Host selection in parasitic birds: are open-cup nesting insectivorous passerines always suitable cuckoo hosts?

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How do potential hosts escape detrimental interactions with brood parasites? Current consensus is that hole-nesting and granivorous birds avoid brood parasites, like common cuckoos *Cuculus canorus*, by their inaccessible nest-sites and food unsuitable for parasites, respectively. Any open-nesting insectivorous hosts are believed to remain open to brood parasite exploitation which leads to the evolution of costly host defences like egg or chick discrimination. In contrast to this coevolutionary scenario, we show for the first time that a previously not studied but seemingly suitable host species escapes brood parasites. The Asian verditer flycatcher *Eumyias thalassinus*, feed newly hatched chicks entirely with beetles and grasshoppers. These are poor quality and hard to digest diet items that are rarely fed to own or cuckoo chicks by regular hosts. Indeed, chick cross-fostering experiments showed that these food items remained undigested by either cuckoos or other sympatric passerines causing them to die quickly. Egg discrimination experiments showed that the flycatcher accepts any foreign eggs. Although most but not all other potential explanations can be safely excluded at present, the most parsimonious historical explanation for these patterns is that the flycatcher exploits a trophic niche that no other sympatric bird can exploit, and that any cuckoo lineages that switch from their original hosts to the flycatcher have no possibilities for establishing viable populations. Thus, the current classification of host suitability based on diet composition may need revision, raising an important cautionary tale for comparative studies and the interpretation of apparent host rejection of parasitic chicks.

Coevolutionary interactions, e.g. those between common cuckoos *Cuculus canorus* and their hosts, are fundamentally constrained by host and parasite life-history traits (Davies 2000, Grim et al. 2011). For example, selection of nest sites may effectively prevent contact – and consequently also coevolution – between the parasite and the potential host (Røskaft et al. 2002). Traditionally the most often cited constraint on host selection is diet: insectivorous passerines are considered suitable hosts whereas seed-eaters that fail to raise cuckoo chicks are considered unsuitable (Rothstein 1976, Moksnes and Røskaft 1995, Soler et al. 1999, Davies 2000).

Here, we report evidence that casts doubts on this traditional view. In a previously unstudied open-cup nesting and insectivorous host, the Asian verditer flycatcher *Eumyias thalassinus*, our chick cross-fostering experiments showed that any foreign passerine or cuckoo chicks did not survive in the flycatcher nests. The majority of potential explanations for early chick deaths were not compatible with our empirical data (Discussion) leaving diet quality as the most viable candidate to explain why foreign chicks died in flycatcher nests. Strikingly, and in contrast to regular cuckoo hosts, the flycatchers fed almost only insects with thick exoskeletons (beetles, grasshoppers) to chicks in the nest. Using egg rejection experiments, we show a complete lack of any anti-parasite defences at the egg stage. These data suggest that the flycatcher did not coevolve with sympatric cuckoos and escapes successful utilization by brood parasites due to its specialized diet. We discuss implications of these findings for comparative studies and classification of host suitability in brood parasite–host coevolutionary studies.

Material and methods

Egg discrimination experiments

We studied flycatchers from April to August 2008–2011 in Kuankuoshui National Nature Reserve (107°02′–14′E,

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†Deceased 20 May 2012.

28°06′–19′N), Guizhou Province, China (Yang et al. 2012). For egg discrimination experiments, we did not use artificial model eggs that might be impossible to reject for puncture-ejector hosts (Martín-Vivaldi et al. 2002). We instead used real russet sparrow *Passer cinnamomeus* eggs painted dark blue with a non-toxic indelible ink pen to appear non-mimetic to flycatcher eggs (Fig. 1). Following established protocols (Grim et al. 2011), we monitored nests daily for six days to determine the response, classified as acceptance (experimental eggs being incubated) or ejection. No nests were deserted.

Chick discrimination experiments

We used eggs or chicks of multiple cuckoo and passerine species to successfully complete 18 heterospecific cross-fostering experiments (Supplementary material Appendix 1, Table A1). Since a particular species may always be atypical
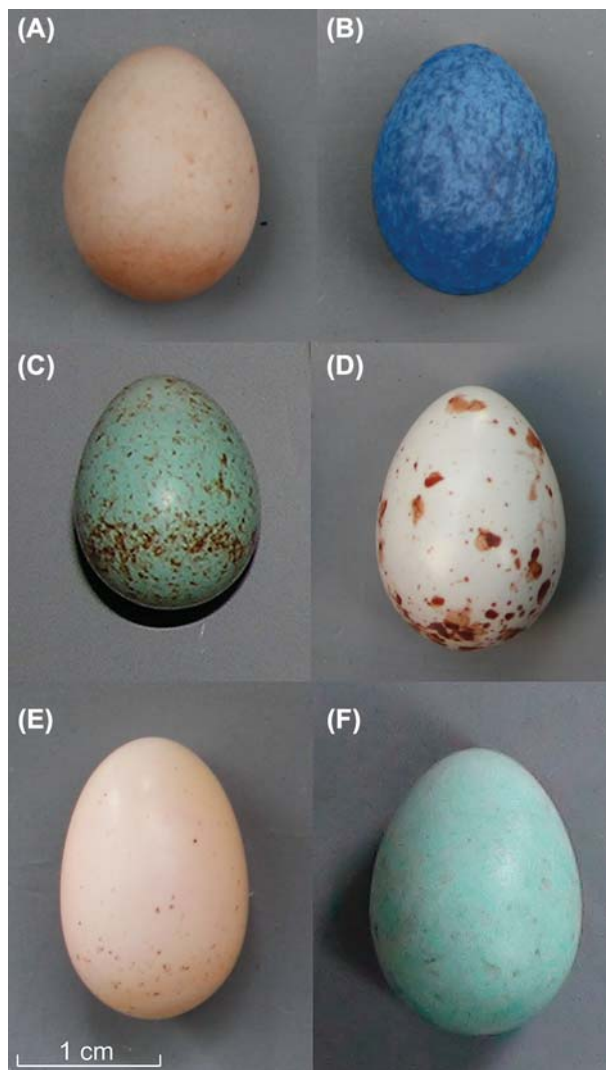

Figure 1. Eggs used in the egg recognition experiments: (A) Asian verditer flycatcher *Eumyias thalassinus*, (B) russet sparrow *Passer cinnamomeus*, painted blue (Methods), (C) daurian redstart *Phoenicurus auroreus*, (D) red-billed leiothrix *Leiothrix lutea*, (E) Himalayan cuckoo *Cuculus saturatus* and (F) common cuckoo *C. canorus*.

of the general ecological and behavioural patterns (Johnson 2002), instead of replicating within a single cross-fostered species, as done in some previous studies (Langmore et al. 2003, Grim 2006a, Grim et al. 2011), we invested research effort into replication among species. This provides a heuristically stronger test than traditional cross-fostering of a single species (Johnson 2002). Because foreign chicks invariably died in flycatcher nests (n = 12), increasing sample sizes at the cost of animal suffering was unwarranted for ethical reasons (Taborsky 2010). We acknowledge that to ensure that cross-fostering itself did not cause nestling death, it would be necessary to perform conspecific cross-fosterings too (Slagsvold 1998, Grim 2007). However, despite an extensive literature search we are unaware of any study that would find that cross-fostering of conspecific chicks per se caused poor chick growth, not to speak of death (Slagsvold 1998), unless the necessity of parental care at the nest is artificially prolonged, which was not the case in our study (cf. Grim 2007).

In egg acceptor hosts we exchanged eggs at the same incubation stage to ensure that cross-fostered eggs hatched synchronously with host eggs. In egg rejecter hosts, exchanges were only conducted during the early nestling period with hatchlings of similar ages. We matched source and target nests within a pair in chick body mass (paired t-test, $t_{14} = 1.38$, p = 0.19).

Ethical concerns were given the highest priority. Experimental procedures were in line with Chinese laws and in agreement with the Animal Research Ethics Committee of Hainan Provincial Education Centre for Ecology and Environment, Hainan Normal Univ. Fieldwork was carried out under the permission from the Forestry Dept of Guizhou Province and Kuankuoshui National Nature Reserve, China. Experiments, including cross-fostering of chicks, were carried out following standard protocols widely used in similar studies (Grim et al. 2011). Since we experienced that foreign chicks invariably died in flycatcher nests, we kept sample sizes to a minimum (Taborsky 2010, Grim et al. 2011).

Results

Natural parasitism and host behaviour at the egg stage

We recorded no cases of parasitism (n = 50 flycatcher nests) despite the fact that the laying period of the flycatcher (April–August) completely overlaps the breeding seasons of the 11 sympatric cuckoo species, including five species of *Cuculus* cuckoos, at our study site (Yang et al. 2012). This apparent absence of parasitism was not a by-product of fast rejection of foreign eggs by flycatchers and hence our inability to detect parasitism: experimentally parasitized fly-catchers accepted all russet sparrow eggs painted non-mimetic blue (n = 18; the flycatcher lays spotted pinkish eggs, Fig. 1). They also accepted the eggs (Fig. 1) of four other species used for cross-fostering experiments (Supplementary material Appendix 1, Table A1). Finally, we did not record any egg losses that might be indicative of egg rejection errors (Davies 2000) at unmanipulated control nests (n = 10).

The absence of cuckoo parasitism in the flycatcher was also not a consequence of the host's nest site selection. The daurian redstart *Phoenicurus auroreus* that breeds in sympatry with the flycatcher in our study area and occupies very similar nesting sites (on buildings or in shadowed rock faces) is heavily parasitized by the common cuckoo (parasitism rate = 15.7%, n = 51 nests; differing significantly from the parasitism rate of the flycatcher: Fisher exact test, p < 0.0001) and often rejects non-mimetic foreign eggs (rejection rate = 73.2%, n = 11; differing significantly from the rejection rate of the flycatcher: Fisher exact test, p = 0.0058).

Host behaviour at the nestling stage

In cross-fostering experiments, all foreign nestlings introduced to flycatcher nests (n = 12), including cuckoo chicks, died within two days (Supplementary material Appendix 1, Table A1). Before they died, cuckoo chicks (n = 3) successfully evicted all host eggs/chicks. Chicks surviving until day 2 (hatching day = 0) appeared sick and inactive. After day 2, all foreign nestlings were found dead in the nest (n = 7), on the ground under the nest (n = 2), or they had disappeared (n = 3). In the last two categories, chicks were most likely removed by parents, which is a standard passerine behavior unrelated to brood parasitism (Davies 2000, Grim 2006a).

We examined the dead nestlings (n = 4) and found that their stomachs were filled with undigested insects with thick exoskeletons, identifiable items including beetles (Coleoptera) and grasshoppers (Orthoptera; Fig. 2). By contrast, all flycatcher nestlings (n = 6) survived after they were introduced into the nests of other passerine species (Supplementary material Appendix 1, Table A1). The results were clear-cut (survival of foreign chicks in flycatcher nests [0% of 12 cases] versus flycatcher chicks in foreign nests [100% of six cases]: Fisher's exact test: p < 0.0001) and consistent across a wide phylogenetic spectrum of species (Supplementary material Appendix 1, Table A1).

Figure 2. A dead common cuckoo nestling filled with insects containing thick exoskeletons that remained undigested.

Discussion

We demonstrate for the first time that an insectivorous open-cup nesting passerine is prevented from long-term coevolution with brood parasites. Asian verditer flycatchers did not neglect foreign chicks (i.e. they fed them), which rejects two major hypotheses that explain poor survival of parasites in nests of hosts: host un-willingness to feed foreign chicks due to their alien phenotype (i.e. evolved nestling discrimination; Langmore et al. 2003), or an inability of foreign chicks to communicate their hunger well to foreign foster species (Schuetz 2005). Alternatively, nest architecture may constrain eviction of host eggs and chicks by the parasite chick (Grim et al. 2009a) leading to fatal competition with host chicks (Grim et al. 2009b). This hypothesis can be excluded as cuckoo chicks were successful evictors in the present study. Brood size can also trigger host decision to desert a single cuckoo chick after it evicted its nestmates (Langmore et al. 2003). This explanation is rejected by the finding that chicks were fed even after they finished evicting host progeny (see full stomachs of dead chicks). Further, hosts may be unable to match provisioning requirements (i.e. diet quantity) of the parasite (Grim 2007). However, this explanation cannot in principle hold for the earliest stages of post-natal ontogeny (because the parasite is initially small and similarly sized to the host's own nestlings), and it is clearly rejected by our empirical data (dead chicks had full stomachs). Theoretically, foreign chicks may not cope with parasites, e.g. mites, in the recipient nests but we did not notice any mites either in nest-cups or on the chicks themselves. However, an unknown disease that is not possible to notice by human sight could kill the cross-fostered nestlings. Similarly to all previous studies (Langmore et al. 2003, Sato et al. 2010, Tokue and Ueda 2010, Delhey et al. 2011) that did not address this possibility, we cannot exclude this explanation although we find it unlikely that a disease would kill 100% of cross-fostered chicks (see also Slagsvold 1998, Grim 2007).

Excluding all these alternatives leaves only one possible explanation, namely diet quality. Indeed, composition of diet that was fed by the Asian verditer flycatcher to nestlings is very unusual. Although cuckoo hosts do feed their chicks occasionally with beetles and grasshoppers these taxa form a negligible part of their diet (less than 5% both in terms of number dominance and mass proportion; Grim and Honza 1997, 2001; Grim unpubl.). In contrast, beetles and grasshoppers formed almost 100% of chick diet in Asian verditer flycatchers. These insect groups are low quality and hard-to-digest prey (Soler 2008). However, we do not know what exactly caused hatchling death. Alternative explanations include that insects were indigestible due to their thick exoskeletons (as preliminary assessed by human vision) or even poisonous. Currently, nothing is known about the natural diet of this flycatcher's own nestlings (our literature search), and thus we also do not know whether this species switches to a different diet when being faced with heterospecific nestlings in its nest.

Despite these questions, that provide exciting options for future research, our findings remain unique because previously documented cases of parasite chick deaths were invariably caused by decreased provisioning in insectivorous

hosts (Langmore et al. 2003, Delhey et al. 2011; other cases reviewed in Grim 2006a, 2011). We also note that the exact mechanistic cause behind diet unsuitability is unknown for hosts of any brood parasite – even in granivorous and frugivorous hosts we do not know what substance(s), including potentially poisonous ones, cause the death of the parasite chick (Rothstein 1976, Middleton 1991, Kozlovic et al. 1996). Our findings of undigested insets in the stomachs of dead chicks parallel findings of Kozlovic et al. (1996) who reported that brown-headed cowbird *Molothrus ater* nestlings that died in the nests of house finches *Carpodacus mexicanus* had in their stomachs mostly 'plant material' that remained 'largely undigested' (p. 255). They concluded that cowbird chick death was caused by cowbird inability to digest plant matter. Under this explanatory paradigm it is possible that also chick deaths in our study were caused by the inability of chicks to digest a diet consisting of exceptionally large proportions of beetles and grasshoppers, no matter what particular substance was causally responsible for chick deaths (see also Soler 2008). However, only feeding experiments will provide definite test of this exciting hypothesis.

The diet of Asian verditer flycatchers seems to cause early death for any foreign chicks raised by this host, including cuckoo chicks. Two scenarios may explain this finding.

First, according to the 'coevolutionary scenario' the flycatcher was frequently parasitized by cuckoos, causing it to evolve egg rejection, and this egg rejection imposed strong selection on cuckoos to evolve perfect egg mimicry, which forced the host to accept foreign eggs. Subsequently coevolution evolved at the nestling stage (Langmore et al. 2003, Grim 2006a). Here, the flycatcher shifted to a new trophic niche, in which cuckoos were unable to respond by evolving new digestive abilities of their chicks and, therefore, they went extinct. This scenario predicts that hosts should show rejection of experimental non-mimetic eggs (but not natural cuckoo eggs, Grim 2011) because antiparasite defences typically persist, although sometimes in lower levels, even in the absence of brood parasitism for long periods (Peer et al. 2011).

Second, according to the 'constraint scenario' the flycatcher exploited its unique dietary niche independently of interactions with brood parasites. Cuckoos that for any reason (e.g. population decline of previously accessible and common hosts) started to utilize the flycatcher failed due to chick diet composition. Therefore, there should be no long-term selection for the evolution of host abilities to reject foreign eggs. Thus, this scenario predicts that hosts should show no egg discrimination.

Two empirical lines of evidence (no egg rejection by the flycatcher, strong egg rejection by sympatric species with similar nest site selection, i.e. the daurian redstart) support the latter 'constraint' scenario. Additionally, it is unlikely that a species would change its trophic niche to starve cuckoo nestlings because such a shift would affect much of the host's ecology and would not affect most of the costs of parasitism because cuckoo nestlings survive sufficiently long to kill all host progeny (Results). Finally, a dietary shift would not diminish selection on the evolution of egg discrimination (Grim 2006a), and thus we should see at least some egg rejection by flycatchers (Davies 2000,

Peer et al. 2011). In contrast, our empirical data show that this species is a pure acceptor of even highly dissimilar foreign eggs. Thus, the most parsimonious explanation seems to be that the flycatcher has never been a regular victim of brood parasites, and therefore has escaped coevolutionary interactions with any of the 11 sympatrically breeding cuckoo species, its specialized diet (a general life-history trait unrelated to parasitism) causing it to be 'primarily unsuitable' (Grim et al. 2011) as a cuckoo host.

Although the physiological adaptations of the flycatcher for digesting the special diet remain to be tested in the future, our experimental data unambiguously show that even open-cup nesting insectivorous passerines can be unsuitable cuckoo hosts. This finding strikingly contrasts with established views (Moksnes and Røskaft 1995, Soler et al. 1999, Davies 2000, Røskaft et al. 2002). Our study also raises an important cautionary tale for the interpretation of documented cases of chick rejection by hosts (Grim 2006a, Sato et al. 2010, Tokue and Ueda 2010) because parasitic chicks may have been sick due to their diet and then removed from the nest by parent hosts, a behavior unrelated to brood parasitism (Grim 2006a). However, the cases where 'little food was found in the stomach of dead nestlings' may represent real neglect of parasites by hosts although phenotypic cues triggering such host differential responses remain to be tested in the future (Delhey et al. 2011, see also Schuetz 2005).

The present study has important general implications for our understanding of brood-parasite–host coevolution. It adds to a growing body of evidence that non-specific general life-history traits can slow down or even prevent coevolution between brood parasites and their hosts (Grim et al. 2011). Our study highlights that simple descriptive categorization of hosts as typically done in comparative studies (Moksnes and Røskaft 1995, Soler et al. 1999), such as 'suitable insect-eating' versus 'unsuitable seed-eating', may sometimes be misleading as a non-insect diet may be suitable for cuckoos (Martín-Gálvez et al. 2005, Grim 2006b), whereas an insect diet may be unsuitable (this study). Instead, rigorous experimental cross-fostering studies, as exemplified by the present work, are needed to explicitly test host suitability and, by implication, the potential for coevolution between parasite and host.

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Table 1 Survival of cross-fostered eggs/chicks of foreign species. Verditer flycatchers either served as hosts (i.e., being experimentally parasitized by cuckoos and other sympatric passerines) or parasites (i.e., being transferred to foreign sympatric heterospecific passerine nests).

Hosts	Parasites	Original clutch size (hosts)	Experimental period (hosts)	Cross-fostering target	No. cross-fostered offspring	Success (parasites)	Duration of time surviving (parasites)
	common cuckoo	4	early incubation	egg	1 egg	dead	< 2 days
	Cuculus canorus	5	early incubation	egg	1 egg	dead	< 1.5 days
	Himalayan cuckoo *Cuculus saturatus*	4	incubation	egg	1 egg	dead	< 1 day
	ashy-throated parrotbill *Paradoxornis alphonsianus*	4	early nestling	nestling	1 nestling	dead	< 1.5 days
	daurian redstart *Phoenicurus auroreus*	3	incubation	egg	3 eggs	dead	< 2 days
Asian verditer flycatcher *Eumyias thalassinus*	green-backed tit *Parus monticolus*	4	early nestling	nestling	4 nestlings	dead	< 1-2 days
	grey bushchat *Saxicola ferrea*	5	early nestling	nestling	1 nestling	dead	< 1.5 days
	red-billed leiothrix	3	egg laying	egg	1 egg	dead	< 2 days
	Leiothrix lutea	4	early incubation	egg	4 eggs	dead	< 2 days
	russet sparrow	5	egg laying	egg	1 egg	dead	< 1.5 days
	Passer cinnamomeus	4	early nestling	nestling	4 nestlings	dead	< 1.5 days
	white-bellied redstart *Hodgsonius phoenicuroides*	5	early nestling	nestling	5 nestlings	dead	< 2 days

Daurian redstart *Phoenicurus auroreus*		4	incubation	egg	4 eggs	fledged	> 13 days
green-backed tit *Parus monticolus*		5	early nestling	nestling	1 nestling	fledged	> 14 days
grey bushchat *Saxicola ferrea*	Asian verditer flycatcher *Eumyias thalassinus*	4	early nestling	nestling	4 nestlings	predated	>= 4 days
red-billed leiothrix *Leiothrix lutea*		3	early nestling	nestling	1 nestling	fledged	> 12 days
russet sparrow *Passer cinnamomeus*		4	egg laying	egg	1 egg	predated	>= 6 days
white-bellied redstart *Hodgsonius phoenicuroides*		3	nestling	nestling	3 nestlings	predated	>= 8 days