

COMMENTS

Chick discrimination versus adaptive parasitic egg acceptance: the egg dilution effect hypothesis revisited

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Coevolutionary interactions between brood parasites and their hosts (Spottiswoode et al. 2012) became a prominent model for the study of antagonistic coevolutionary arms races (Dawkins & Krebs 1979). Despite considerable recent advances in this field, some aspects of host and parasite biology can only be described as enigmatic. Although our understanding of host egg discrimination and resulting parasite egg mimicry is well advanced, until recently, there was a conspicuous lack of studies focussing on chick discrimination and the resulting chick mimicry (Grim 2007a).

Since 2010, a series of important empirical studies have documented various cases in which parasite chicks have been deserted, starved or even ejected alive from host nests (Honza et al. 2010; Sato et al. 2010b; Shizuka & Lyon 2010; Tokue & Ueda 2010; Delhey et al. 2011; Grim et al. 2011; Hegemann & Voesten 2011; Shizuka & Lyon 2011; Soler & de Neve 2012; Yang et al. 2013; Sato et al. 2015; Yang et al. 2015; Sánchez-Martínez et al. 2017; Grim & Rutila in press). Other studies have revealed fascinating novel details about previously known chick discrimination systems (including fledgling discrimination: De Mársico et al. 2012; Soler et al. 2014), namely for the first time objectively quantifying parasite-host chick mimicry (Langmore et al. 2011) and even discovering previously unthought-of mechanisms of chick rejection (prenatal learning: Colombelli-Négrel et al. 2012, 2014). Although it is generally difficult to determine the causes and consequences of such (apparent) chick discrimination (Lichtenstein 2001; Schuetz 2005a,b; Anderson & Hauber 2007), these studies finally allow a more robust assessment of the conditions that favour or constrain the evolution of chick discrimination (Grim in press).

An integral and important part of these efforts has

always been the use of theoretical models (Lotem 1993; Planqué et al. 2002; Lawes & Marthews 2003; Grim 2006b; Britton et al. 2007) combined with discussions (Rothstein 1982; Redondo 1993; Grim 2005, 2011, 2013). The most recent model, “the egg dilution effect hypothesis” (Sato et al. 2010a) attempted to explain why the Large-billed Gerygone *Gerygone magnirostris* discriminates Little Bronze-Cuckoo *Chalcites minutillus* chicks (by ejection), but accepts cuckoo eggs (Sato et al. 2010b). The egg dilution model suggested that hosts may adaptively decide to accept a first-laid parasite egg, even though they might be cognitively able to discriminate the foreign egg (Soler et al. 1999, but see Hauber 2014), and postpone the rejection of the parasite into the nestling period. However, what is the adaptive value of this sophisticated hypothetical strategy? Accepting the first egg increases the total clutch size and consequently may benefit the hosts if the second-laying parasite female removes the egg of the first parasite female. Thus, the principle of the model parallels the classic dilution effect in the context of predation (Munro & Bédard 1977).

Sato et al. (2010a) formulated their model to specifically explain patterns of host defences in the Large-billed Gerygone versus Little Bronze-Cuckoo system. However, using data from a study system to create a model that explains only that very same data represents a tautology (Peters 1991). It should be stressed that Sato et al. (2010a) did not commit this mistake as they related their model to other study systems, specifically to all evicting cuckoos, i.e., cuckoos that instinctively evict host progeny (Honza et al. 2007; Grim et al. 2009) (see Sato et al. 2010a: pp. 117–118, Fig. 2, Appendix 1), which confirms that the model should apply generally (at least to evicting cuckoos). Notably, the egg dilution model has already been empirically applied in a different study of the Chalk-browed Mockingbird *Mimus saturninus* versus Shiny Cowbird *Molothrus bonariensis* system

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(Gloag et al. 2012; but see below).

On the one hand, I applaud Sato et al. (2010a) for realizing that dilution effects and resulting “safety in numbers” might theoretically represent an important yet so far ignored aspect of the ecological setting that moulds the evolution of egg rejection and, indirectly (as modelled by the egg dilution effect) other related strategies such as chick discrimination. On the other hand, when assessing the validity of any biological model we need to keep in mind several cautionary notes: (1) a model is only as good as its assumptions; (2) a model’s internal validity does not imply external validity, i.e., the logical coherence of a model does not automatically imply that the model is empirically correct; this is because no biological model can in principle take into account all relevant parameters that play roles under natural conditions; (3) the most fundamental question is whether empirical data do or do not support the model’s assumptions and predictions.

Sato et al. (2010a) listed five assumptions of their egg dilution effect model (their p. 116). I will show that each of these five conditions is either unlikely (conditions 1, 2, 3, 5) or never (4) met with in the real world in any brood parasite-host system; therefore, the egg dilution model cannot be applied generally. Furthermore, data from the Large-billed Gerygone versus Little Bronze-Cuckoo system are also at odds with the egg dilution effect model’s assumptions, showing that the model in its published form does not even explain the specific parasite-host system that inspired it.

ASSUMPTIONS

1) “Nests are parasitized twice and only after the host clutch is completed”

The core of the model rests on the occurrence of multiple parasitism. To find repeated parasitism events in the same nest requires very high egg parasitism rates (e.g., Moskát & Honza 2002). Therefore Sato et al. (2010a) reviewed parasitism rate estimates from previous studies (their Appendix 1) to support this assumption of their model. There are multiple issues with this data.

For the Reed Warbler *Acrocephalus scirpaceus* for example, the authors (Sato et al. 2010a) listed five estimates of parasitism rates by the Common Cuckoo *Cuculus canorus*. There are at least three problems here. First, checking the second reference revealed that Langmore et al.’s (2005) paper does not contain

any data on parasitism rates. Second, the Reed Warbler estimates range from 9 to 55%; however, only the value of 55% would count as a high parasitism rate that could regularly lead to evolutionary relevant rates of multiple parasitism. Notably, this outlier is based on the smallest sample size by far of the estimates cited from Wyllie (1981) (see his Table 17). Weighting by sample size gives an average parasitism rate of only 17%. Checking a more representative study of 16 different reed warbler populations across continental Europe (Stokke et al. 2007) gives an estimate four times lower: ~5%. Indeed, even parasitism rates “of 0.15 are likely to be quite high for cuckoos” (Broom et al. 2008). Third, even the estimate of ~5% based on data from Stokke et al. (2007) might be too high to give a reliable general picture. For most host populations and species, typical rates of Common Cuckoo parasitism *per host species* are given in single digit percentage values (Davies 2000, p. 120: 2–5%). Sato et al. (2010a) could only arrive at dramatically higher average values based on biased data selection: only regularly parasitized populations were included; their Appendix 1 does not contain a single non-parasitized host population. This is a major omission because many host populations, and in some hosts perhaps even the majority of populations, are allopatric, i.e., parasitism rates are often or even typically zero (Stokke et al. 2007; Moskát et al. 2008; Grim et al. 2011; Samas et al. 2014). Ignoring such populations artificially inflates estimates of parasitism rates and overestimates the potential for multiple parasitism.

Similarly, for the Great Reed Warbler *Acrocephalus arundinaceus* (Appendix 1 in Sato et al. 2010a) the single parasitism rate referred to is 51%. This represents one of the highest values ever reported for any Common Cuckoo host and surely is not typical for the species (e.g., Trnka & Grim 2014 and references therein). For example, Moskát and Honza (2002) reported a parasitism rate of 64%, which they rightly called “an unusually high frequency” in their “heavily parasitized” population. Such parasitism rates are not only extreme, but *cannot* be typical for a host species because such heavily parasitized populations represent population sinks that must be maintained by continuous immigration of hosts from other less parasitized, and consequently more productive, populations (Barabás et al. 2004; Moskát et al. 2008). I stress that this argument is not limited to these specific illustrative examples. The argument applies to any host of any brood parasite, including

all species of evicting cuckoos listed by Sato et al. (2010a, Appendix 1).

What matters for the evolution of a host's defences is the *general* parasitism pressure on the whole host species, whose populations are connected by gene flow (geographic mosaic theory of coevolution: Thompson 2005). In contrast, the parasitism rates that are typically reported in scientific publications are from long-term studies of *specific* populations that were non-randomly selected by researchers exactly because they show parasitism rates that are high enough to allow the collection of sufficient sample sizes. Therefore, general parasitism rates for hosts of the Common Cuckoo and other parasites listed by Sato et al. (2010a, Appendix 1) are at least one (or even two) orders of magnitude lower (Davies 2000) than those reported by Sato et al. (2010a). This means that the chances of double (not to mention triple) parasitism are negligible in virtually all hosts of the Common Cuckoo and most other brood parasites. This argument agrees well with empirical data as seen from almost any study of any cuckoo host, multiple parasitism is a rare phenomenon and not reported in the majority of studies. Even in the most heavily parasitized populations, the majority of nests do *not* contain multiple cuckoo eggs (Moskát & Honza 2002).

Multiple parasitism might be common in some populations of hosts parasitized by non-cuckoo parasites, e.g., *Molothrus* cowbirds (Trine et al. 1998; Gloag et al. 2012). However, this is not relevant because Sato et al. (2010a) aimed their model specifically at hosts of parasites that (a) belong to Cuculidae, and that are (b) evicting host offspring; the authors did not indicate whether their model could be extended to other, e.g., non-evicting parasites (but see Gloag et al. 2012). They cited only data from various cuckoo-host systems (Appendix 1), but all parasitism rate estimates were inflated because non-parasitized populations were omitted in all cases (see above).

I conclude that the parasitism rates that were cited and deemed to support the egg dilution effect model are selectively biased, clearly non-representative, and extremely overestimated. Just as the Large-billed Gerygone versus Little Bronze-Cuckoo system is not representative of avian brood parasites and their hosts in respect to chick discrimination (most hosts do not reject foreign chicks), it is also not representative in respect of parasitism rates and multiple parasitism (most hosts of brood parasites do not suffer such

extreme parasitism rates as the Large-billed Gerygone). This reflects generally poor citing practices in ecology – ~25% (!) of cited sources do not provide the apparent support (Todd et al. 2007) – and calls for more responsibility on the part of authors, referees, and editors.

In the second part of condition (1), for the egg dilution effect model to work, it is assumed that parasitism takes place “*only after the host clutch is completed*”. This condition is not supported, to my knowledge, in any host of any brood parasite. Generally, the overwhelming majority of parasitic egg laying occurs during the host laying period, not after clutch completion, and this holds true for any brood parasite (e.g., Wyllie 1981; Mermoz & Reboresda 1999; Davies 2000; Moksnes et al. 2000; Hanley et al. 2016; M. Kysučan & T. Grim extensive unpublished data from the Common Redstart *Phoenicurus phoenicurus* versus Common Cuckoo system, Samaš et al. 2016). Even Sato et al. (2010a) cite papers that reject this unrealistic assumption: e.g., two model cuckoo species studied by Brooker and Brooker (1989) laid the majority of their eggs *before* the hosts began incubating (13 out of 14 eggs and 8 out of 11 eggs, respectively, p. 537 in Brooker & Brooker 1989).

2) Rejecters “*regularly eject the first cuckoo egg before the second cuckoo lays her egg*”

This condition is also unlikely to be fulfilled by most hosts. The Great Reed Warbler, for example, is perhaps the only Common Cuckoo host that does suffer regular multiple parasitism in some populations (Moskát & Honza 2002). It shows exceptionally fine-tuned egg discrimination (as best shown by perfect mimicry in cuckoo eggs: Igic et al. 2012), yet Great Reed Warblers delay their ejection of natural cuckoo eggs on average by four days (and up to 10 days) after the onset of incubation (Fig. 2 in Hanley et al. 2016). Rejection of foreign eggs during incubation is common and not specific to Great Reed Warblers (Grim et al. 2014 and references therein). Thus, hosts almost always reject eggs during incubation, not during laying, and cuckoos almost always lay during the laying (not the incubation) period of the host. This empirical pattern pre-empts assumption (2).

I acknowledge that in special cases the second cuckoo may remove the egg of the first cuckoo, as reported in the Large-billed Gerygone versus Little Bronze-cuckoo system (Gloag et al. 2014). However, in this system hosts do not eject any *naturally laid*

cuckoo eggs, thus making this assumption empty under natural non-experimental conditions.

3) “*Hosts eject cuckoo eggs and nestlings without mistakes*”

Although this may be feasible in some hosts (error-free chick discrimination: Grim et al. 2003; Grim 2007b; Langmore et al. 2009b), it does not apply in most hosts. Most hosts make some mistakes (just as birds commit mistakes in any recognition task in nature, e.g., feeding of chicks: Tanaka et al. 2005). Rejection errors have been amply documented for host responses to eggs (Samas et al. 2014; reviewed in Stokke et al. 2016), and to chicks (Shizuka & Lyon 2010). More importantly, even Large-billed Gerygone themselves often “killed their own young,” a fact explicitly interpreted as a “recognition error” by Sato et al. (2010b). Thus, assumption (3) does not hold even in the system that the egg dilution effect aspired to explain.

4) “*Eggs and nestlings do not die other than when ejected by the host and the cuckoo*”

This condition is effectively impossible in any host due to the high nest predation rates typically found in all passerines. Open-nesting passerines suffer notoriously high predation rates, irrespective of the climatic zone in which they occur (Remeš et al. 2012).

Cavity (or closed nest) nesters (such as *Gerygone* spp.) suffer less predation but, as authors of the egg dilution effect model themselves stress in a further paper (Sato et al. 2010c) “predation rates are typically higher in tropical lowlands” and mangroves (inhabited by Large-billed Gerygone) “experience higher nest predation rates than do other habitat types in the region”. Thus, the authors’ own empirical data reject the assumption of their own model.

5) “*Hosts... eject cuckoo nestlings before they damage the host brood*”

This condition is supported in only one host, the Mangrove Gerygone *Gerygone laevigaster* (but with very small samples, $n=2$: Tokue & Ueda 2010). The condition is unlikely to apply generally, because chick discrimination among hosts of evicting cuckoos is delayed and typically happens after the eviction of host eggs and chicks by the cuckoo has already been completed. Specifically, Horsfield’s Bronze-cuckoo *Chalcites basalis* nestlings deserted by host Superb Fairy-wrens *Malurus cyaneus* were 3–6 days old (Langmore et al. 2003), long after the cuckoo

chicks had killed all of the host progeny. Similarly, the Common Cuckoo nestlings deserted by host Reed Warblers described by Grim et al. (2003), were 14–15 days old, and thus long after the hosts had lost their progeny due to being evicted by the parasite (Common Cuckoo chicks typically finish “cleaning” the host nest when 3–4 days old: Hauber & Moskát 2008; Anderson et al. 2009; Grim et al. 2009).

Little Bronze-cuckoo nestlings ejected by Large-billed Gerygone were 1–3 days old (Table 1 in Tokue & Ueda 2010), yet the hosts did not often save their own progeny because either their progeny were already absent from the nest when the hosts ejected the cuckoo chick, or they accidentally ejected their own progeny with the cuckoo chick (as inferred from Table 1 in Sato et al. 2010b). These delays in host defences against chicks are perhaps typical overall and chick discrimination may even be postponed to the post-fledging period: for example, the South American Baywing *Agelaioides badius* rejects non-mimetic Shiny Cowbird *Molothrus bonariensis* young only after the parasites have fledged, thus paying the full cost of parasite egg incubation and chick provisioning up until fledging (De Mársico et al. 2012; see also Soler et al. 2014).

ADDITIONAL ISSUES

Sato et al.’s (2010b) discussion section also suffers multiple problems. Some claims are presented without any empirical support, e.g. “The evolutionary lag hypothesis is implausible, as it appears sufficient evolutionary time for the occurrence and selection of the necessary mutation(s) for nestling ejection behavior has passed”. The authors simply claim this without showing any data. Indeed, I strongly suspect that it is actually impossible to provide reliable data to support such a claim (Grim & Stokke 2016).

Furthermore, the discussion of egg acceptance via “the bill-size constraint” is insufficient because there is no reason to assume that hosts have only two choices: to grasp the foreign egg, or to desert the parasitized nest. Gerygones could also choose to puncture foreign eggs, as many similarly-sized hosts of brood parasites do worldwide (Davies 2000). I note that desertion should be a viable strategy for Gerygones because re-nesting is less costly in the tropics (Langmore et al. 2003), where the *Gerygone* clade lives, than in the temperate zone – and even there desertion is a common response to parasitism (e.g., to conspecific parasitism: Samas et al. 2014).

RELAXATION OF MODEL CONDITIONS

It could be argued that any of the strict conditions that Sato et al. (2010a) considered could be relaxed. For example, Sato et al. (2010a) explicitly applied their model specifically to hosts of evicting cuckoos and did not discuss whether their model could be applied to other, e.g., non-evicting parasites or not. Gloag et al. (2012) applied the egg dilution model to non-virulent (*sensu* Kilner 2005) *Molothrus* parasites without indicating that the condition (5) (see above), is not fulfilled in their study system. Still, Gloag et al. (2012) concluded that their findings were in line with the egg dilution model. This indirectly suggests that (a) assumption (5) could indeed be relaxed or that (b) the model is too vague. As a general rule in science, models, hypotheses, and predictions must be specific enough to allow researchers to falsify them – e.g., via rejecting the assumption(s) of a model, which then calls for restructuring of the model and new empirical tests (Peters 1991). Models that “hold,” even when their assumptions do not hold, are useless (Peters 1991). Therefore, the contradiction in assumption (5) between Sato et al. (2010a) and Gloag et al. (2012) indicates that clarification of the conditions that facilitate, or prevent, egg dilution effects is necessary to specify to which study system(s) the model applies in the first place.

Assumption (3) might hold in some systems (Grim 2007b; Langmore et al. 2009b), but not in others (Stokke et al. 2016), including the system that inspired the proposal of the egg dilution model (Sato et al. 2010b). However, to make the model useful the relaxation of this assumption must be modelled explicitly – simply assuming that it might be relaxed then makes such an assumption redundant (Peters 1991). It is the responsibility of the authors of any scientific model to prove whether and how simplifying the conditions of the model affects its conclusions.

CONCLUSIONS AND RECOMMENDATIONS

The conditions required for the egg dilution model to work do not hold generally (even among evicting cuckoos), severely limiting the potential applicability of the model. More specifically, the conditions are not even fulfilled in the host-parasite system for which the model was proposed (i.e., Large-billed Gerygone versus Little Bronze-cuckoo system). Although the egg dilution model is logically consistent, it is difficult to imagine any real parasite-host system for

which it could work under natural and realistic conditions (note that Gloag et al.’s (2012) results do not provide a valid counterargument because their study system did not fulfil all assumptions of the egg dilution effect model). This underlines the general need for theoretical models to obey biological reality. For example, because we know that hosts do commit rejection errors under natural conditions in both parasitized and non-parasitized nests (Stokke et al. 2016), theoretical models must take this biological fact into account (as correctly done, e.g., by Mikami et al. 2015). Furthermore, parameter values should reflect biological reality: thus, for example, assuming a predation rate of a mere 15% (as done by Broom et al. 2008) is completely unrealistic for open-nesting passerines that are typical hosts of most cuckoos and cowbirds. Models that “work” only under unrealistic theoretical assumptions are of little value.

I find it striking that Sato et al. (2010b) completely ignored almost all previous models for the phenomenon they tried to explain. As stated above, there is a long tradition of theoretical formal or verbal modelling and discussions of conditions that prevent or allow the evolution of chick discrimination. Ironically, Sato et al. (2010b) cited only one of them – Lotem (1993) –, which is problematic theoretically (unnecessarily constrained and unrealistic assumptions, see Grim 2006b) and, more importantly, consistently *not* in line with empirical evidence for chick discrimination in nature (Planqué et al. 2002; Kilner 2005; Grim 2006a,b, 2011, in press). Therefore, it is incorrect to cite Lotem (1993) as an explanation for apparent prevalence of foreign chick acceptance among brood parasite hosts (Grim in press).

In their paper, Sato and colleagues (Sato et al. 2010a) expressed their wonderment as to why hosts that reject chicks do not reject eggs. First, the acceptance of parasite eggs that are quite similar to host eggs (Fig. 1 in Sato et al. 2010b) may not be very surprising, especially in closed and consequently poorly lit nests (Langmore et al. 2009a; Gloag et al. 2014). Second, and even more importantly, the patterns of a trade-off between egg- and chick-related defences is exactly what we should find under natural conditions if theoretical models – not cited by the authors of the egg dilution effect model – have some merit. Specifically, the rarer enemy model (Grim 2006b) explicitly predicted that *only* acceptors of natural parasite eggs should evolve chick discrimination (see also Langmore et al. 2003). Mathematical models (Planqué et al. 2002; Britton et al. 2007) support

this view. Indeed, almost all host-parasite systems in which chick discrimination or chick mimicry have been observed or suspected were limited to acceptors of natural parasite eggs (Table 1 in Grim 2006b). A large number of studies from the last decade consistently supports this pattern (Table 30.1 in Grim in press). Therefore, the claim that “The previously proposed hypotheses seem insufficient to explain the observed nestling ejection behaviour in the absence of egg rejection in the Large-billed Gerygone” (Sato et al. 2010b) is simply wrong. The previously proposed rarer enemy effect (Grim 2006b) and strategy blocking models (Britton et al. 2007) have explained this pattern very well.

I hope that the types of problems outlined and discussed here will represent a useful cautionary note for future theoretical and empirical studies of brood parasitism. These recommendations should improve our chances of disentangling the various patterns of host defence strategies.

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