



# 0 Host selection in parasitic birds: are open-cup nesting insectivorous passerines always suitable cuckoo hosts? 53

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20 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. 70

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35 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). 75

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45 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 80

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95 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. 90

## Material and methods 100

### Egg discrimination experiments

We studied flycatchers from April to August 2008–2011 in Kuankuoshui National Nature Reserve (107°02′–14′E, 105

52 <sup>†</sup>Deceased 20 May 2012.

0 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

15 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

of the general ecological and behavioural patterns (Johnson 2002), instead of replicating within a single cross-fostered species, as done in some previous studies (Grim 2006a, Langmore et al. 2003, 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 University. Fieldwork was carried out under the permission from the Forestry Department 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 flycatchers 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 ( $n = 10$ ).



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*.

0 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  
 5 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  
 10 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

15 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  
 20 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  
 25 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  
 30 (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  
 35 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 1 Table A1).



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60 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  
 65 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 unwillingness to feed  
 foreign chicks due to their alien phenotype (i.e. evolved nest-  
 70 ling 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  
 75 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  
 80 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  
 85 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  
 90 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  
 95 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  
 100 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  
 105 terms of number dominance and mass proportion; Grim  
 and Honza 1997, 2001; Grim unpubl. data). 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.  
 110 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  
 115 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  
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0 hosts (Langmore et al. 2003, Delhey et al. 2011; other cases  
1 reviewed in Grim 2006a, 2011). We also note that the  
2 exact mechanistic cause behind diet unsuitability is  
3 unknown for hosts of any brood parasite – even in  
4 granivorous and frugivorous hosts we do not know what  
5 substance(s), including potentially poisonous ones, cause  
6 the death of the parasite chick (Rothstein 1976, Middleton  
7 1991, Kozlovic et al. 1996). Our findings of undigested  
8 insects in the stomachs of dead chicks parallel findings of  
9 Kozlovic et al. (1996) who reported that brown-headed  
10 cowbird *Molothrus ater* nestlings that died in the nests  
11 of house finches *Carpodacus mexicanus* had in their  
12 stomachs mostly ‘plant material’ that remained ‘largely  
13 undigested’ (p. 255). They concluded that cowbird chick  
14 death was caused by cowbird inability to digest plant  
15 matter. Under this explanatory paradigm it is possible that  
16 also chick deaths in our study were caused by the inability  
17 of chicks to digest a diet consisting of exceptionally large  
18 proportions of beetles and grasshoppers, no matter what  
19 particular substance was causally responsible for chick  
20 deaths (see also Soler 2008). However, only feeding experi-  
21 ments 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.

25 First, according to the ‘coevolutionary scenario’ the fly-  
26 catcher was frequently parasitized by cuckoos, causing it  
27 to evolve egg rejection, and this egg rejection imposed  
28 strong selection on cuckoos to evolve perfect egg mimicry,  
29 which forced the host to accept foreign eggs. Subsequently  
30 coevolution evolved at the nestling stage (Langmore et al.  
31 2003, Grim 2006a). Here, the flycatcher shifted to a new  
32 trophic niche, in which cuckoos were unable to respond  
33 by evolving new digestive abilities of their chicks and, there-  
34 fore, they went extinct. This scenario predicts that hosts  
35 should show rejection of experimental non-mimetic eggs  
36 (but not natural cuckoo eggs, Grim 2011) because anti-  
37 parasite defences typically persist, although sometimes in  
38 lower levels, even in the absence of brood parasitism for  
39 long periods (Peer et al. 2011).

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

49 Two empirical lines of evidence (no egg rejection by the  
50 flycatcher, strong egg rejection by sympatric species with  
51 similar nest site selection, i.e. the daurian redstart) support  
52 the latter ‘constraint’ scenario. Additionally, it is unlikely  
53 that a species would change its trophic niche to starve  
54 cuckoo nestlings because such a shift would affect much of  
55 the host’s ecology and would not affect most of the costs  
56 of parasitism because cuckoo nestlings survive sufficiently  
57 long to kill all host progeny (Results). Finally, a dietary  
58 shift would not diminish selection on the evolution of  
59 egg discrimination (Grim 2006a), and thus we should see  
60 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.

61 Although the physiological adaptations of the flycatcher  
62 for digesting the special diet remain to be tested in the  
63 future, our experimental data unambiguously show that  
64 even open-cup nesting insectivorous passerines can be  
65 unsuitable cuckoo hosts. This finding strikingly contrasts  
66 with established views (Moksnes and Røskaft 1995, 67  
68 Soler et al. 1999, Davies 2000, Røskaft et al. 2002).  
69 Our study also raises an important cautionary tale for the  
70 interpretation of documented cases of chick rejection  
71 by hosts (Grim 2006a, Sato et al. 2010, Tokue and Ueda  
72 2010) because parasitic chicks may have been sick due to  
73 their diet and then removed from the nest by parent hosts,  
74 a behavior unrelated to brood parasitism (Grim 2006a).  
75 However, the cases where ‘little food was found in the  
76 stomach of dead nestlings’ may represent real neglect of  
77 parasites by hosts although phenotypic cues triggering  
78 such host differential responses remain to be tested in the  
79 future (Delhey et al. 2011, see also Schuetz 2005).

80 The present study has important general implications  
81 for our understanding of brood-parasite–host coevolution.  
82 It adds to a growing body of evidence that non-specific  
83 general life-history traits can slow down or even prevent  
84 coevolution between brood parasites and their hosts (Grim  
85 et al. 2011). Our study highlights that simple descriptive  
86 categorization of hosts as typically done in comparative  
87 studies (Moksnes and Røskaft 1995, Soler et al. 1999), such  
88 as ‘suitable insect-eating’ versus ‘unsuitable seed-eating’,  
89 may sometimes be misleading as a non-insect diet may  
90 be suitable for cuckoos (Martín-Gálvez et al. 2005, Grim  
91 2006b), whereas an insect diet may be unsuitable (this  
92 study). Instead, rigorous experimental cross-fostering  
93 studies, as exemplified by the present work, are needed to  
94 explicitly test host suitability and, by implication, the  
95 potential for coevolution between parasite and host.

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