

COMMENT

Low virulence of brood parasitic chicks: adaptation or constraint?**ORNITHOLOGICAL
SCIENCE**© The Ornithological Society
of Japan 2006Tomas GRIM[#]*Department of Zoology, Palacky University, tr. Svobody 26, CZ-771 46 Olomouc, Czech Republic*

Chicks of some brood parasitic species severely decrease hosts' fitness through various behavioural strategies (e.g. eviction of host eggs or chicks, direct killing by pecking, aggressive begging) leading to the death of host progeny (Davies 2000). However, nestlings of some other parasitic species are more tolerant and raised in the presence of host offspring. In contrast to previous theory, which focused on the benefits of parasitic intolerance to host chicks, Kilner (2005) importantly drew attention to the costs of virulence. Although the killing of host progeny may be beneficial in terms of avoiding the cost of sharing or competing for parental care with host offspring, it might have also associated costs: by killing hosts young the parasite also kills its "helpers" in soliciting of parental care. Both comparative and experimental evidence suggests that the Brown-headed Cowbird (*Molothrus ater*) chick may benefit from the presence of a few—but not too many—host nestlings because a larger brood elicits higher parental feeding frequencies and the cowbird chick is able to outcompete host offspring to monopolize these extra feeds (Kilner 2003; Kilner et al. 2004). In addition, Kilner (2005) attempted to explain patterns of virulence and tolerance to host young by parasitic chicks in a wider context, i.e. across other brood parasite-host systems.

The idea of a trade-off between benefits and costs of virulence toward host chicks is brilliant, however, I will show that (i) most evidence presented by Kilner (2005) as supportive of the hypothesis may be explained more parsimoniously in other ways, (ii) the author did not consider a substantial body of evidence that goes against her hypothesis in at least some parasitic species, and (iii) to understand inter-specific variation in parasitic chicks virulence it is

necessary to consider not only trade-offs between costs and benefits of particular chick behaviours (Kilner 2005) but also physical and other constraints on the evolution of chick-killing strategies. Despite the following criticisms I believe that studies such as Kilner (2005) are important because they foster more research in an area so far neglected in the study of parasitic chicks (Grim 2006b).

**COSTS, BENEFITS AND CONSTRAINTS ON
PARASITIC CHICK TOLERANT AND
VIRULENT BEHAVIOUR**

Kilner (2005) importantly stresses that we have to consider both benefits and costs of parasitic chick tolerance towards host young. However, there is a third "side of the coin" that must be considered too—the constraints which set limits on chick behaviour.

For instance, why do Great Spotted Cuckoos (*Clamator glandarius*) not evict their nest-mates? Kilner (2005) correctly rejects the evolutionary lag explanation (p. 56) which is anyway an explanation of the last resort (Davies 2000). However, she does not consider the most obvious and non-adaptive explanation: Great Spotted Cuckoo chicks hatch in the nests of large hosts (magpies *Pica pica* and other corvids). The eviction of large host eggs and chicks may simply not be an option for the small parasitic chick in a deep corvid nest (Wyllie 1981, p. 151; Davies 2000, p. 98; Payne 2005, p. 147). The same holds for hole-nesters (Rutilla et al. 2002). There is some evidence that the eviction behaviour in the nests of some hosts is costly in terms of time (Nakamura 1990), impaired growth (Kleven et al. 1999), the risk of suicide by self-eviction (Molnar 1944; Wyllie 1981) and may even result in starving to death when the cuckoo chick concentrates on trying to evict the host nestlings (Soler 2002, p. 421). Under such

(Received 24 February 2006; Accepted 26 May 2006)

[#] E-mail: tomas.grim@upol.cz

physical constraints, the energy invested in eviction in large nests could be wasted. Instead, the Great Spotted Cuckoo chick uses an alternative and very successful strategy—it eliminates its competitors through exaggerated begging and wasting the food that could be otherwise taken by its competitors (Redondo 1993; Redondo & Zuniga 2002).

Kilner (2005) further discussed two other species of cuckoos. Common Koel (*Eudynamys scolopacea*) chicks indeed sometimes do not evict host young. Noticeably, they “tolerate” host’s young only in the nests of large body hosts (*Corvus*, *Urocissa*) in India while in Australia they parasitize smaller hosts and evict their nestmates (Davies 2000; Payne 2005). The mechanism of non-eviction in Indian subspecies may simply be an unsuccessful eviction (but this hypothesis needs testing). In addition, chicks of the Channel-billed Cuckoo (*Scythrops novaehollandiae*) can hardly be described as “benign” (Kilner 2005, p. 56): “Nestling hosts usually disappear within a week. The nestling cuckoo may crowd and starve them without evicting them...” (Payne 2005, p. 385). It seems that parasitic offspring in all three species discussed are “tolerant” to host offspring most likely because physical constraints imposed by host/nest selection by adult parasites. In my view, an ancestral evicting mutant of the Great Spotted Cuckoo or the Channel-billed Cuckoo would simply not be favoured by selection in the environment of large hosts due to too large energetic costs of eviction (see also Kleven et al. 1999; Rutila et al. 2002; Soler 2002). Intraspecific variability in the eviction behaviour of the Common Koel correlated with host body size is in line with this constraint hypothesis. However, to fully evaluate the alternatives, experimental evidence is needed about the potential growth and survival benefits of nestmate tolerance at the earliest nestling stages of Common Koels and Channel-billed Cuckoos.

NO COSTS OF KILLING OF HOST YOUNG FOR COMMON CUCKOO CHICKS

Kilner (2005, p. 57) argued that provisioning of Common Cuckoo (*Cuculus canorus*) chicks by Reed Warblers (*Acrocephalus scirpaceus*) is relatively slow for “a parasite that is unconstrained by kinship in its demands for food”. According to Kilner (2005) this low provisioning rate “is unlikely to be explained by a constraint on the part of the Reed Warblers” and thus may reflect a cost of virulence for the cuckoo chick that killed host young and thus lost their assis-

tance in obtaining enough food. This explanation is falsified by four lines of evidence.

(i) Indirect but suggestive evidence is that differences in the qualitative composition of diet delivered to cuckoo vs. host chicks probably reflect exhaustion on the part of Reed Warbler fosterers feeding the parasite (Grim & Honza 1997, 2001). The raising of a Cuckoo chick until fledging seems to be highly costly and hosts would be most likely unable to rear both their young and the parasitic chick if Common Cuckoos were non-evicting parasites.

(ii) The data on the growth of cuckoo chicks in other host species clearly reject the hypothesis that cuckoo chicks are somehow constrained and unable to grow faster in the Reed Warbler nests (cf. Kilner 2005, pp. 57–58). Cuckoo chicks have a capacity to reach about one third more mass in nests of a regular host, the Great Reed Warbler (*A. arundinaceus*; Kleven et al. 1999), and a rarely used host, the Song Thrush (*Turdus philomelos*; Grim 2006a), at the same age as in the nests of the Reed Warbler. This shows directly that the constraint is not on the part of the cuckoo but the Reed Warbler. Therefore, the slow growth of cuckoo chicks and their relatively “low” provisioning in the nests of Reed Warblers is not caused by cuckoos’ internal constraints but by the hosts’ inability (or non-willingness, Grim et al. 2003; Grim 2006c) to increase their feeding rates in the long term. Both the decreased foraging selectivity (Grim & Honza 2001) and growth patterns of parasitic chicks (Kleven et al. 1999; Grim 2006a) suggest that there is no spare provisioning capacity in host Reed Warblers that could be further exploited by cuckoo chicks. Although Brooke and Davies (1989) suggested that Reed Warblers might increase their feeding rates above those for the normal brood their experiments were probably too short-term to make the test rigorous.

(iii) The presence of a single gape in the nest (Kilner 2005, p. 57) is also unlikely to explain the low feeding rate because Reed Warblers “follow exactly the same integration rule when provisioning a single cuckoo in their nest as when feeding a brood of their own young” (Kilner et al. 1999, p. 667). In other words, number of open mouths *per se* does not influence provisioning rates by Reed Warblers. Cuckoo chicks behaviour is affected by host provisioning rules not because a cuckoo chick has a *single* gape but because it has a *small* gape for its body size.

(iv) Both observational (Rutilla et al. 2002) and experimental (Soler 2002; Martin-Galvez et al. 2005) evidence clearly showed that cuckoo chicks are very

poor competitors for parental care when accompanied by hosts own brood (either due to unsuccessful eviction of host progeny from too deep or hole nests or due to the experimental change in competitive environment).

To sum up, tolerance towards host young could not be beneficial for the Common Cuckoo chick in theory (i–iii) and it is not beneficial in reality (iv). The high virulence of cuckoo chicks is adaptive and clearly non-costly in terms of lost assistance of host chicks in obtaining sufficient amounts of food.

REJECTION OF THE PARASITIC CHICK BY HOSTS IS NOT A COST OF PARASITE'S INTOLERANCE TO HOST YOUNG

Kilner (2005, p. 58) argued that an additional cost of parasitic chick intolerance to host progeny may be rejection by hosts of the parasitic chick (see the section “2) Rejection by hosts” in that paper). Under this scenario the brood size of one resulting from parasite chick eviction of host progeny would trigger rejection (e.g., desertion) of the parasite chick. Therefore, chick rejection by the host can be critical for the evolution of virulence in parasite chicks: it would select against the parasite chick virulence. To support this scenario Kilner (2005) discussed results of Langmore et al. (2003). However, Kilner's (2005) re-interpretation of Langmore et al. (2003) data is distracting: “by killing host young, the parasite abolishes the hosts' inclination to deliver food at the nest entirely” (Kilner 2005, p. 58). As cuckoo chick rejections by hosts in that study were not explained as a by-product of brood reduction or desertion of uneconomically small one chick broods (as experimentally shown by Langmore et al. 2003) then it follows that by evicting host progeny the parasitic chick cannot specifically trigger host rejection response. Langmore et al. (2003) explicitly argued (p. 159 “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”) that the sole occupancy of the nest is *not* (contrary to Kilner 2005, p. 60) cue responsible for desertion of parasitised broods. Also in Reed Warbler vs. Common Cuckoo system where there is some evidence for chick discrimination (Grim et al. 2003) the brood size of one does not trigger desertion of the nest (Davies 2000; Grim et al. 2003; Grim 2006b, 2006c).

Further arguments by Kilner (2005, pp. 58–59) are

based on an assumption that hosts learn the appearance of their eggs and chicks. Although two influential experimental papers by Lotem et al. (1992, 1995) and his theoretical model (Lotem 1993) lead to the generally accepted impression that hosts learn the appearance of their eggs, the majority of empirical studies rejected the hypothesis—in all other common cuckoo host species than the Great Reed Warblers from Lotem et al. studies there is no evidence for age effects—and hence learning—on the egg discrimination abilities (Davies & Brooke 1988; Stokke et al. 1999; Marchetti 2000; Soler et al. 2000; Amundsen et al. 2002; Stokke et al. 2004). Thus, the arguments presented in the section “2) Rejection by hosts” may apply only in few hosts that learn appearance of their eggs but not in the majority of hosts that show experience-independent egg discrimination.

According to Lotem's (1993) model, hosts of evicting parasites—like the common cuckoo—should not be expected to discriminate against parasitic chicks. It is inappropriate that Kilner (2005, p. 59) presents results of Langmore et al. (2003) as a “serious challenge to Lotem's (1993) hypothesis”. The model was based on an *assumption* that the host learns egg and chick appearance. This assumption is clearly not met in the bronze-cuckoo (*Chrysococcyx* spp.)—Superb Fairy-wren (*Malurus cyaneus*) system where there is no evidence of imprinting and parent age effects on chick desertion (Langmore et al. 2003). Lotem's (1993) model “will be falsified if nestling discrimination is exhibited by hosts in which only the parasitic nestling remains in the nest, and if discrimination in this case is *learned*” (Lotem 1993, p. 744; emphasis added). This seems not to be the case in Superb Fairy-wrens (see also Grim 2006b, 2006c).

The comparison of *Vidua* and Shiny Cowbird (*Molothrus bonariensis*) systems with bronze-cuckoo system seems to imply that only the bronze-cuckoo host “unambiguously reject parasitic nestlings in favour of constructing a new nest” (Kilner 2005, p. 60). Literally, this is undisputable but it should not mean that only Superb Fairy-wrens reject alien chicks. Both *Vidua* and Shiny Cowbird chicks are reared *along* host chicks. In *Vidua* species there is good evidence that these parasites are mimetic and thus one cannot expect to observe their rejection under natural conditions (for review see Grim 2005, 2006b, for a case study Schuetz 2005). In the former system, host estrildids sometimes clearly reject (by refusing to feed) some of cross-fostered alien non-mimetic chicks which then die and are removed by

hosts while hosts own chicks remain in the nest (Payne et al. 2001). Thus, there is no reason for hosts for “constructing a new nest”. In the latter system, host Bay-winged Cowbirds (*Agelaioides badius*) refuse to feed non-mimetic Shiny Cowbird fledglings that probably die shortly after fledging outside the nest (Fraga 1998). Thus, hosts do not need to construct new nests after rejection of alien chicks in both systems. This does not have any bearing on the observations that both species unambiguously reject some parasitic chicks. Finally, also Reed Warblers in at least one frequently parasitised population fulfil the definition of chick rejection: they desert some old parasitic chicks which die and hosts sometimes start to build a new nest immediately after desertion of parasitized nests (Grim et al. 2003; Grim 2006c). Moreover, there are various other systems where chick discrimination was observed or is suspected due to circumstantial evidence (Redondo 1993; Grim 2006b). Thus, adaptive host response to parasitic chicks is much more frequent than Kilner (2005) implies. Fairy-wren vs. bronze-cuckoos system is not the first system where chick discrimination was found nor is it the only such system (for review see Grim 2006b). Perhaps most importantly, after taking into account the research effort in egg vs. chick studies there is no big difference in the “rarity” of chick in comparison to egg rejection behaviour (Grim 2006b) contrary to the generally accepted view in the literature (see any paper or book on brood parasitism mentioning chick discrimination).

To sum up, there is no evidence that parasite chick virulence is costly because it reveals “the parasite’s identity to hosts who then stop feeding it completely” (Kilner 2005, p. 60).

EFFECTS OF HOST BREEDING STRATEGY ON PARASITIC CHICK VIRULENCE

Kilner (2005, p. 62) predicted that the chick-killing brood parasites should show larger body size than their fosterers (although it is not clear whether *adult* body size or *chick* body size are discussed—this difference is of critical importance as pinpointed by Dearborn & Lichtenstein 2002, pp. 367–368). This hypothesis is based on possible costs and benefits for the parasitic chick but does not consider other important factors, namely (i) physical constraints imposed e.g. by host nest design and (ii) host breeding strategy. If the Common Cuckoo would parasitize hosts, e.g. thrushes of the genus *Turdus*, whose chicks are

larger than itself after hatching then the Cuckoo would not be virulent. This would be not because it would not need to monopolize all the parental care at the nest (as suggested by Kilner 2005) but because it would hatch in a deep nest and would be accompanied by large and quickly growing host chicks. Virulent behaviour, e.g. eviction, would simply not be an option under such physical constraints. Survival of the Cuckoo would then depend on the host breeding strategy: a Cuckoo chick would survive in the nests of clutch adjusters (who prefer to feed smaller chicks within the brood, Soler 2001, 2002) but it would die in the nests of brood reducers (who disfavour smaller chicks, Soler 2001, 2002). There is some experimental evidence in favour of this hypothesis (Soler 2002, Grim 2006a).

Most Common Cuckoo hosts are small passerines seemingly supporting Kilner (2005) hypothesis that chick-killing should evolve in systems with high parasite/host body-size ratio. However, in the nests of smaller hosts, the Cuckoo would thrive in nests of brood reducers (because it would be the largest chick in the brood) while it would have problems to obtain sufficient feeding in nests of clutch adjusters where parents would be—from cuckoo’s point of view—“distracted” by smallest chick(s) in the brood. Therefore, in the nests of small brood reducers there is no need to evolve energetically costly (Kleven et al. 1999) and risky (Wyllie 1981) chick-killing strategy of evicting behaviour—host preference for large chicks would work well enough taking into account the existence of parasitic adaptations such as a shorter incubation period and a more exaggerated begging behaviour. Most Cuckoo hosts show clutch adjusting strategy (Soler 2002) and the Cuckoo’s evicting behaviour seems to be an adaptation to obtain all the care otherwise provided for the whole host brood. But the reason for the cuckoo’s eviction behaviour is not the magnitude of the parasitic chick’s provisioning requirements (as predicted by Kilner 2005) but its inability to withstand the competition with host young (Molnar 1944; Rutila et al. 2002; Soler 2002; Martin-Galvez et al. 2005). Possible effects of parasite/host body size ratio on parasitic chicks virulence seems to depend more on host breeding strategies than on parasite chick provisioning demands (as hypothesised by Kilner 2005).

CONCLUSIONS

The exaggerated begging by non-evictor brood

parasitic young and their fast growth frequently results in starvation and early death of host young (Redondo 1993), which is in contradiction with predicted (Kilner 2005) benefits from non-eviction of host young. In my opinion, both comparative and experimental data strongly suggest that parasitic young in most parasitic species do not get any benefits from the presence of host young (e.g., in the *Cuculus* cuckoos). If there were any benefits of tolerance to host young they are most likely too small to outweigh both the benefits of elimination of host young (Redondo 1993) and the costs of tolerance of host young (Rutila et al. 2002; Soler 2002; Martin-Galvez et al. 2005). Kilner (2005, p. 58) also argued that the high virulence of parasite young which leads to reduction of brood size to one may increase the risk of parasite chick rejection by hosts. However, Langmore (2003), Grim et al. (2003) and Grim (2006b, 2006c) show that this rejection of intolerant parasite young by hosts does not seem to be a cost of parasite chick virulence. Further, the prediction that “the chick-killing brood parasites should be substantially larger than their hosts, whereas more benign brood parasites and their hosts should be more closely matching in size” (Kilner 2005, p. 62) also stems from alternative hypotheses, namely “physical constraints on eviction” hypothesis (this paper) and “host breeding strategy” hypothesis (Soler 2002) which seem to explain observed patterns of parasitic chick virulence in some host-parasite systems more parsimoniously than Kilner (2005) “cost of killing host young” hypothesis. Therefore, together with the trade-off idea Kilner (2005) suggested, constraints could be crucial for our understanding of interspecific variance in parasitic chick virulence. I believe that idea-rich paper by Kilner (2005) and the present paper will inspire more research in the neglected chick stage of parasite-host coevolution (Grim 2006b).

ACKNOWLEDGMENTS

I thank M. Soler, F. Takasu and others for comments on earlier versions of the MS. My work is supported by grants MSM6198959212 and GACR 206/03/D234.

REFERENCES

- Brooke ML & Davies NB (1989) Provisioning of nestling cuckoos *Cuculus canorus* by reed warbler *Acrocephalus scirpaceus* hosts. *Ibis* 131: 250–256.
- Davies NB (2000) *Cuckoos, cowbirds and other cheats*. T & AD Poyser, London.
- Dearborn DC & Lichtenstein G (2002) Begging behaviour and host exploitation in parasitic cowbirds. In: Wright J & Leonard ML (eds) *The evolution of begging*. pp 361–387. Kluwer, Dordrecht.
- Fraga RM (1998) Interactions of the parasitic screaming and shiny cowbirds (*Molothrus rufoaxillaris* and *M. bonariensis*) with a shared host, the bay-winged cowbird (*M. badius*). In: Rothstein SI & Robinson SK (eds) *Parasitic birds and their hosts*. pp 173–193. Oxford Univ Press, New York.
- Grim T (2005) Mimicry vs. similarity: which resemblances between brood parasites and their hosts are mimetic and which are not? *Biol J Linn Soc* 84: 69–78.
- Grim (2006a) Cuckoo growth performance in parasitized and unused hosts: not only host size matters. *Behav Ecol Sociobiol* 60: 716–723.
- Grim T (2006b) The evolution of nestling discrimination by hosts of parasitic birds: why is rejection so rare? *Evol Ecol Res* 8: 1–18.
- Grim T (2006c) Experimental evidence for chick discrimination without recognition in a brood parasite host. *Proc R Soc Lond B*: doi: 10.1098/rspb.2006.3731.
- Grim T & Honza M (1997) Differences in parental care of reed warbler (*Acrocephalus scirpaceus*) in its own nestlings and parasitic cuckoo (*Cuculus canorus*) chicks. *Folia Zool* 46: 135–142.
- Grim T & Honza M (2001) Does supernormal stimulus influence parental behaviour of the cuckoo's host? *Behav Ecol Sociobiol* 49: 322–329.
- Grim T, Kleven O & Mikulica O (2003) Nestling discrimination without recognition: a possible defence mechanism for hosts towards cuckoo parasitism? *Proc R Soc Lond B* 270: S73–S75.
- Kilner RM (2003) How selfish is a cowbird nestling? *Anim Behav* 66: 569–576.
- Kilner RM (2005) The evolution of virulence in brood parasites. *Ornith Sci* 4: 55–64.
- Kilner RM, Madden JR & Hauber ME (2004) Brood parasitic cowbird nestlings use host young to procure resources. *Science* 305: 877–879.
- Kilner RM, Noble DG & Davies NB (1999) Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature* 397: 667–672.
- Kleven O, Moksnes A, Røskoft E & Honza M (1999) Host species affects the growth rate of cuckoo (*Cuculus canorus*) chicks. *Behav Ecol Sociobiol* 47: 41–46.
- Langmore NE, Hunt S & Kilner RM (2003) Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature* 422: 157–160.
- Lotem A (1993) Learning to recognize nestlings is maladaptive for cuckoo *Cuculus canorus* hosts. *Nature*

- 362: 743–745.
- Lotem A, Nakamura H & Zahavi A (1992) Rejection of cuckoo eggs in relation to host age—a possible evolutionary equilibrium. *Behav Ecol* 3: 128–132.
- Lotem A, Nakamura H & Zahavi A (1995) Constraints on egg discrimination and cuckoo-host co-evolution. *Anim Behav* 49: 1185–1209.
- Martin-Galvez D, Soler M, Soler JJ, Martin-Vivaldi M & Palomino JJ (2005) Food acquisition by common cuckoo chicks in rufous bush robin nests and the advantage of eviction behaviour. *Anim Behav* 70: 1313–1321.
- Molnar B (1944) Cuckoo in the Hungarian plain. *Aquila* 51: 100–112.
- Nakamura H (1990) Brood parasitism of the cuckoo *Cuculus canorus* in Japan and the start of new parasitism on the azure-winged Magpie *Cyanopica cyana*. *Jap J Ornithol* 39: 1–18.
- Payne RB (2005) *The cuckoos*. Oxford Univ Press, Oxford.
- Payne RB, Woods JL & Payne LL (2001) Parental care in estrildid finches: experimental tests of a model of *Vidua* brood parasitism. *Anim Behav* 62: 473–483.
- Redondo T (1993) Exploitation of host mechanisms for parental care by avian brood parasites. *Etología* 3: 235–297.
- Redondo T & Zuniga JM (2002) Dishonest begging and host manipulation by *Clamator* cuckoos. In: Wright J & Leonard ML (eds) *The evolution of begging*. pp 389–412. Kluwer, Dordrecht.
- Rutila J, Latja R & Koskela K (2002) The common cuckoo *Cuculus canorus* and its cavity nesting host, the redstart *Phoenicurus phoenicurus*: a peculiar cuckoo-host system? *J Avian Biol* 33: 414–419.
- Schuetz JG (2005) Low survival of parasite chicks may result from their imperfect adaptation to hosts rather than expression of defenses against parasitism. *Evolution* 59: 2017–2024.
- Soler M (2001) Begging behaviour of nestlings and food delivery by parents: the importance of breeding strategy. *Acta Ethol* 4: 59–63.
- Soler M (2002) Breeding strategy and begging intensity: influences on food delivery by parents and host selection by parasitic cuckoos. In: Wright J & Leonard ML (eds) *The evolution of Begging*. pp 413–427. Kluwer, Dordrecht.
- Soler M, Palomino JJ, Martin-Vivaldi M & Soler JJ (2000) Lack of consistency in the response of Rufous-tailed Scrub Robins *Cercotrichas galactotes* towards parasitic Common Cuckoo eggs. *Ibis* 142: 139–158.
- Wyllie I (1981) *The cuckoo*. Batsford, London.