

## Costs of virulence for brood parasitic young: a clarification

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I invite Kilner's response to my commentary. Although I do not object her re-interpretation of constraints as a special sort of costs ("Physical constraints are simply one mechanism by which costs on chick-killing are imposed", Kilner 2006, p. 244), there remain some points that need clarification.

### PHYSICAL CONSTRAINTS AND CHICK-KILLING

Kilner (2006) rebuts my "physical constraints on chick eviction" with several observations that show that "Even large host chicks may be evicted with relative ease".

First, in my original comment (Grim 2006a) I probably did not make entirely clear that I was interested more in *nest design* (i.e. size, shape, structure, see also p. 240 in "Effects of host breeding strategy" section) than in host chick body size *per se* (which is probably not very important unless being coupled with large nests). This hypothesis of "nest design as a constraint on chick eviction" is supported by data from Common Cuckoos (*Cuculus canorus*) parasitizing a small host, the hole-nesting Redstart (*Phoenicurus phoenicurus*). Although the cuckoo does show evicting behaviour in the nests of that host the eviction works very poorly there – only a half of cuckoo chicks succeed in killing all host progeny by eviction (Rutila et al. 2002). Even less successful are eviction attempts in nests with a smooth inner surface (e.g. the Song Thrush, *Turdus philomelos*) and/or a deep nest cup (e.g. the Fieldfare, *T. pilaris*). Although the cuckoo chicks are able to evict even relatively big eggs and chicks from nests of other hosts with shallow nests they were unable to evict any eggs (even experimentally added eggs much smaller than those of *Turdus* hosts) and chicks from the nests of both the Song Thrush and Fieldfare (T. Grim, M. Honza, A. Moksnes, C. Moskát, E. Røskaft, in prep.).

Second, there is no disagreement between my and Kilner's (2006) view in that "Physical constraints are ... unlikely to prevent the evolution of chick-killing by brood parasitic young, but they may well influence the means of execution" because in my original commentary I wrote specifically about *eviction* behaviour by parasite chick (not about chick-killing in general) and I explicitly claimed that physical constraints may lead to other than eviction mechanisms of chick-killing ("chick uses an alternative and very successful strategy – ... exaggerated begging" (Grim 2006a, p. 238).

### COSTS OF VIRULENCE IN COMMON CUCKOO CHICKS

(i) I agree that the limitation of parental abilities on the part of reed warbler hosts does not rule out potential signalling limitations in cuckoo chicks. The former limitation is supported by the observation that Reed Warblers are able to raise a cuckoo chick to a much higher fledging mass than under normal conditions if the parasite chick is cross-fostered to their unparasitized nest after being fed for some period (~ 10 days) in another nest. Thus, parents in the recipient nest are relieved from a substantial amount of parental care and, perhaps consequently, show an ability to invest more into the parasite chick which supports the contention that the constraint is, at least partly, on the part of the Reed Warblers (T. Grim, M. Pozgayova, unpubl. data).

(ii) The apparent discrepancy between Kilner (2006) and Grim (2006a) on cuckoo chick growth is just misunderstanding – Kilner wrote about *signalling* constraints whereas Grim (2006a) wrote about *growth* constraints; note that the term "signalling" did not appear in Grim (2006a) at all.

(iii) The single gape displayed at parasitized nests indeed does not explain the low feeding rate to cuckoos. Reed warblers adjust their feeding frequencies to the call rate of the brood and the total gape area of the brood with no respect to the number (single or any other) of gapes which contribute to this total gape area. In other words, number of open mouths per se does not influence provisioning rates by Reed Warblers (as indicated by the absence of a term “number of gapes” in the feeding frequency formula by Kilner et al. 1999, p. 668). Cuckoo chicks behaviour is affected by host provisioning rules not because a cuckoo chick has a *single* gape but because it has a very *small* gape for its body size. Moreover, the relatively small gape of the cuckoo chick is not only compensated (Kilner 2005, p. 57) by supernormal begging call rates but even over-compensated: a cuckoo chick receives significantly more food than same sized warbler chick (Grim & Honza 2001) and, consequently, grows significantly faster than an average four-chick host brood (T. Grim unpubl. data).

(iv) I certainly did not claim that “virulence cannot be adaptive if killing host young is costly, because the better strategy then would be to tolerate host young” (Kilner 2006). Obviously, *every* behaviour is costly whereas only *some* behaviours provide any benefits. To rephrase my original point, even if a presence of host young had increased a total delivery of food to the parasitized nest (Martin-Galvez et al. 2005) it is of no use to the cuckoo chick because the benefit goes to host nestlings and not to the parasite chick as experimentally shown by Martin-Galvez et al. (2005). Therefore, the increment in provisioning of the nest with both cuckoo and host young in comparison to the cuckoo alone cannot be interpreted as a benefit to the cuckoo and cannot be lost by evicting host young. Thus, the eviction of host young does not constrain but improves cuckoo’s ability to solicit care in the Martin-Galvez et al. (2005) study.

#### **PARASITIC CHICK REJECTION BY HOSTS**

My original claim that “by evicting host progeny the parasitic chick cannot *specifically* trigger host rejection response” (Grim 2006a) is not rejected by Kilner’s (2006) response. First, Langmore et al. (2003) indeed explicitly argued that the sole occupancy of the nest is *not* the only cue responsible for desertion of parasitised broods: “Our experiment shows that cuckoo chick desertion is not simply a by-product of a life-history strategy to avoid wasting time on single chick broods” (Langmore et al. 2003, p. 159). Second, although some host single-chick broods too were deserted it does not follow that the corresponding percentage of alien cuckoo chicks were deserted *because* they were perceived by fosterers as a single-chick broods. Langmore et al. (2003, p. 159) showed that the cue for desertion can be the structure of begging calls. Thus, *all* rejected non-mimetic cuckoo chicks might be deserted because of the acoustical cues whereas *all* rejected single-chick host broods might be deserted because of other reasons, e.g. brood size of one. Similarly, parasitic egg is ejected, by some host species, because of its size and/or colour whereas own host egg is sometimes rejected because of entirely different reasons, e.g. because it is cracked (Grim 2006b). Obviously, identical behaviours may frequently be triggered by various cues.

My suggestion that nestling discrimination is not learned (=imprinted) in the Superb Fairy-wren was based on results of Langmore et al. (2003), specifically the absence of any evidence for misimprinting and parent age effects on chick desertion (“Females that accepted a Horsfield’s bronze-cuckoo nestling did not abandon a lone fairy-wren chick in a later breeding attempt”, p. 159). These authors themselves interpreted their findings as “no evidence to support [misimprinting] view” (p. 159).

Further, desertion of cuckoo chicks – at least in some cases (Grim et al. 2003) – cannot be explained by high costs of parental care or by an inability of widowed member of a host pair to raise the large parasite chick as hypothesized by Kilner (2006). The experimental result that parasite chicks are deserted because of time-restrictive pre-programmed parental care (Grim 2006a) also shows that recognition is not necessary for discrimination (cf. Kilner 2006). Interestingly, reduction of brood size to one due to cuckoo chick evicting its nestmates is not a cost of virulence for the common cuckoo – host desertion was not triggered by brood size of one (Grim 2006a).

Finally, I feel it is fair to stress that the idea of host breeding strategies explaining interspecific variation in parasite chick virulence is not my “own explanation” (Kilner 2006, p. 246) but intellectual credits go to M. Soler (Soler 2002).

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