Evicting cuckoo nestlings from the nest: a new anti-parasitism behaviour

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As avian brood parasitism usually reduces hosts' reproductive success, hosts often exhibit strong defence mechanisms. While such host defences at the egg stage (especially egg rejection) have been extensively studied, defence mechanisms at the nestling stage have been reported only recently. We found a previously unknown anti-parasitism behaviour in the large-billed Gerygone, which is a host species of the little bronze-cuckoo, a host-evicting brood parasite. The hosts forcibly pulled resisting nestlings out of their nests and dumped them. Although it has been suggested that defence mechanisms at the nestling stage may evolve when host defence at the egg stage is evaded by the parasite, the studied host seems to lack an anti-parasitism strategy at the egg stage. This suggests that the evolutionary pathway may be quite different from those of previously studied cuckoo–host systems. Future research on this unique system may give us new insights into the evolution of avian brood parasitism.

Keywords: anti-parasitism strategy; avian brood parasitism; bronze-cuckoo; host–parasite coevolution; nestling ejection

1. INTRODUCTION

Since brood-parasitic cuckoos usually reduce their host's reproductive success, hosts exhibit strong defence behaviour against parasitism (Wyllie 1981). The ejection of cuckoo eggs from host nests is one such defence mechanism, but it depends on hosts having the ability to reliably discriminate cuckoo eggs (Davies 2000). If cuckoo eggs slip through the hosts' detection system, and hatch, hosts typically accept the cuckoo nestlings and take care of them until they reach independence (Wyllie 1981).

Why do hosts accept cuckoo nestlings? One hypothesis is that learning to recognize parasitic nestlings is costly (recognition error outweighing benefit) and thus maladaptive for hosts (Lotem 1993). However, two recent studies have shown that two host species have defence mechanisms against cuckoo nestlings (Grim *et al.* 2003; Langmore *et al.* 2003). These hosts recognize that their brood has been parasitized by using cues such as the begging call of the cuckoo

nestling (Langmore *et al.* 2003) or the unusually prolonged parental care (Grim *et al.* 2003), and abandon such nests. It has been suggested that this defence mechanism at the nestling stage should evolve when host defence at the egg stage has been breached by the parasite and is beneficial for hosts because they avoid futile parental investment (Langmore *et al.* 2003). However, the hosts cannot rescue their progeny. Thus, in theory, hosts should rescue their progeny by selectively ejecting cuckoo nestlings from their nest before the cuckoo young ejects the hosts' brood, but such has never been reported, to our knowledge, until now.

In this paper, we report this previously unknown behaviour in host species of an Australian bronze-cuckoo, and discuss whether it represents an anti-parasitic strategy. Using video cameras, we successfully recorded the moment when host birds ejected live cuckoo chicks from their nests.

2. MATERIAL AND METHODS

The little bronze-cuckoo (*Chrysococcyx minutillus*) is common in mangroves and rainforests of tropical Australia and Southeast Asia, and specializes in parasitizing warblers of the genus *Gerygone* (Higgins 1999; Noske 2001). Our study was conducted in mangroves in Darwin, Northern Territory, Australia, where we focused on the main Australian host species, the large-billed Gerygone (*Gerygone magnirostris*) (Brooker & Brooker 1989). Parasitism rates were very high: during 2000–2002, the cuckoos parasitized 41 per cent of the nests of this species (Mulyani 2004), and 36 per cent (K. Tokue 2007–2009, unpublished data). Soon after the cuckoo hatches, it physically ejects any host eggs and chicks. Interestingly, the cuckoo's eggs appear very different from those of their hosts (figure 1), while the cuckoo's chicks, which have blackish-coloured skin and white down on the dorsal surface, closely resemble the nestlings of these hosts (figure 1). Nestling mimicry in the host–Vidua systems is based on being accepted by the foster parents (Payne 2005) and facilitate in parasite young competing for parents' provisioning (Schuetz 2005; but see also Hauber & Kilner 2007). These conditions cannot explain the nestling similarity of the present system because the cuckoo evicts the host's eggs and young soon after hatching.

We searched for host's nests during 4 years (2006–2009) and recorded behaviours during the nestling stage at 22 nests (523 h); 11 parasitized (254 h) and 11 unparasitized (268 h) with video cameras (Canon mini-DV FV30 and FV M200). The recording period was from the expected hatching date to the day of nestling ejection event or to the fifth day since hatching of parasitic young. The average recording time for each nest was approximately 7 h d^{−1}.

3. RESULTS

Out of 22 nests, we succeeded in capturing live nestling(s) being ejected by an adult host at five different host nests (one case was an unparasitized nest, four cases were parasitized nests, table 1). In two cases, only a cuckoo nestling was removed. In two other cases, only a host nestling was evicted. In the fifth case, both cuckoo and host nestlings and a host egg were ejected. In all cases, the host dragged the resisting nestling(s) from the nest, and dropped it under the nest, presumably resulting in its death (see electronic supplementary material S1). Although only two of the adult hosts from the five nests were marked with colour rings, we concluded that the five adults were different individuals, judging from their nest position and breeding year. These two marked individuals were known to be the owners of the nests from which they ejected nestlings because they incubated the eggs in those nests.

No other types of rejection were captured on the video in the other 17 nests. Host young fledged in four out of 10 unparasitized nests. In two nests, outcomes

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Figure 1. Picture of an Australian brood parasite and its host: (a) little bronze-cuckoo nestling (left) and egg (right); (b) large-billed Gerygone nestling (left) and egg (right).

Table 1. Details and outcomes of nests from which nestlings were ejected. C, cuckoo; H, host.

number	nest contents when first nestling was ejected				who was ejected		outcome
	C egg	C young	H egg	H young	C	H	
1	—	1	2	—	1	0	failure
2 ^a	—	1	—	—	1	—	failure
3	—	—	—	3	—	1	two host young fledged
4 ^a	2	—	—	1	0	1	one cuckoo fledged
5	—	1	2	—	1	2 ^b	failure, entire brood ejected

^aBoth adults at the nests were colour-banded for individual recognition.
^bOne young and one egg ejected.

are not known, while the rest of the unparasitized nests failed to produce any young. By contrast, cuckoo young fledged from two parasitized nests, host young fledged from two nests (cuckoo egg/young disappeared from nest) and from three nests young disappeared before the day that they were expected to fledge.

4. DISCUSSION

This is, to our knowledge, the first report of cuckoo hosts physically ejecting cuckoo nestlings from their nests, although nestling rejection (i.e. nest abandonment by hosts containing parasite young) has been reported previously (Grim *et al.* 2003; Langmore *et al.* 2003). We speculate that this ejection behaviour is an anti-parasitism strategy, for the following reasons. First, at least two confirmed nest owners ejected live nestlings from their nest, suggesting that this behaviour was not infanticide by intruders. Second, the morphological similarity between the nestling of the cuckoo and that of its host (figure 1) suggests that this is a consequence of the host’s ability to discriminate odd looking cuckoo nestlings, comparable to the outcome seen in cuckoos mimicking hosts’ eggs to avoid detection (Brooke & Davies 1988).

However, the present study did not provide sufficient evidence to show that the host adults rescued progeny from host-evicting cuckoo young. Rather, some of them killed their own young, but this is to be expected since similar recognition errors are known in egg-ejecting host species (e.g. Davies & Brooke 1988). Therefore, we need to examine whether the hosts are able to achieve higher fitness by ejecting cuckoo nestlings even with the cost of ejecting their own young.

The evolutionary trajectory of this probable anti-parasitism strategy at the nestling stage may be quite different from that of abandonment of parasitized nests at the same stage. Langmore *et al.* (2003) suggested that defence mechanisms at the nestling stage would evolve only after host defence at the egg stage had been breached by the parasite. Interestingly, our hosts seem to lack any anti-parasitism strategy at the egg stage (the cuckoo egg does not mimic host eggs, figure 1). In fact, we observed only one case of egg ejection in our 4 years of research, and this happened when the egg did not hatch after the full incubation period (table 1, no. 5).

These factors suggest that the host may have bypassed the egg rejection strategy and went straight to the evolution of nestling ejection strategy. The lack of egg rejection, and the evolution of nestling ejection, may be owing to a coincidence, or constraints such as small bill size (Rohwer & Spaw 1988), physical structure of the nest, e.g. domed nest (Brooker *et al.* 1990; Langmore *et al.* 2009b) or some other flexible strategies by the host (Langmore *et al.* 2009a). Future research on this apparently unique system may give us new insights into the coevolution of avian brood parasitism.

The Charles Darwin University Animal Ethics Committee and the Conservation Commission of the Northern Territory issued permits to trap and colour-band birds.

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