A stab in the dark

NIGEL DENNIS/AFRICA IMAGERY

Female Greater Honeyguides lay eggs that mimic the size and shape of those of their chosen host.

The sight of an exhausted small songbird raising the gargantuan offspring of a brood parasitic impostor has raised questions for bird-watchers ever since Aristotle contemplated cuckoos in Ancient Greece. A diminutive wagtail perched on the back of the gaping cuckoo chick it is feeding is a typical and defining image.

But some of Africa's most intriguing parasitic interactions take place concealed within the gloom of holes in trees or termite mounds, in the nests of barbets, woodpeckers, hoopoes, starlings and bee-eaters. These species are the victims of honeyguides, remarkably odd birds whose fascinating traits include their famous interactions with honey-gathering humans and their ability to digest beeswax, as well as their brood-parasitic exploitation of other species. The young honeyguide has long been known to be murderous: it hatches equipped with a bayonet-like, hooked bill which it uses to lacerate to death any host nest-mates that might compete with it for the care of its unsuspecting foster parents.

Because host parents stand to lose their entire brood in this way, they have a strong incentive to detect whether a honeyguide egg has been smuggled into their clutch, but how can they do so in the darkness of a tree hole? Although honeyguides may be unable to see in the nest cavities, they might be able to feel, and eggs could be distinctive to the touch instead of the eye. The various hosts of Greater Honeyguide *Indicator indicator*, for example, differ greatly in egg size and shape, ranging from the small, round eggs of bee-eaters to the large, tapered ones of hoopoes.

Fitztitute affiliate Claire Spottiswoode and Zambian ornithologist and egg expert John Colebrook-Robjent have been studying honeyguides in southern Zambia. They found that eggs laid by different female Greater Honeyguides vary subtly according to the species they are parasitising, mimicking the size and shape of their hosts' eggs. This is very possibly analogous to the host-specific variation in egg colour and patterns found in cuckoos.

The selfishness of Greater Honeyguides does not stop at infanticide, however. Females further ensure that their offspring will enjoy the undivided attention of their foster parents by puncturing one or several eggs of the host clutch when they lay their own. However, here they face a trade-off, because if they puncture eggs too heavily, this may cause the host to realise that it has been parasitised and therefore abandon the nest. It turns out that honeyguides take the biggest risks when the potential rewards are greatest, for example when their own eggs are being laid late relative to the host clutch (which may result in the honeyguide's egg hatching too late, or not at all).

In the arms race between parasite and host, hosts defend themselves, and one defence mechanism useful against honeyguides is the strengthening of their eggshells. Good evidence has emerged that thicker-shelled and rounder (thus more puncture-resistant) eggs are favoured by selection imposed by parasitic honeyguides. Indeed, there are signs of natural selection operating in front of our eyes. Despite being parasitised by a honeyguide, individual Little Bee-eater *Merops pusillus* host-females laying thicker-shelled eggs were more likely to raise their own young successfully, suggesting that the host eggs survive the bill-stabs of the laying honeyguide.

This process is also reflected on an evolutionary timescale, because honeyguide host species (for example, Striped Kingfishers *Halcyon chelicuti*) have substantially thicker eggshells than closely related species such as Grey-headed Kingfishers *H. leucocephala*, which are not parasitised by honeyguides. Thus it seems that the arms race between parasite and host continues, with adaptation and counter-adaptation at work beneath the eggshell surface, deep in a dark nest hole. □

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