 2000, p. 186)

[a] Trnka et al. (2012)

[b] Antonov et al. (2010)

[c] Parasite and host eggs very similar (Davies 2000; Payne 2005), making rejection of natural parasite eggs unlikely

[d] Brooker and Brooker (1989)

[e] Includes ca. 15 host–parasite species pairs where parasite chick mimicry seem to have evolved independently (Davies 2000)

[f] No evidence of natural cuckoo egg rejection but experimental data not available (M. L. Hall, pers. comm.)

[g] Briskie (2003). Only artificial models, sample sizes small ($n = 3$)

[h] Hosts included two *Leptopogon* spp. and one *Mionectes* sp. No naturally laid parasite eggs were ejected. Observed desertion rates of parasitized nests (5 out of 9) did not differ statistically (Fisher’s exact test: $p = 0.64$) from rates expected (3 out of 9) for this sample of nests ($n = 9$) from background desertion rates at control nests (21 out of 63). The pavonine cuckoo does not show evicting behaviour but kills host progeny via bill hook; thus, it is raised alone just like chicks of evicting cuckoo species are

[i] Ca. 10% cowbird eggs disappeared but host own eggs disappeared at the same rate (10%; hosts remove their own eggs punctured by cowbirds). Experiments in different populations did not reveal any egg rejection by hosts (Delhey et al. 2011)

[j] Payne et al. (2001)

[k] Supplemental Information from Sato et al. (2015) suggests no specific rejection of parasite eggs

[l] M. Soler, pers. comm.

[m] Blackbirds reject roughly half of non-mimetic and mimetic models and even conspecific eggs (Samas et al. 2014); responses to natural cuckoo eggs were not tested so far and are hard to predict because blackbirds do not reject foreign eggs based on absolute cue dissimilarity discrimination thresholds but show colour categorization (Hanley et al. 2017). Cuckoo chicks cross-fostered into blackbird nests die soon, even after evicting host progeny; this is unlikely to be explained by unsuitable diet (Grim et al. 2011) and calls for more research

**Fig. 29.1** (**a**) Deserted Horsfield's bronze cuckoo (*Chalcites basalis*) chick (3–4 days old) in a superb fairywren (*Malurus cyaneus*) nest in Australia (nest and chick moved from original position to facilitate photography). (**b**) Deserted common cuckoo (*Cuculus canorus*) chick (14 days old) in a reed warbler (*Acrocephalus scirpaceus*) nest in the Czech Republic. (**c**) Deserted common cuckoo chick (17 days old) in a common redstart (*Phoenicurus phoenicurus*) nest with a deserted host chick (same age) after other host chicks fledged in Finland. Photo credits: (**a**) N. Langmore, (**b**) O. Mikulica, (**c**) T. Grim

hatched chicks. At least in some nests, the cuckoo and host chicks coexist for several days, in some hosts regularly, and even up to fledging (Chap. 16). This provides as much time (or much longer, in host–parasite mixed broods) as is needed for host responses to cuckoo eggs (Hanley et al. 2016).

Further, I am going to discuss, chronologically, only potentially viable explanations (for unviable ones see Grim 2006).

### 29.2.1 Misimprinting Model

Lotem (1993) assumed that hosts imprint on both their eggs and chicks for the lifetime. Given his model assumptions, he showed that in hosts of evicting parasites, costs of misimprinting on parasite chicks are higher than benefits of correct imprinting on own chicks. Due to its elegant simplicity, the model was generally accepted as a good explanation for why hosts do not reject foreign chicks.

Theoretically, the generality of misimprinting model is limited because it may apply only under special conditions (Planqué et al. 2002; Grim 2006; Britton et al. 2007). The model did not take into account rejection costs and errors and was based on poorly supported assumptions. Specifically, misimprinting model assumed, without any empirical evidence, that *chick* recognition is only learned and innate recognition is improbable. Today, there is good empirical evidence for innate recognition in various biological contexts (egg, adult, enemy, etc.; Grim 2006), including chick recognition (Langmore et al. 2003, 2009). Misimprinting model also assumed, with limited empirical evidence, that *egg* recognition is based on imprinting. However, the majority of studies do not support this contention (Soler et al. 2013b and references therein). Recognition, even innate one, is not strictly necessary for chick discrimination (Grim et al. 2003; Schuetz 2005a). At the time of publication, the model was apparently in line with empirical data because chick discrimination seemed to be more prevalent in non-evicting parasites; today, the opposite is true: most cases of chick discrimination come from evicting parasites (Table 29.1).

I suspect that the misimprinting model, although admirable for its parsimony, might be partly responsible for low research effort on chick discrimination: it took the absence of chick discrimination for granted and by providing an explanation for the *absence* of the phenomenon it apparently made chick discrimination a "closed case". This view is in line with the fact that its publication did not elicit any empirical tests of chick discrimination. Today, both theoretical reasons and empirical data make it clear that the misimprinting model should no longer be considered a viable *general* explanation for the lack or (apparent?) rarity of chick discrimination. In contrast, alternative models (rarer enemy, strategy blocking) fit empirical data well.

### 29.2.2 Rarer Enemy Model

The rarer enemy model (Grim 2006) is an extension of the classic verbal model, the rare enemy effect (Dawkins 1982). Although parasite eggs are rare enemies, parasite chicks are even rarer enemies. This is primarily because host interactions with chicks are pre-empted by host removing potential parasite chicks before they hatch (egg rejection) and also via parasite egg infertility and nest failure due to predation or inclement weather; even egg acceptors face parasite chicks less often than eggs (this point has not been considered in any other theoretical model). All these factors additively decrease *effective* parasitism rate during the chick stage. The core of the rarer enemy idea is that these factors prevent parasitism rate at the chick stage to reach the threshold that selection pressures must overcome in order to positively select for chick discrimination (Fig. 1 in Grim 2006). The view that it is hosts themselves that create low parasitism rate at the chick stage (via egg rejection) fundamentally differs from alternative explanations. Although the model is "only" verbal, each step of the suggested coevolutionary dynamics is supported by published mathematical models (Fig. 1a–f in Grim 2006).

The rarer enemy model explicitly predicted that chick discrimination should evolve mostly in hosts that are forced to accept parasite eggs from any reason (egg mimicry, crypsis, shared diet effects on egg colour, phylogenetic and physical constraints, etc.; Grim 2002, 2005). Novel evidence accumulated after the model was published (Grim 2006) consistently supported the model (Grim 2011): the most persuasive evidence for chick discrimination came from pure acceptors of natural parasitism (Table 29.1). Still, the model predicted coexistence of imperfect egg and imperfect chick discrimination (Grim 2006). An example of this might be provided by reed warblers (*Acrocephalus scirpaceus*) from a population where hosts always accept cuckoo eggs unless they directly witness the cuckoo during laying (Moksnes et al. 2000) and sometimes desert cuckoo chicks (Grim et al. 2003; Fig. 29.1b). Indeed, this population may experience a strong parasitism pressure only recently (Igic et al. 2012).

The idea can be extended to other stages of the host–parasite arms race. For example, also successful nest defence pre-empts selection pressure on both egg and chick rejection: e.g. "sitting on the nest" by yellow warblers (*Setophaga petechia*) blocks parasite access to the nest (Hobson and Sealy 1989) and might explain why these hosts accept foreign eggs. Testing this hypothesis will require data on *natural* host–parasite interactions during laying (Moksnes et al. 2000; see Chap. 18). Dummy experiments are useful for other purposes, e.g. enemy recognition studies (Hobson and Sealy 1989), but useless in this respect because they cannot determine if the parasite female is deterred by hosts or not. Further, a trade-off between earlier and later defences can work not only at the host species/population level (as discussed so far) but at individual level too. Here, the rarer enemy effect predicts that females that are egg rejecters should be more likely chick acceptors, whereas egg acceptors should be more chick discriminating; note that female is the sex responsible for discrimination of both eggs and chicks in most birds (Davies 2000; Langmore et al. 2003).

### 29.2.3 Strategy Blocking Model

The mathematical model (Britton et al. 2007; see also Planqué et al. 2002 for a less general version of the model) is based on an idea that adaptiveness of a particular strategy is context-dependent, i.e. its fitness is affected by the frequency of other strategies in "defence portfolios". Britton et al. (2007) showed that a strategy might be adaptive on its own but can get prevented ("blocked") by another ("blocking") strategy. For example, the model suggested that a population of naive hosts (i.e. non-defending acceptors of both egg and chick parasites) can be invaded by

**Table 29.2** Differences between rarer enemy and strategy blocking models. See the original studies for rationales

| Prediction | Rarer enemy (Grim 2006) | Strategy blocking (Britton et al. 2007) |
|---|---|---|
| Egg rejection is blocked by chick rejection | No | Yes |
| Chick rejection can coexist with egg rejection | Yes | No |
| Patterns of host defences under natural conditions | Only acceptors of natural (but not necessarily experimental) parasite eggs should show chick discrimination | No explicit prediction |

egg rejecter strategy but such a population of egg rejecters would not be later invaded by either chick rejecters or all rejecters (i.e. rejecters of both eggs and chicks). The crucial and contra-intuitive insight is that a mixed strategy of rejecting both eggs and chicks is maladaptive and cannot invade a population of either egg rejecters or chick rejecters (at least given the model structure).

Strategy blocking is similar to rarer enemy effect but there are important differences between the two (Table 29.2). Essentially, the two models can be seen as a one-sided (rarer enemy) vs. double-sided (strategy blocking) trade-off between strategies within a defence portfolio. The two models are clearly different from other models both conceptually and in their predictions (e.g. Lotem 1993; Redondo 1993; Lawes and Marthews 2003; Sato et al. 2010a). Future modelling and empirical studies are needed to clarify which conditions best explain patterns of chick discrimination observed in nature.

### 29.2.4 Egg Dilution Model

The final published theoretical explanation of conditions necessary for the evolution of chick discrimination takes into account multiple parasitism. Sato et al. (2010a) suggested that hosts in populations where multiple parasitism is common may adaptively accept a first-laid parasite egg (even though they can discriminate the foreign egg) and delay the rejection of the parasite into the chick period. The rationale is that not rejecting the first parasite egg increases the total clutch size and the second-laying parasite female might remove the egg of the first female, effectively helping hosts with rejecting the first parasite. However, the assumptions of the model are unlikely to occur empirically in most brood parasite–host systems, severally limiting its applicability and making it an unlikely general explanation for chick discrimination patterns (Grim 2017).

## 29.3 Empirical Evidence

Australian hosts, superb fairywrens (*Malurus cyaneus*), desert parasite chicks (Langmore et al. 2003) and fine-tune their innate chick rejection via learning (Langmore et al. 2009). This has resulted in an evolution of admirable level of both acoustic (Langmore et al. 2008) and visual mimicry (Langmore et al. 2011). The last study found beautiful similarity between chicks of several host–parasite pairs, suggesting that chick discrimination may be much more widespread than thought previously (Table 29.1).

Reed warblers desert some nests where the brood, be it a cuckoo (Grim et al. 2003) or own chicks (in nests with experimentally prolonged nestling period), needs longer care than host own brood under natural conditions (Grim 2007b). Such preprogrammed parental care represents "discrimination without recognition" because warblers do not recognize their vs. foreign chicks (Davies 2000) yet are able to get rid off of the parasite. As argued by Soler et al. (2013a), deserting cuckoo nestlings is unlikely a by-product of host fledgling process: altricial species decrease feeding to force nestlings to leave the nest but this "forcing" behaviour does not result in chick death.

Recently, chick discrimination by ejection (i.e. host parent grasped a cuckoo chick and removed it from its nest) was video-recorded in three gerygone species (Table 29.1). This provides direct evidence that physical constraints are impotent as an explanation for acceptance of foreign chicks (as already supported by indirect evidence: Grim 2006). Additionally, there is an older observational and experimental evidence of foreign chick discrimination from another gerygone species (McLean and Rhodes 1991). A closely related thornbill (*Acanthiza*) host is parasitized by apparently mimetic cuckoo chicks (Table 29.1). This phylogenetic distribution (Nyári and Joseph 2012) suggests that chick discrimination may represent an ancestral trait in the Acanthizidae; clearly, other related species in this clade deserve more attention. The same holds for various *Malurus* fairywrens (Langmore et al. 2003, 2011; Colombelli-Négrel et al. 2016).

Some of these cases (Table 29.1) unambiguously represent chick rejection, while others may be more parsimoniously explained as by-products of host general life history traits, namely, indigestible food, nest design, etc. (Grim et al. 2011). More important than the origin of (apparent) chick discrimination is its effects on parasite–host coevolutionary dynamics: for example, fosterer non-willingness to feed a chick with phenotype different from host chicks effectively results in chick discrimination (lowered parasite fitness, improved host fitness: this is certain) no matter what was the evolutionary origin of that behaviour (host–parasite coevolution, parent–offspring conflict, sibling competition, exploitation of preexisting preferences, etc.: this is uncertain). Thus, even general life history traits (Grim et al. 2011) might contribute to host avoidance or diminishing of misplaced investment into alien chicks (Soler 2008; Yang et al. 2013; Grim et al. 2017).

Despite increasing empirical evidence, there is completely untapped cornucopia of potentially relevant study systems. These include the many introduced host populations that were typically released from parasite pressures (reviewed in Grim and Stokke 2016). Such efforts will allow to study phylogenetic patterns of host responses to foreign chicks (Wang and Kimball 2012), their covariation with other host traits (Trnka and Grim 2014), and determining conditions which favour or constrain the evolution of chick discrimination (Britton et al. 2007). Empirical studies are fundamental, including metareplication, i.e. repeating the same study design across phylogeny, space and time (Grim et al. 2011; Grim and Stokke 2016). For example, Soler et al. (2013a) replicated the study of Grim (2007b) and found no evidence for the preprogrammed parental care in their model species. Empirical studies at nestling stage should be integrated with studies of all other stages of parasite and host life cycles: ignoring a life cycle stage can produce wrong conclusions, e.g. highly biased fitness estimates (Chap. 16). Comprehensive “all stages” approach was attempted rarely (Grim et al. 2011; Li et al. 2016; Chap. 16) and never really satisfactorily so far.

## 29.4 Constraints on Our Understanding of Host Defences

Understanding of chick discrimination has been hindered by both inappropriate methods in empirical research and prejudices in theoretical considerations. For the development of this field, it is essential that these errors are well understood and avoided in the future.

### 29.4.1 Non-experimental Data

An observation that hosts accept *natural* parasite chicks does not mean the host does not possess chick rejection abilities. Just like egg mimicry forces egg rejecters to accept (Igic et al. 2012), chick mimicry forces chick rejecters to accept (Langmore et al. 2011). Observations are inconclusive and cannot be used as evidence for the absence of chick discrimination—this flawed way of reasoning was standard in the past. The sole way to discover whether a host shows chick discrimination is experimental, either cross-fostering of various chicks with divergent phenotypes (Grim and Samaš 2016) or manipulation of host and parasite phenotypes (Redondo 1993).

An observation that parasite chicks are similar to host ones does not necessarily imply that chicks are mimetic. Host progeny (eggs, nestlings, fledglings) may resemble parasite progeny from various reasons other than mimicry (Grim 2005). Recent common descent of host and parasite will likely create a superficial—and flawed—impression of mimicry and indirectly of discrimination. This highlights the crucial importance of experiments, especially in the cases of mere “Phenotypic similarity” (Table 29.1). For example, for half a century at least (Voipio 1953), the rufous morph of the common cuckoo female was assumed to mimic falcons (*Falco* spp.). However, a closer examination of plumage patterns and cues known to be used by hosts for enemy recognition casts doubts on the hypothesis. Indeed, experimental data reject it (Trnka et al. 2015). This case warns us to infer mimicry from mere similarity, i.e. without experimental manipulations (Grim 2013).

Parasite chicks can die very soon after hatching and may easily go undetected (Delhey et al. 2011). Parasite chicks can also perish shortly before (Grim et al. 2003; Fig. 29.1c) or even after fledging (De Mársico et al. 2012); such cases might easily by misinterpreted as "parasite successful" because avian ecologists often use artificial cut-off points to score nest fates before fledging.

### 29.4.2 Preferential Feeding of Super-Chicks

If we adopt a view that parents *always* prefer larger, higher quality or more vigorously begging chicks (host exploitation hypothesis: Redondo 1993; see also Tanaka and Ueda 2005), then cuckoo chick discrimination will seem impossible—a parasite chick is almost always larger immediately after the emergence from the egg and begs more than host chicks do (Redondo 1993). What are the consequences of such constrained assumptions? Consistent parental/fosterer preference for a larger chick inevitably leads to ever-increasing discrepancy between the size of the largest chick (fed more and more) and the smaller chick (fed less and less); such a positive feedback leads to brood reduction (starvation or even death of smaller chicks). Even without any empirical data, this scenario seems unlikely to apply generally. Indeed, only some birds prefer to feed larger chicks, creating size asymmetries and leading to brood reduction (brood reducers *sensu* Soler 2002), whereas others prefer an egalitarian distribution of food, creating evenly sized broods and avoiding brood reduction (clutch adjusters *sensu* Soler 2002). The common cuckoo has specialized in parasitizing "clutch adjusters" species, and therefore cuckoo chicks need to be alone in the host nest, which makes egg eviction a compulsory strategy (Soler 2002; Grim et al. 2009a; Chap. 16).

### 29.4.3 Potential Cues for Chick Discrimination

Altricial chicks show low variation overall, and parents recognize them via their signals of need and quality (begging), creating a "blind alley" situation for the evolution of chick discrimination (Redondo 1993). I have refuted this argument previously (Grim 2006). Since then, a large body of evidence accumulated, showing that cues for potential chick discrimination are indeed more varied than realized previously (Table 29.3) and are present for the whole time after the parasite emerges from the egg, from hatchlings, through nestlings, to fledglings (for the last stage, see Chap. 30 and Tyller et al. 2018). Even for conspecific chicks, there is evidence of individual-level cues and recognition based on such fine-scale cues, in both parasitic and non-parasitic taxa (Kilner 2006; Shizuka and Lyon 2010, 2011; Levréro et al. 2009). For example, juvenile gapes, the skin, and feathers reflect UV-part of the light spectrum at least in some passerine nestlings and fledglings, and parents use these signals to adjust their provisioning (Tanner and Richner 2008 and references therein).

**Table 29.3** Diversity of potential chick discrimination cues, exemplified by the common cuckoo

| Cue | Host | Parasite | Reference |
|---|---|---|---|
| **Brood size** | Several chicks | Single chick | Anderson and Hauber (2007) |
| **Body size** | Normal | Larger | Wyllie (1981) |
| **Colour** | | | |
| Skin | Normal | (Different) | Wyllie (1981) |
| Gape | Normal | (Different) | Noble et al. (1999) |
| Natal down | (Present) | Absent | Harrison (2002) |
| Plumage | Normal | Different | Voipio (1953) |
| **Sound** | | | |
| Begging calls | Normal | (Different) | Butchart et al. (2003) |
| Host absent vocalizations | Absent | Present | Šicha et al. (2007) |
| **Behaviour** | | | |
| Eviction | Absent | Present | Anderson et al. (2009) |
| Wing-shaking | Symmetrical | Asymmetrical | Grim (2008) |
| **Smell** | | | |
| Skin smell | Normal | ? | No studies yet |
| Repulsive secretions | Absent | Present | Trnka et al. (2016) |
| **Demands** | | | |
| Length of care | Normal | Protracted | Grim (2007b) |
| Intensity of care | Normal | Elevated | Grim et al. (2003) |

“Normal” refers to non-parasitized host nests. Parentheses denote traits when the cuckoo chick is different from host chicks in some hosts but not in others

### 29.4.4 Adaptiveness of Late Chick Discrimination

What is the benefit of late chick desertion for the host that has already lost its own progeny? Previous mistaken investment does not imply that additional investment is adaptive. What matters is future benefits, regardless of previous (“sunk”) costs (see the concept of “Concorde fallacy”: Dawkins and Carlisle 1976). This applies not only to late chick discrimination (Grim et al. 2003) but also to even later fledgling discrimination (De Mársico et al. 2012; Soler et al. 2014). Mistakenly invested costs are continuously increasing every single day the host cares for foreign nestlings (including conspecific nestlings: Shizuka and Lyon 2010; Samas et al. 2014). Therefore every single day the host avoids such care adds to the host’s fitness.

**Concluding Remarks and Future Directions**

To move the field forward, it is now essential to focus on discovering more chick discrimination systems and then build theoretical models that could be informed by *quantitative* estimates of *empirically* determined costs and benefits. Both observational and experimental approaches will be necessary, including manipulation of chick phenotypic traits, cross-fostering of parasites

(continued)

and both conspecific and heterospecific chicks as controls. Laboratory studies might be important too but should be validated by experiments under natural conditions to confirm that laboratory results are not biased due to artificial environment in captivity.

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