Evidence of Adaptations and Counter-Adaptations Before the Parasite Lays Its Egg: The Frontline of the Arms Race

17

William E. Feeney

Abstract

The interactions between avian brood parasites and their hosts provide tractable model systems to study coevolutionary processes under natural conditions. Here, I review evidence of reciprocal adaptations and counter-adaptations in brood parasites and hosts that are deployed prior to the parasite depositing its egg in the host nest: the 'frontline' of the arms race. Unlike interactions at latter stages of the nesting cycle, frontline interactions primarily concern adult brood parasites and adult hosts, offering opportunities to study how exchanges between these species influence adult phenotypes. Placing emphasis on recent advances, I discuss how frontline interactions have shaped the life histories, behaviours, morphologies and physiologies of adult brood parasites and adult hosts. Similar to latter stages of the nesting cycle, frontline interactions comprise diverse adaptations and counter-adaptations that appear to be a product of coevolution and are important for determining the outcome of the exchanges between these species. Further investigation of these interactions is essential for categorizing the diversity of adaptations and counter-adaptations at this stage of the nesting cycle and expanding our understanding of how adaptations and counter-adaptations at all stages of the nesting cycle evolve in relation to one another.

W. E. Feeney (✉)
School of Biological Sciences, University of Queensland, Brisbane, QLD, Australia
e-mail: w.feeney@uq.edu.au

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17.1 Introduction

Humans have demonstrated a deep and lasting interest in the natural habits of the avian brood parasites. Their unmistakeable calls are recognized as synonymous with seasonal change throughout Europe, Asia and Australia (Lai 1998; Davies 2000; Gray and Fraser 2013); one acts as foraging partner with humans in sub-Saharan Africa (Spottiswoode et al. 2016); and references to their parasitic breeding habits are evident throughout the world's folklores, languages and mythologies (Lai 1998; Davies 2000; Gray and Fraser 2013; Møller et al. 2017). Throughout history myriad explanations have been proposed to rationalize why these species never tend to their offspring (Davies 2000). Of these, natural selection prevailed (Darwin 1859), and these systems have since become models for studying the ecological and evolutionary ramifications of species interactions under natural conditions (Rothstein 1990; Davies 2000; Feeney et al. 2014).

Research is currently being conducted on parasite–host systems that include representatives from each of the seven brood parasite lineages (Sorenson and Payne 2005) and on species pairs that inhabit every continent except for Antarctica (where none occur, Davies 2000). We know that the cost of hosting a parasite varies across species pairs (Kilner 2005) and that the benefits of hosting a parasite can outweigh the costs under some circumstances (Canestrari et al. 2014). The ecological consequences of these interactions can be globally conspicuous, predicting broad patterns of trait diversity such as small clutch sizes (Hauber 2003) and cooperative breeding (Feeney et al. 2013) in hosts, as well as hawk mimicry (Gluckman and Mundy 2013) and plumage polymorphisms (Thorogood and Davies 2013) in parasitic cuckoos. The depth of coevolution between these species is also becoming clear, with data now demonstrating that coevolved adaptations and counter-adaptations are evident at all stages of the host's nesting cycle (reviewed in Feeney et al. 2014; Soler 2014)

In this chapter, I will discuss the interactions between avian brood parasites and hosts that occur prior to the parasite laying its egg in the host's nest: the 'frontline' of the arms race (Welbergen and Davies 2009). These exchanges are of utmost importance, as a parasite's reproductive output hinges on its ability to successfully deposit eggs in host nests, and successful deterrence of adult parasites offers the first opportunity for hosts to defend their nests. Unlike reciprocal adaptations and counter-adaptations at latter stages of the nesting cycle, frontline interactions primarily concern adult brood parasites and hosts, offering opportunities for selection to shape adult phenotypes of the involved species as well as their natural histories. Following a recent review of this topic (Feeney et al. 2012), I will discuss evidence of how coevolution has affected the life histories, behaviours, morphologies and physiologies of brood parasites and hosts. However, to minimize any unnecessary overlap, this chapter will place emphasis on new research as well as research that was not heavily discussed in Feeney et al. (2012). Discussion of traits will be conducted in a roughly chronological order.

17.2 Life Histories

17.2.1 Breeding Phenology

Parasitism can only occur if there is breeding synchrony between parasite and host. Despite being inherently difficult to demonstrate, evidence suggests that some host species, or populations of hosts within species, may have shifted their breeding phenologies to avoid breeding in synchrony with parasites. Brooker and Brooker (1989) were the first to compare breeding records of Australian cuckoos and their hosts and found numerous examples of hosts starting breeding before their cuckoos arrived or ending after they left, consistent with the hypothesis that hosts shift their breeding phenology to minimize overlap with cuckoos. Medina and Langmore (2016) built on this and found that early-laying yellow-rumped thornbills (*Acanthiza chrysorrhoa*) were parasitized significantly less than late breeders. Similar trends have been found in other host species (see Middleton 1977; Campomizzi et al. 2013 for similar evidence in hosts of the brown-headed cowbird (*Molothrus ater*); Table 17.1).

Research into the effects that climate change has had on bird breeding behaviours may offer insights into effectiveness and potential evolutionary consequences of this putative defence. Notably, migratory parasites are likely more vulnerable to shifts in host breeding phenology compared to their resident counterparts, as they are less able to track their host's breeding schedule (Saino et al. 2009; Møller et al. 2011b; Péron et al. 2016). Those that are unable to effectively track host laying may be forced to switch hosts (Møller et al. 2011b; Péron et al. 2016) or face a reduction in their abundance (Saino et al. 2009). Host switching, in turn, may promote hybridization of closely related parasite species (Péron et al. 2016) or divergence into distinct 'races' (gentes) (Møller et al. 2011a) or species (Sorenson et al. 2003; Péron et al. 2016). Together, these studies suggest that shifts in host breeding phenology could provide an extremely effective defence against brood parasitism, especially in parasite–host systems that comprise migratory parasites and resident hosts, and could have dire evolutionary repercussions for the parasites.

If parasites and hosts do breed in synchrony, hosts may tactically adjust their laying dates to minimize their likelihood of parasitism or exhibit compensatory breeding behaviours to mitigate the cost of parasitism if it does occur. As parasites are constrained by their laying schedules, synchronous breeding in host communities reduces the likelihood of any individual being parasitized through a 'swamping' or 'dilution' effect (Clark and Robertson 1979; Martínez et al. 1996; Massoni and Reboreda 2001). Parasites can counter these traits with behaviours, such as the tactical destruction (i.e. 'farming') of host nests (e.g. Hoover and Robinson 2007; Swan et al. 2015), which forces renesting and offers an opportunity for subsequent parasitism (see Chap. 15; Table 17.2). If parasitism does occur, hosts may double-brood in an attempt to compensate for their lost reproductive success. Recently, Louder et al. (2015b) found that parasitism by brown-headed cowbirds prompts

Table 17.1 Life-history phenotypes that affect the interactions between brood parasites and hosts

	Trait	Purpose	Key reference(s)
Host	Shifted breeding phenology	Mismatch breeding synchrony between parasite and host	Álvarez (1996)* Middleton (1977) Brooker and Brooker (1989) Soler et al. (2012)* Campomizzi et al. (2013) Boves et al. (2014) Medina and Langmore (2016)*
	Compensatory breeding	Dilute the cost of parasitism	Louder et al. (2015b)*
	Synchronous breeding by multiple hosts	Dilute the likelihood of parasitism	Clark and Robertson (1979) Martínez et al. (1996) Massoni and Reboreda (2001)
	Deceptive nest architecture	Decrease the perceived quality of the nest	Soler et al. (1999)
	Defensive nest architecture	Obstruct parasite access/ minimize their likelihood of successful parasitism	Rutila et al. (2002)* Grim et al. (2011)*
	Cryptic nest architecture/ placement	Minimize the likelihood of the parasite discovering the nest	Burhans (1997) Clarke et al. (2001) Jelínek et al. (2014)
	Unappealing nest location	Minimize the likelihood of parasitism through placement near aggressive or noxious heterospecifics	Clark and Robertson (1979)
	Breeding mode	Facilitates nest defence	Brown and Lawes (2007) Wiley (2012) Trnka and Prokop (2011) Canestrari et al. (2009)

Asterisk (*) indicates a manipulative experimental component. Parasite counter-adaptations to these adaptations tend to be behavioural (e.g. strategic targeting of nests and nest farming) and are therefore in Table 17.2

Table 17.2 Behaviours that affect the interactions between brood parasites and hosts

	Trait	Purpose	Key reference(s)
Parasite	Increased spatial memory	Facilitates effective parasitism	White et al. (2009)* Guigueno et al. (2014*, 2015*)
	Strategic targeting of host nests	Increases the likelihood of successful parasitism	Soler et al. (1995a*, 1999) Moskát and Honza (2000) Honza et al. (2002) Grant and Sealy (2002) McLaren and Sealy (2003) Skjelseth et al. (2004) Langmore and Kilner (2007) Polačiková et al. (2009)
	Flexible adjustment of nest searching strategies	Optimizes nest location	Woolfenden et al. (2003) Strausberger and Ashley (2005) Jelínek et al. (2014)
	Discreet nest monitoring behaviour	Lowers the likelihood of the host detecting the parasite	Álvarez (1993) Øien et al. (1996) Honza et al. (2002)
	Fast egg laying	Lowers the likelihood of the host detecting the parasite at the nest	Davies (2000)
	Nest farming	Destroy host nests to force renesting	Hoover and Robinson (2007)* Swan et al. (2015)*
	Tactical destruction of host eggs during laying	Provide a less competitive environment for the brood parasite's offspring	Spottiswoode and Colebrook-Robjent (2007) Fiorini et al. (2014)* Gloag et al. (2013)
	Mafia behaviours	Force acceptance of parasite egg (s) through retaliatory nest destruction following egg rejection	Soler et al. (1995b)* Hoover and Robinson (2007)*
Host	Specific recognition and denotation of brood parasites	Facilitates parasite-specific defences	Hobson and Sealy (1989)* Uyehara and Narins (1995)*

(continued)

Table 17.2 (continued)

	Trait	Purpose	Key reference(s)
			Gill and Sealy (2004)* Gill et al. (1997*, 2008*), Welbergen and Davies (2008)* Feeney et al. (2013)*
	Tactical use of social and personal information	Optimizes defences against brood parasites	Hauber and Russo (2000) Davies et al. (2003)* Davies and Welbergen (2009)* Campobello and Sealy (2011)* Welbergen and Davies (2012)* Feeney and Langmore (2015)* Thorogood and Davies (2016)*
	Decreasing time spent near the nest	Provides fewer opportunities for parasites to locate their nest	Banks and Martin (2001)
	Mobbing behaviours	Physically deter brood parasites from accessing host nests	Welbergen and Davies (2009)* Feeney et al. (2013)* Gloag et al. (2013)
	Nest protection behaviours	Physically blocking access to the nest	Hobson and Sealy (1989)*

Asterisk (*) indicates a manipulative experimental component compensatory double-brooding in prothonotary warblers (*Protonotaria citrea*). They also found that double-brooding females are often parasitized during their subsequent breeding attempt, suggesting that cowbirds may be promoting and then exploiting compensatory breeding behaviours to maximize their own reproductive success (Table 17.2).

17.2.2 Nest Architecture and Placement

When hosts and parasites breed sympatrically, hosts can also lower their likelihood of parasitism with defensive nest architectures or by building their nests in areas that are less likely to be located by parasites. In an elegant series of studies, Soler et al. (1995a, 1998, 1999, 2001) demonstrated that deceptive nest architectures can be employed by hosts in response to brood parasitism. They showed that in magpies (*Pica pica*), nest size is a sexually selected trait that correlates with reproductive success (Soler et al. 2001), that great spotted cuckoos (*Clamator glandarius*) preferentially parasitize larger magpie nests (Soler et al. 1995a), and that magpies that breed in sympatry with cuckoos have smaller nests than those in allopatry (Soler et al. 1999), together suggesting that brood parasitism is influencing sexually selected traits in these populations.

Hosts can also choose nesting sites that lower their likelihood of being parasitized. Individual parasites vary in their nest-searching behaviours and patterns of host use and can vary these behaviours according to the abundance of suitable host nests (Table 17.2). Hosts can respond by building nests that counter typical parasitic searching strategies, such as building nests that are removed from vantage points (e.g. ‘perch proximity’ hypothesis, Øien et al. 1996; Hauber and Russo 2000) or by increasing their defences when nesting in higher-risk areas (Welbergen and Davies 2012). Alternatively, hosts may place nests in locations that are less desirable to potential parasites, such as near aggressive interspecifics (Clark and Robertson 1979). Whether these kinds of interspecific associations lower the likelihood of brood parasitism awaits experimental investigation.

Alternatively, hosts could build secretive nests (e.g. Burhans 1997; Clarke et al. 2001; Jelínek et al. 2014) or nests that obstruct parasite access to minimize their likelihood of parasitism (Rutila et al. 2002) (Table 17.1). Notably, cavity nests also appear to obstruct parasites from depositing their eggs, and their design may also inhibit the nestling parasite’s competitiveness after hatching (e.g. Rutila et al. 2002, also see Grim et al. 2011). This may explain why cavity nesters are so rarely hosts of the common cuckoo (*Cuculus canorus*) (Moksnes and Røskaft 1995).

17.2.3 Breeding Modes

A recent series of studies has demonstrated that host breeding mode can facilitate defences against brood parasitism (Table 17.1). While the behavioural mechanism that underpins parasite deterrence varies (e.g. decreasing the opportunity for parasitism, Canestrari et al. 2009; or facilitating host aggression, Feeney et al. 2013), they cumulatively suggest that more defence is better defence (however see Ursino et al. 2011). Recently, Feeney et al. (2013) found that brood parasitism and cooperative breeding evolve together; however, they were not able to determine the direction of the relationship.

17.3 Behaviour

17.3.1 Cognitive Adaptations

Considerable research has been and continues to be conducted into the cognition of brood parasites and hosts. In parasites, investigation of brain morphologies tends to show that they have relatively large hippocampal regions areas that are generally associated with spatial memory (see Chap. 11). A recent series of experimental and field-based studies on the brown-headed cowbird built on these findings and has demonstrated that females have a more accurate spatial memory than males (Guigueno et al. 2014), are able to assess host nest readiness to maximize laying synchrony (White et al. 2009) and that they can remember and target particular host individuals, within and between seasons, that have a history of successfully raising cowbird offspring (Louder et al. 2015a; also see Guigueno et al. 2015; Astié et al. 2015; de la Colina et al. 2016). Similarly, a variety of studies have demonstrated that parasites can strategically choose nests according to the perceived quality of the host parents or nest (Table 17.2) in addition to those that are perceived to be less likely to elicit defences (Avilés et al. 2006) or have a lower likelihood of being depredated (Soler et al. 2014a, b). Some also appear able to change their nest-searching strategy according to the availability of nests (e.g. Jelínek et al. 2014). Together, these studies suggest that cognitive adaptations have played an important role in facilitating parasitic life histories and that these traits may have been further shaped through interactions with hosts.

Similar evidence of cognitive adaptations is evident in hosts. For example, it is becoming clear that at least some hosts recognize brood parasites as unique threats and produce alarm calls that denote parasites in order to elicit specific defences (Table 17.2). At least some can also learn to respond to the sight of a parasite (Davies and Welbergen 2009; Langmore et al. 2012; Feeney and Langmore 2013) and use personal and social information to adjust their behaviours in order to minimize their likelihood of being parasitized (Table 17.2). To date, these studies have tended to focus on the interactions between one host and its primary parasite. However, most brood parasite–host pairs coexist with other parasites and hosts (Davies 2000; Feeney et al. 2013), and while they may have preferred hosts, a variety of parasite species rarely use one host species exclusively (Davies 2000). Therefore, hosts species that exist in these environments may eavesdrop on one another to acquire information about the local risk of parasitism and/or cooperate with one another when defending their nests.

17.3.2 Stealth and Detection

By and large, parasites and hosts appear to increase their respective likelihoods of successfully parasitizing host nests, or dodging parasitism, by minimizing the likelihood of interacting with one another. Evidence suggests that hosts can lower the likelihood of parasites discovering their nests by decreasing the amount of time they spend around them (Banks and Martin 2001) and by producing complex versus simple vocalizations, which may be difficult for parasites to use as location cues (Garamszegi and Avilés 2005). Parasites also tend to be secretive around host nests (however, not always Gloag et al. 2013; Soler et al. 2014a, b). For example, a combination of monitoring, experimental, video and radio telemetry studies suggests the common cuckoo monitors nests from distant perches (Álvarez 1993; Øien et al. 1996), increases the amount of time spent monitoring a nest the day of host laying (Honza et al. 2002), lays eggs extremely quickly (Davies 2000) and adjusts nest-searching strategies according to the availability of host nests (Table 17.2). In turn, hosts use various sources of direct and indirect information to gauge the risk of being parasitized (Table 17.2). Notably, Thorogood and Davies (2016) recently demonstrated that reed warblers (*Acrocephalus scirpaceus*) use a combination of personal and social information to inform their deployment of defences at latter stages of the nesting cycle. Parasites can further minimize the likelihood of host recognition through a variety of morphological adaptations, which will be discussed in more detail below (see Sects. 17.4.1 and 17.4.2).

17.3.3 Aggression

Hosts and parasites also use physical aggression to defend or gain access to the nest. While not universal, most host species aggressively mob brood parasites that approach their nests (Table 17.2). This behaviour can deter parasitism from occurring (Welbergen and Davies 2009; Feeney et al. 2013) and can even result in the death of the parasite (Gloag et al. 2013). In general, physical aggression appears to be an effective defence against brood parasitism (Welbergen and Davies 2009; Feeney et al. 2013; Fig. 17.1); however, at least some parasites appear able to withstand vicious mobbing while they lay their eggs (e.g. Neudorf and Sealy 1992; Gloag et al. 2013; Soler et al. 2014a, b) or may even incite mobbing in order to gain information about the location of a nest (e.g. Robertson and Norman 1976; Strausberger 1998, but see Gill et al. 1997). Species that do not exhibit evidence of mobbing tend to be small-bodied species that rush to and sit on their nest when the risk of parasitism is high in an attempt to block parasite access (e.g. Hobson and Sealy 1989; Medina and Langmore 2016; but see Gloag et al. 2013; Soler et al. 2014a, b for notable exceptions).

Adult parasites can also use aggressive and violent behaviours to increase the likelihood of their offspring surviving. These adaptations have been best studied in the cowbirds, which have been shown to puncture host eggs to assess nest suitability for parasitism (Massoni and Reboreda 1999), destroy host clutches in order to force

Fig. 17.1 Australian superb fairywrens (*Malurus cyaneus*) mobbing a taxidermied shining bronze-cuckoo (*Chalcites lucidus*) in Canberra, Australia. Photo: William Feeney

renesting (Peer and Sealy 1999; Hoover and Robinson 2007; Dubina and Peer 2012; Swan et al. 2015) and destroy eggs during laying to minimize the competition faced by their chicks after hatching (e.g. Gloag et al. 2013; Fiorini et al. 2014; also see Spottiswoode and Colebrook-Robjent 2007 for a reference to similar behaviours in the greater honeyguide (*Indicator indicator*) and Soler and Martínez 2000 for references to similar behaviours in the great spotted cuckoo). Several parasites have also been suggested to monitor host nests following parasitism and destroy clutches that reject their eggs (e.g. 'mafia' behaviours, Soler et al. 1995b; Hoover and Robinson 2007). These kinds of manipulative behaviours appear to be more common in less virulent parasite species, where hosts do not always surrender their entire reproductive effort through hosting a parasite (but see Peer et al. 2013) and the parasite may therefore not be required to prioritize discretion near the nest (see Chap. 15).

17.4 Morphology

17.4.1 Camouflage

Parasites that are detected near host nests risk being vigorously attacked (Table 17.2) and forfeiting information about the host's risk of parasitism, which may result in an increased likelihood of defences being deployed at latter stages of the nesting cycle (Davies and Brooke 1988; Peer and Sealy 2004; Langmore et al. 2009). Similarly, conspicuous hosts risk becoming easy targets (Banks and Martin 2001; Garamszegi and Avilés 2005). Selection should therefore favour cryptic phenotypes in adult brood parasites and hosts.

Brood parasites exhibit a suite of behaviours that minimize their likelihood of being detected while monitoring host nests (Øien et al. 1996; Honza et al. 2002), and the effectiveness of these behaviours could be increased through cryptic morphological phenotypes. Recent phylogenetic analyses have provided some support to the observation that brood parasites tend to have dull plumages, suggesting that these attributes may be a product of coevolution with hosts (Payne 1967; Krüger et al. 2007; Medina and Langmore 2015). Notably, Krüger et al. (2007) found that, in contrast to other cuckoos, the *Clamator* cuckoos had evolved showier plumages, which may reflect their more conspicuous behaviours around host nests (Macías-Sánchez et al. 2013; Soler et al. 2014a, b; but see Medina and Langmore 2015). Breast barring, which is associated with hawk mimicry in a variety of parasitic cuckoos (Gluckman and Mundy 2013), may also serve to facilitate camouflage while monitoring host nests from tree branches.

17.4.2 Deceptive Plumages

The common cuckoo has become a model for understanding the ecology and evolution of deceptive plumage phenotypes in avian brood parasites. This species exhibits two distinct plumage polymorphisms: a grey and rufous morph (Davies 2000). The grey morph bears a striking resemblance to Eurasian sparrowhawks (*Accipiter* spp.), while the rufous morph has been noted to resemble Eurasian kestrels (*Falco tinnunculus*) (Davies and Welbergen 2008; Thorogood and Davies 2012; Trnka et al. 2015). Numerous studies have demonstrated that both host and non-host species are cautious when presented with models of grey morph cuckoos (Table 17.3), confirming that this cuckoo has evolved mimicry to facilitate parasitism. By contrast, mixed and negative support for mimicry has been found regarding mimicry in the rufous morph (Honza et al. 2006; Trnka et al. 2015). These studies instead support findings that plumage polymorphisms can evolve as a further counter-adaptation against hosts transmitting knowledge of cuckoos throughout a

Table 17.3 Morphological phenotypes that affect the interactions between brood parasites and hosts

	Trait	Purpose	Key reference(s)
Parasite	Dull plumages	Suspected to decrease parasite conspicuousness	Krüger et al. (2007) Medina and Langmore (2015)
	Showy plumages in males	Suspected to assist in male distraction behaviours	Krüger et al. (2007)
	Plumage mimicry	Promotes mistaken identity between the cuckoo and the harmful (Batesian) or harmless (Aggressive) model	Davies and Welbergen (2008)* Trnka and Prokop (2012)* Gluckman and Mundy (2013) Feeney et al. (2015)* Møller et al. (2015)
	Plumage polymorphisms	Decreases the likelihood of information transmission about the presence of the rare morph	Honza et al. (2006)* Thorogood and Davies (2012*, 2013) Trnka et al. (2015)*

Asterisk (*) indicates a manipulative experimental component population (Tables 17.2 and 17.3). This correlated evolution of mimicry and polymorphisms across a wide array of parasite species suggests that this series of coevolved adaptations and counter-adaptations is relatively common among parasite–host systems (Krüger et al. 2007; Thorogood and Davies 2013; Gluckman and Mundy 2013; Tanaka 2016).

Deceptive plumages also appear to exist in other brood parasite species (Table 17.3); however, they remain largely unstudied. Putative examples include drongo-cuckoos (*Surniculus* spp.) mimicking drongos (*Dicrurus* spp.) (Duckworth 1997), Wahlberg's honeyguide (*Prodotiscus regulus*) mimicking small grey flycatchers (Muscicapidae) (Payne 1967) and cuckoo-finches (*Anomalospiza imberbis*) mimicking female *Euplectes* weavers (Feeney et al. 2015). These putative examples of plumage mimicry largely await formal examination (for an exception, see Feeney et al. 2015).

17.4.3 Weapons and Armoury

Despite numerous studies suggesting that violent interactions between brood parasites and hosts may be common at host nests (Table 17.2), almost no research has investigated whether these interactions have selected morphological weaponry and armoury. Adaptations such as thicker skin or denser bones may be present in a variety of brood parasites (Moksnes et al. 2000; Gloag et al. 2013; Soler et al. 2014a, b); however, they await investigation.

17.5 Physiology

Evidence of physiological adaptations resulting from brood parasite–host coevolution remains scarce. Investigation of these kinds of adaptations at this stage of the nesting is largely limited to fast parasite laying, internal egg incubation, and investigation of immune function and hormone profiles in parasites (Dufty et al. 1987; Davies and de Brooke 1988; Kattan 1997; Mermoz and Reboreda 2003; Birkhead et al. 2011; Hahn et al. 2013; Merrill et al. 2013). Building on this, a recent study by Jung et al. (2016) investigated the testosterone profiles of adult common and lesser cuckoos (*C. poliocephalus*) throughout the breeding season and found that they largely resembled those that would be expected in non-brood parasites (also see Dufty et al. 1987).

Concluding Remarks and Future Directions

Frontline interactions, similar to those at latter stages of the nesting cycle, provide tractable opportunities to study coevolutionary processes under natural conditions. Though, unlike interactions at the egg, chick and fledgling

(continued)

stages, frontline interactions primarily concern adult brood parasites and adult hosts, offering opportunities to investigate how selection imposed on hosts by brood parasites, and vice versa, shapes adult phenotypes of the involved species. Recent research has and continues to demonstrate the ecological and evolutionary repercussions of frontline coevolution between these species, such as their ability to explain broad patterns of trait diversity in hosts (Feeney et al. 2013) and parasites (Thorogood and Davies 2013; Gluckman and Mundy 2013). However, they also offer unique avenues for future research, such as further investigation of the causal links between brood parasitism and host breeding systems (Table 17.1), how interactions between adult brood parasites and hosts affect behaviours at latter stages of the nesting cycle (Table 17.2) and whether the cost of brood parasitism has selected cryptic vocal or plumage phenotypes in hosts (Table 17.3). Ultimately, like interactions at other stages of the nesting cycle, a deeper understanding of frontline interactions is key to realizing the ecological and evolutionary repercussions of these iconic relationships.

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