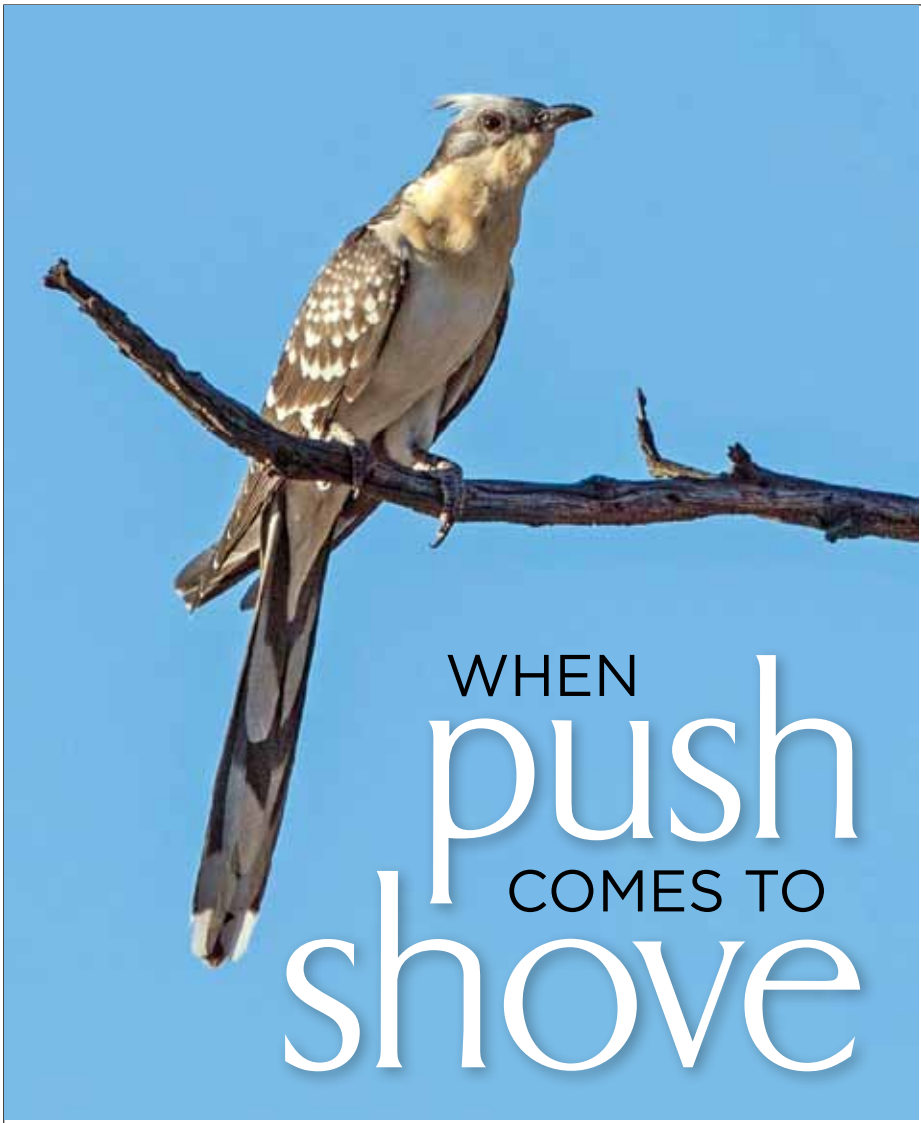

WHEN push COMES TO shove

ALBERT FRONEMAN

The evolution and persistence of brood parasitism in birds has long fascinated biologists, and the study of these relationships has provided some of the best examples of co-evolutionary arms races because of the high stakes involved. At best, chicks of parasitic species tend to be larger and more demanding than the host's chicks, resulting in few host chicks surviving to fledge. And at worst, the parasites turn on their nest mates, killing them before they have a chance to compete. Because accepting foreign eggs and chicks directly reduces the number of offspring a host produces, selection strongly favours hosts that reject them.

As a result, most new hosts rapidly evolve defences against brood parasites. Several studies have shown how host species learn to recognise and reject 'foreign' eggs if they are exposed to a novel brood parasite, and the level of discrimination tends to be correlated with the intensity of parasitism. It is equally well known that many brood parasites have responded by evolving sophisticated egg matching, making it hard for hosts to detect foreign eggs. Hosts can counteract egg mimicry by either becoming extremely discriminating or by varying the pattern of their own eggs, making it harder for the parasite to match an individual's pattern.

This was recently demonstrated for two common hosts of the Cuckoo Finch *Anomalospiza imberbis* in Zambia (Spottiswoode & Stevens 2011, *Proc. R. Soc. B* 278: 3566–73). The eggs of Tawny-flanked Prinias *Prinia subflava* vary greatly in appearance among clutches, whereas those of Red-faced Cisticolas *Cisticola erythrops* are less variable. Cuckoo Finches thus manage to provide a better match to the cisticola's eggs, yet both species reject roughly half of all Cuckoo Finch eggs, because the cisticolas are more discriminating.

Egg matching applies not only to colour and pattern, but also to egg size and shape. This is particularly critical in species such as honeyguides that target cavity-nesting hosts, for whom visual appearance might be less important in the darkness of tree holes or underground burrows (see Spottiswoode et al. 2011, *PNAS* 108: 17738–42). And despite the sometimes farcical disparity in chick and parent size, the attempt at concealment by at least some brood parasites continues into the chick stage. This has been shown recently for the bronze-cuckoos *Chalcites* of Australasia, where each species mimics its most common host's skin and down colour to reduce the risk of host rejection or desertion (Langmore et al. 2011, *Proc. R. Soc. B* 278: 2455–63).

The need for deception may even continue after parasite chicks have fledged. Mársico et al. 2012 (*Proc. R. Soc. B* 279: 3401–8) show that the South American >

above *A study in Europe suggests that Great Spotted Cuckoos 'punish' hosts that reject their eggs or chicks.*

right *Cuckoo Finch eggs (top row) closely match those of their hosts (bottom row), but are better able to match those of Red-faced Cisticolas than the more variable eggs of Tawny-flanked Prinias.*

CLAIRE SPOTTISWOODE

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A newly hatched African Cuckoo chick ejects one of its host's eggs from the nest.

Baywing *Agelaioides badius* only tolerates the mimetic fledglings of the Screaming Cowbird *Molothrus rufoaxillaris*, a specialist brood parasite of the Baywing. Most young Shiny Cowbirds *M. bonariensis*, which don't resemble young Baywings, are abandoned and die if they are cross-fostered to Baywing hosts.

Yet vexing questions remain. Not all brood parasites have eggs that match those of their hosts, so why don't their victims discriminate against these eggs? Biologists have argued this might be because the host hasn't had sufficient time to evolve a rejection response (an evolutionary lag) or because the level of discrimination is a balance between the costs of parasitism and the danger of accidentally rejecting your own eggs (an evolutionary equilibrium).

But evidence is emerging for a third, more sinister explanation for some species tolerating the presence of parasites in their broods – Mafia-style enforcement. Several brood parasites are known to eat the eggs and chicks of host species. This has been interpreted as a mechanism to 'farm' potential hosts. A female cuckoo has to lay her egg in a host nest early in the incubation period; nests found later in the breeding cycle are useless to her. By causing such attempts to fail, she stimulates the parents to breed again, giving her the chance to parasitise them.

But this callous behaviour is only part of the story. Some brood parasites appear to specifically target the nests of hosts that eject their eggs. This was first reported in Great Spotted Cuckoos *Clamator glandarius* in Spain (Soler et al. 1995, *Evolution* 49: 770–5). Female cuckoos repeatedly check the nests of Eurasian Magpies *Pica pica* in which they had laid their eggs, and often destroy nests in which the magpies have rejected a cuckoo egg or chick.

EVIDENCE IS EMERGING FOR A THIRD, **MORE SINISTER EXPLANATION** FOR SOME SPECIES TOLERATING THE PRESENCE OF PARASITES IN THEIR BROODS – **MAFIA-STYLE ENFORCEMENT**

More recently, Brown-headed Cowbirds *M. ater* have been shown to destroy more than half the nests of Prothonotary Warblers *Protonotaria citrea* from which their eggs have been removed (Hoover & Robinson 2007, *PNAS* 104: 4479–83). This is more than twice the rate at which cowbirds destroy unparasitised nests to create additional laying opportunities. Such strong-arm tactics tip the selection scales in favour of hosts retaining a parasite chick, because they can raise at least some of their own offspring. In the case of the warblers, pairs that accept a cowbird in the family raise 60 per cent more chicks on average than those that eject a cowbird's egg. The strong-arm tactic is less likely to work in species where the parasite chick kills all its nest mates, such as honeyguides and some cuckoos, because the benefits of rejecting always outweigh the costs.

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