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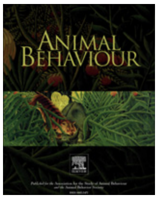

Review

The frontline of avian brood parasite–host coevolution

William E. Feeney [a,*], Justin A. Welbergen [a,b], Naomi E. Langmore [a]

[a] *Evolution, Ecology and Genetics, The Research School of Biology, The Australian National University, Canberra, Australia*
[b] *Centre For Tropical Biodiversity & Climate Change, James Cook University, Townsville, Australia*

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The interactions between avian interspecific brood parasites and their hosts provide tractable and informative systems for investigating coevolution. Generally, these investigations have emphasized the egg and chick stages of the coevolutionary arms race; however, recent studies demonstrate that coevolution operates at all stages of the host nesting cycle and emphasize the importance of reciprocal adaptations prior to deposition of the parasite egg in the host nest: the 'frontline' of the arms race. Here we review the diversity of adaptations at the frontline and its implications for our understanding of brood parasite–host relationships. Coevolution at the frontline can fundamentally shape the life histories, morphologies, physiologies and behaviours of both brood parasites and their hosts, and influences the trajectories and outcomes of their subsequent coevolutionary interactions. We advocate the incorporation of frontline interactions in empirical and theoretical investigations of brood parasite–host arms races to provide a more holistic understanding of the coevolutionary processes in these systems.

Brood parasites foist the cost of raising their offspring onto other individuals. Obligate interspecific brood parasitism is a life history strategy recognized in birds, fishes, arachnids and insects (where it is known commonly as 'social parasitism'; Sato 1986; Davies 2000; Boulton & Polis 2002; Cervo et al. 2004). The reproductive cost of hosting a parasite selects for defensive host adaptations, which in turn select for counteradaptations in the parasite (Davies 2000; Kilner & Langmore 2011), binding host and parasite in a coevolutionary arms race (Dawkins & Krebs 1979). These relationships often exhibit distinct and tractable adaptations and counteradaptations, facilitating their use as experimental systems for studying coevolutionary processes (Rothstein 1990; Brandt et al. 2005; Cervo 2006).

AVIAN BROOD PARASITE–HOST COEVOLUTION

Investigation of avian brood parasite–host coevolution has most notably focused on reciprocal adaptations at the 'egg stage' (e.g. Brooke & Davies 1988; Langmore et al. 2009b; Spottiswoode & Stevens 2011) and the 'chick (or 'nestling') stage' of the arms race (e.g. Langmore et al. 2003; Tanaka & Ueda 2005; Remeŝ 2006; Grim 2007; Sato et al. 2010). For example, many hosts have evolved the ability to reject foreign eggs from their nests (Brooke & Davies 1988; Moskát et al. 2002; Lahti 2006). In response, brood parasites have evolved counteradaptations including mimicry of host eggs (Avilés et al. 2010; Spottiswoode & Stevens 2010; Stoddard & Stevens 2010), cryptic eggs (Marchant 1972; Langmore et al. 2009b) and thickened eggshells (Brooker & Brooker 1991; Antonov et al. 2009). Likewise, some host species have evolved the ability to reject parasite chicks (Langmore et al. 2003; Grim 2007; Sato et al. 2010; Tokue & Ueda 2010), which has selected for mimicry of host young by some species of cuckoos (Langmore et al. 2003, 2008, 2011; Sato et al. 2010).

Host defences at the egg stage may salvage the host's own breeding attempt if the parasite egg is successfully removed from the nest; however, brood parasites typically remove a host egg from the nest before laying their own, so parasitism still carries a cost to the host in this case (Chance 1940; Davies 2000). Likewise, host defences at the chick stage can prevent wasteful investment in parasite young (Langmore et al. 2003) and might even salvage some host young (Sato et al. 2010; Tokue & Ueda 2010); however, defences at this stage of the breeding cycle again fail to prevent all reproductive losses to the host. By contrast, host defences that prevent the parasite from inserting her egg in the nest may protect the host's entire breeding attempt, and successful deployment of such defences at the frontline is therefore potentially the most advantageous line of defence.

The 'Frontline' of Brood Parasite–Host Coevolution

The 'frontline' (Welbergen & Davies 2009) of an avian brood parasite–host coevolutionary arms race is defined as the coevolved

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[*] Correspondence: W. E. Feeney, Evolution, Ecology and Genetics, The Research School of Biology, The Australian National University, Acton, Canberra, ACT 0200, Australia.
E-mail address: william.feeney@anu.edu.au (W. E. Feeney).

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adaptations in the brood parasite and its host that are employed prior to insertion of the parasite egg in the host nest. Despite some early interest in investigating adaptations at this level of the arms race (Swynnerton 1918; Edwards et al. 1949; Robertson & Norman 1976), the most informative and extensive studies have been conducted in recent years (e.g. Gill & Sealy 2004; Hoover & Robinson 2007; Krüger et al. 2007; Welbergen & Davies 2008, 2009, 2011, 2012; Davies & Welbergen 2009; Trnka & Prokop 2011, 2012; Langmore et al. 2012).

As in other stages of the coevolutionary arms race, interactions at the frontline have given rise to coevolved adaptations in brood parasites and their hosts (Soler 1990; Soler et al. 1995; Hoover & Robinson 2007; Krüger et al. 2007; Welbergen & Davies 2011). These adaptations can have profound implications for the life histories (e.g. Brown & Lawes 2007; Canestrari et al. 2009), morphologies (e.g. Garamszegi & Avilés 2005; Davies & Welbergen 2008), physiologies (e.g. Birkhead et al. 2011) and behaviours (e.g. Norman & Robertson 1975; Davies & Welbergen 2009) of both brood parasites and their hosts. Adaptations at this level of the arms race may also influence the evolution of adaptations at later stages of the arms race, resulting in a diversity of adaptive portfolios (Petit 1991; Gill et al. 1997; Kilner & Langmore 2011; Grim et al. 2011).

HOST ADAPTATIONS AND BROOD PARASITE COUNTERADAPTATIONS

Here we outline adaptations evolved by brood parasites to maximize their chances of gaining access to host nests, and the reciprocal adaptations of their hosts to prevent parasitism. Adaptations that are currently thought to have facilitated the evolution of brood parasitism (e.g. small brain and body size and internal egg incubation among the cuckoos, see Krüger et al. 2007; Boerner & Krüger 2008; Birkhead et al. 2011) extend beyond the scope of this review and will not be discussed in depth. Likewise, both brood parasites and hosts may show attributes of life history, morphology or behaviour that provide benefits in brood parasite–host interactions, but that are not necessarily the outcome of brood parasite–host coevolution (e.g. predator defences). We have restricted our discussion to those adaptations that show some evidence of being the outcome of an evolutionary arms race between brood parasites and hosts. The content of this review reflects the bias in the literature towards studies of brood parasitic cuckoos and cowbirds. There is less available information on frontline adaptations in brood-parasitic honeyguides, finches and ducks and their hosts, but where possible this information is included and discussed.

Life History Attributes

Nest placement

Hosts can reduce the probability of parasitism locally through nest placement and nest structure, while brood parasites can improve the chances of successful parasitism with careful selection of host nests. Brood parasites may require vantage points to locate host nests (‘nest exposure’ and ‘perch proximity’ hypotheses; Freeman et al. 1990; Alvarez 1993; Moskát & Honza 2000; Antonov et al. 2006; Røskaft et al. 2002b; Welbergen & Davies 2012), although this is not universal (Barber & Martin 1997; Brown & Lawes 2007; Fiorini et al. 2009). Thus it has been suggested that hosts can reduce parasitism risk by building nests far from vantage points (e.g. Øien et al. 1996; Moskát & Honza 2000; Røskaft et al. 2002b; Antonov et al. 2007; Patten et al. 2011; but see Clotfelter 1998), but this is yet to be tested, for example by comparing nest placement in parasitized and unparasitized populations.

Hosts may also reduce the probability of parasitism by building near species that could deter parasites. For example, Clark & Robertson (1979) found that yellow warblers, *Dendroica petechia*, nesting in the vicinity of red-winged blackbirds, *Agelaius phoeniceus*, suffered less parasitism than those nesting far from red-winged blackbirds. This was attributed to the high levels of aggression exhibited by red-winged blackbirds towards cowbirds (Clark & Robertson 1979). Some brood parasite hosts, such as yellow-rumped thornbills, *Acanthiza chrysorrhoa*, and a variety of weaverbirds (Ploceinae), build their nests beneath the large nests of eagles and other predatory birds (Moreau 1942; Higgins & Peter 2002), and some weaverbirds build their nests close to those of stinging insects (Moreau 1942). However, the idea that hosts may gain protection against brood parasites by nesting near aggressive or dangerous species awaits formal testing.

Nest structure

If the cost of brood parasitism is sufficiently high, hosts may evolve nest structures or architectures that deter parasitism. In theory, hosts could influence the likelihood and costs of brood parasitism by building nests that (1) inhibit access by the parasite (Davies 2000), (2) are deceptive (Soler et al. 1999a; Galligan & Kleindorfer 2008) and/or (3) reduce the success of the parasite chick (Rutila et al. 2002; Grim et al. 2011).

Cavity nests may constrain access by brood parasites, particularly where there is a substantial size discrepancy between parasite and host. For example, Rutila et al. (2002) found that common cuckoos, *Cuculus canorus*, had low breeding success when parasitizing cavity-nesting redstarts, *Phoenicurus phoenicurus*. The low rate of cuckoo success was attributed to the cavity nests, which made laying difficult for the cuckoo (cuckoo eggs were often found outside the nest cup), and low rejection rates of host chicks by the cuckoo chick (46% of cuckoo chicks were unable to eject all host eggs/chicks). Nest cohabitation between cuckoo and host chicks often resulted in high rates of cuckoo death from starvation as a result of nestling competition (Rutila et al. 2002). Although this experiment was conducted using artificial nestboxes, it may explain why relatively few cavity-nesting species are parasitized compared to other potential hosts (Moksnes & Røskaft 1995). Similarly, cavity nests may impede large cuckoo chicks from exiting the nest owing to the small entrance. Although cavity nesting may provide an effective defence against brood parasitism, it is also likely to represent a general defence against nest predation.

Other nest structures may also inhibit access by brood parasites. For example, some African weaver birds build nest tubes up to 30 cm in length, which appear to provide protection from both predation and brood parasitism (Crook 1963; Davies 2000; A.K. Lindholm, personal communication). Nest tubes occur more frequently among species that are regularly parasitized (Freeman 1988; Davies 2000) and there are reports of Diederik cuckoos, *Chrysococcyx caprius*, becoming trapped while trying to enter the nests (Davies 2000), suggesting that these structures may be an adaptive response to brood parasitism. Comparison of predation and parasitism in sham-manipulated nests versus nests with tubes removed might prove a fruitful avenue of research to investigate the relative influence of predation and parasitism on the evolution of nest tubes.

Hosts may also deceive brood parasites about the quality or location of their nests. Brood parasites should choose hosts that maximize the likelihood of successfully rearing their chick (Wiley 1988; Woolfenden et al. 2003; Langmore & Kilner 2007; Grim et al. 2011). Therefore, hosts could decrease the likelihood of parasitism by constructing seemingly unappealing nests. In magpies, nest size correlates with reproductive success (Soler et al. 1998; Soler et al. 2001). Large nest size is also preferred by its primary brood parasite, the great spotted cuckoo, *Clamator glandarius* (Soler et al. 1995). This has selected for smaller nest size in