



Parasite Adaptations During the Nestling and Fledgling Stages

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Abstract

Young of altricial brood parasites are fully dependent on their foster parents for a considerable period of time before being able to survive on their own. Therefore, they are expected to exhibit traits that allow them to avoid host defences and manipulate host's parental behaviour to their favour. Many morphological, physiological and behavioural traits have been proposed as adaptations for brood parasitism based on their apparent selective advantage for parasitic chicks. In this chapter, we describe and discuss these putative adaptations to examine, in the light of available evidence, whether or not those traits have evolved specifically to increase parasites' fitness. We show that whereas some adaptations are well-supported and indisputable, other traits require a closer scrutiny taking into account the parasite's evolutionary history before concluding that they are true adaptations for brood parasitism. We propose some future directions for research on key adaptations to parasitism and coevolutionary interactions between parasites and their hosts during the nestling and fledgling stages.

30.1 Introduction

Successful parasitism requires that young parasites generate the appropriate signals to elicit provisioning from their foster parents and deal with competition within the brood. It has long been recognized that parasitic nestlings possess many behavioural

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and physiological traits that allow them to secure parental care and manipulate host's parental behaviour (Payne 1977; Rothstein 1990). These include nestmate-killing behaviours, early hatching, rapid growth rates and/or exuberant begging displays (Payne 1977; Rothstein 1990; Redondo 1993; Davies 2000). Despite their intuitive selective advantage, however, these putative adaptations should be tested taking into account the parasite's evolutionary history before concluding that they have evolved specifically for brood parasitism (Mermoz and Ornelas 2004; Birkhead et al. 2011).

In theory, the fitness costs imposed on hosts by parasitic nestlings that either kill or outcompete host young may set the stage for a coevolutionary arms race, where hosts evolve defences against parasitic nestlings and parasites evolve counter-adaptations that select for improved host defences and so on (Rothstein 1990). However, it was assumed until recently that nestling rejection was unlikely to evolve when hosts have to learn the appearance of their own young during the first breeding attempt because the costs of incurring recognition or rejection errors would outweigh the benefits of this defence (Lotem 1993; Lawes and Marthews 2003; Grim 2006a). Today, new evidences for the evolution of host adaptations against parasitic chicks and reciprocal counter-adaptations in parasite populations (i.e. chick mimicry) are driving a paradigm shift (Langmore et al. 2003; Grim 2007, 2011; Soler 2009; Sato et al. 2010; De Marsico et al. 2012; Feeney et al. 2014; Chap. 29).

Davies (2011) has coined the terms 'trickery' and 'tuning' to distinguish between parasite's traits that have evolved as a result of coevolutionary interactions with its host (trickery) and traits that have not coevolved with host defences but which enhance parasite's success (tuning). For instance, mimicking host-specific cues to avoid host discrimination would be trickery (see also Grim 2005), whereas adjusting begging displays to better exploit host's sensory preferences would be tuning (Davies 2011). The trickery-tuning distinction may become diffuse when failure to tune into host's life history ultimately results in parasite's death or when parasite tuning might also lead to reciprocal adaptations (Davies 2011). However, it provides a useful framework to pinpoint co-evolved adaptations in parasites and their hosts, which has historically been a major focus of research on avian brood parasitism (Rothstein 1990).

Trickery and tuning adaptations similar to those observed at the nestling stage can also appear during the post-fledging period since fledgling parasites depend on their hosts for several weeks before attaining nutritional independence. Juveniles of obligate brood parasites also face another major challenge: at some point, they must abandon their foster parents and meet their conspecifics to continue their life cycle. Obviously, they are adapted to do so, or those species would not exist! However, how juvenile parasites recognize their own kind remains poorly understood (Goth and Hauber 2004). Indeed, very little is known about parasites' biology after they fledge from host nests. The paucity in research during this critical life period arises from the difficulties associated with tracking mobile juveniles. Despite this, recent insights into the social interactions and dispersal patterns of parasitic juveniles suggest potential adaptations at this last stage of the nesting cycle (Soler and Soler 1999; Hauber et al. 2000, 2001; Hauber 2002; Soler et al. 2014a; Louder et al. 2015).

Here we review the main proposed adaptations for brood parasitism at the nestling and fledgling stages (Tables 30.1 and 30.2). We describe how young

Table 30.1 Overview of proposed adaptations for brood parasitism at the nestling stage

Challenges to solve	Proposed adaptations	Study species	Adaptive role supported?	References
Deal with intra-brood competition	Early hatching	Common cuckoo (<i>Cuculus canorus</i>), African cuckoo (<i>C. gularis</i>) and honeyguides (<i>Indicator indicator</i>)	No	Birkhead et al. (2011) Honza et al. (2001, 2015)
		Cowbirds (<i>Molothrus</i> spp.)	No	McMaster and Sealy (1998) Mermoz and Ornelas (2004)
		Great spotted cuckoo (<i>Clamator glandarius</i>)	No	Soler (1990)
	'Nestmate-killing' behaviour	Old World cuckoos (Family Cuculidae) Honeyguides (Family Indicatoridae) Striped cuckoo (<i>Tapera naevia</i>)	Yes	Kilner (2005) Hauber and Moskát (2008) Grim et al. (2009) Spottiswoode and Koorevaar (2012) Wang and Kimball (2012)
Grow optimally in host nests	Rapid growth rates	Cowbirds	No	Mermoz and Ornelas (2004) Remeš (2010)
		Great spotted cuckoo	No	Soler and Soler (1991)
	Increased digestive efficiency	Great spotted cuckoo	Partially	Soler et al. (2014b)
Stimulate parental care	Exaggerated begging displays/Tuning into host's sensory preferences/ Displaying conspicuous traits (e.g. wing patches, palatal papillae)	Common cuckoo	Partially	Kilner et al. (1999) Madden and Davies (2006)
		Great spotted cuckoo (<i>Clamator glandarius</i>)	Partially	Soler et al. (1999) Soler et al. (1995a)
		Cowbirds	Mixed evidence	Lichtenstein (2001) Dearborn and

(continued)

Table 30.1 (continued)

Challenges to solve	Proposed adaptations	Study species	Adaptive role supported?	References
				Lichtenstein (2002) Rivers et al. (2010, 2013) Gloag and Kacelnik (2013)
		Horsfield's hawk cuckoo (<i>Cuculus fugax</i>)	Partially	Tanaka and Ueda (2005) Grim (2008)
Avoid host defenses	Chick mimicry	Horsfield's bronze cuckoo (<i>Chalcites basalis</i>)	Presumably yes	Langmore et al. (2003, 2011)
		Little bronze cuckoos (<i>Chrysococcyx minutillus</i>)	Partially	Sato et al. (2010), Tokue and Ueda (2010)
		Whydahs and indigobirds (<i>Vidua</i> spp.)	Mixed evidence	Payne et al. (2001) Schuetz (2005a, b) Hauber and Kilner (2007)

Selected references provide evidence either supporting or not the hypothesized adaptation. 'Partially' supported means that empirical data suggest a fitness benefit of the proposed adaptation, but comparative phylogenetic studies are lacking. 'Mixed evidence' means conflicting results about the putative adaptive role

parasites can solve the problem of securing parental provisioning from hatching to independence and discuss, in the light of available evidence, whether those seemingly adaptive traits have evolved specifically as trickery or tuning adaptations for brood parasitism. Finally, we suggest future directions for research on brood parasitism at the nestling and fledgling stages.

30.2 Proposed Parasite Adaptations During the Nestling Stage

30.2.1 Early Hatching

Hatching earlier than host chicks can be key to the survival of parasitic young, because it ensures that nestling parasites have the size advantage needed to either eject host nestmates or compete with them for food. The notion that early hatching represents an adaptation to brood parasitism stems from long-standing observations

Table 30.2 Overview of proposed adaptations for brood parasitism at the fledgling stage

Challenges to solve	Proposed adaptations	Study species	Adaptive role supported?	References
Securing parental care out of the nest	Exaggerated begging signals/tuning into host's sensorial preferences	Brown-headed cowbird (<i>Molothrus ater</i>)	Partially	Woodward (1983) Sealy and Lorenzana (1997) Rasmussen and Sealy (2006)
		Great spotted cuckoo (<i>Clamator glandarius</i>)	No	Soler et al. (2014a)
	Joined dispersal	Great spotted cuckoo	Partially	Soler et al. (1995b, 2014a)
	Change to better caregivers	Great spotted cuckoo	Partially	Soler et al. (2014a, c)
Avoiding host discrimination	Host fledgling mimicry	Screaming cowbird (<i>M. rufoaxillaris</i>)	Yes	Fraga (1998) De Mársico et al. (2012)
Conspecific recognition	'Password' for species recognition	Brown-headed cowbird	Partially	King and West (1977) Graham and Middleton (1988) Hauber et al. (2001)
		Great spotted cuckoo	No	Soler and Soler (1999)
		Indigobirds (<i>Vidua funerea</i> and <i>V. purpurascens</i>)	Presumably yes	Payne et al. (2000) DaCosta and Sorenson (2014)
	Self-referencing	Brown-headed cowbird	Partially	Hauber et al. (2000)
	Facilitation by adult parasites	Brown-headed cowbird	Mixed evidence	Hahn and Fleischer (1995) Hauber (2002) Louder et al. (2015)

(continued)

Table 30.2 (continued)

Challenges to solve	Proposed adaptations	Study species	Adaptive role supported?	References
		Great spotted cuckoo	Partially	Soler and Soler (1999) Soler et al. (1995b)

Selected references provide evidence either supporting the hypothesized adaptation or not. ‘Partially’ supported means that empirical data suggest a fitness benefit of the proposed adaptation, but comparative studies are lacking. ‘Mixed evidence’ means that different studies showed conflicting results

that parasite eggs hatch sooner than would be allometrically expected for their size (Hamilton and Orians 1965; Payne 1977; Briskie and Sealy 1990). Early hatching might be achieved via maternal traits (e.g. internal incubation; Chap. 20) or via the rapid development of parasite embryos themselves.

Researchers have looked to characteristics of parasite’s eggshells for evidence of rapid embryo growth, with equivocal results. The eggs of brown-headed cowbirds (*Molothrus ater*) are more porous than those of two closely related non-parasitic icterids, consistent with cowbird eggs achieving the high rates of gas flux needed for rapid embryo growth (Jaeckle et al. 2012). However, a phylogenetic analysis of cowbirds and their relatives found no evidence that these parasites had shorter-than-expected incubation times (Mermoz and Ornelas 2004). In common cuckoos (*Cuculus canorus*), eggshells are *less* porous than those of non-parasites, which would not favour rapid growth but might instead help them conserve the energetic reserves needed for hatching (Portugal et al. 2014). Indeed, hatching from parasite eggs, which are typically thicker shelled than those of non-parasites, may require its own adaptations, such as stronger hatching muscles (Honza et al. 2001, 2015).

30.2.2 Host-Attuned Growth Rates

Host species broadly differ in life history traits, provisioning effort, and predation pressures, all of which can affect the survival and growth of parasitic chicks. Given that growth patterns may have important consequences for fitness, the question arises of whether parasites are attuned to grow optimally in host nests.

Two major drivers of growth rates in birds are nest predation risk (Martin et al. 2011; Mainwaring and Hartley 2012) and within-brood competition (Royle et al. 1999). Parasitic chicks may benefit from growing as fast as possible if this reduces their exposure to predation (Remeš and Martin 2002; Remeš and Matysiokova 2016) and/or increases their competitive ability (Royle et al. 1999). However, empirical data do not support this expectation. Rather, growth rates vary within parasite species depending on host characteristics and brood size. For instance, brown-

headed cowbird nestlings grow faster when parasitizing host species with shorter nestling periods (Kilpatrick 2002; Remeš 2010) and shiny cowbird (*M. bonariensis*) nestlings grow more rapidly in nests of small- and medium-sized hosts (De Mársico et al. 2010; Gloag et al. 2012; but see Tuero et al. 2013). In addition, a comparative study indicates that cowbirds have not evolved faster growth rates than their non-parasitic relatives (Mermoz and Ornelas 2004). Similarly, common cuckoo nestlings show considerable variation in growth rate among host species, probably due to differences in provisioning rates or host quality (Kleven et al. 1999; Butchart et al. 2003; Grim 2006b). Common cuckoo nestlings also showed decreased growth rates when they were forced to compete with host nestmates in mixed broods (Hauber and Moskát 2008; Grim et al. 2009; Geltsch et al. 2012), which further indicate that growth dynamics of parasite nestlings can be constrained by the rearing environment.

Parasitic nestlings could achieve rapid growth rates via increased digestive efficiency relative to host nestlings. Soler et al. (2014b, 2017) examined this putative adaptation by analysing the digestive performance of hand-fed great spotted cuckoo (*Clamator glandarius*) nestlings and those of its primary host, the magpie (*Pica pica*). Great spotted cuckoo nestlings usually grow faster than magpies and ingest more food under similar conditions (Soler and Soler 1991; Soler et al. 1995a, 2014b). Nevertheless, controlled biochemical analyses of nestlings' faeces failed to support the hypothesis of better nutrient assimilation in cuckoos, suggesting that faster growth rates result from parasite's higher competitive ability rather than increased digestive efficiency (Soler et al. 2017).

30.2.3 Nestmate-killing Behaviour

Young of obligate brood parasites are expected to behave selfishly since they are not constrained by kin selection (Hamilton 1964). A striking example is the nestmate-killing behaviour found in most Old World cuckoos (Jenner 1788; Honza et al. 2007), honeyguides (*Indicator* spp.; Spottiswoode and Koorevaar 2012) and the striped cuckoo (*Tapera naevia*) (Morton and Farabaugh 1979). Nestmate-killing behaviours typically result in parasite nestlings becoming the sole occupants of the nest, hence its most obvious benefit is to monopolize parental care (Kilner 2005; Hauber and Moskát 2008; Grim et al. 2009). Various adaptive explanations have been proposed for nestmate-killing in brood parasites (reviewed in Kilner 2005; see also Soler 2002), but none of them can fully account for the phylogenetic distribution of this trait (Wang and Kimball 2012; see also Grim 2006c).

What are the evolutionary origins of nestmate-killing in obligate brood parasites? Is it linked to obligate siblicide? Wang and Kimball (2012) examined this link. They found that clades of parasite species exhibiting nestmate-killing behaviours were nested within clades containing obligate siblicidal species and, conversely, clades with 'nestmate-acceptor' parasites did not feature siblicidal behaviour (Wang and Kimball 2012). The exception is the genus *Clamator*, which do not exhibit nestmate-killing but occurs within a larger clade containing nestmate-killing parasites

(Wang and Kimball 2012). The evolution of virulence in obligate brood parasites may have resulted from a predisposition for nestmate killing in certain lineages combined with ecological and evolutionary constraints (Wang and Kimball 2012; Fulmer and Hauber 2016). Nevertheless, the adaptiveness of nestmate-killing likely depends on multiple factors including host's food allocation strategies and the competitive ability of parasitic chicks (Soler 2002; Kilner et al. 2004; Rivers 2007; Gloag et al. 2012; Soler and de Neve 2013).

30.2.4 Exaggerated Begging Displays

Nestling birds communicate their need through begging displays that comprise visual (posturing and coloured gapes) and vocal signals (begging calls). Begging signals have been hypothesized to carry honest information about offspring need because they convey direct (i.e. energy expenditure, predation risk) and indirect fitness costs (i.e. competition with full- or half-sibs) to nestlings (Godfray 1995; Kilner and Johnstone 1997). Hence, it is expected that nestlings will beg at intensities that reflect their hunger level (i.e. short-term need) and body condition (i.e. long-term need) (Budden and Wright 2001).

Early ornithologists have noticed that parasitic nestlings beg louder than host young (e.g. Friedmann 1929; Fig. 30.1). These observations found empirical support from studies showing exaggerated begging displays in different parasite species (Gochfeld 1979; Kilner et al. 1999; Soler et al. 1999; Rivers 2007). This exaggeration involves not only acoustic signals but also visual ones, such as body stretching, conspicuous gape colours (Álvarez 2004), wing-shaking (Grim 2008) or wing patches that simulate extra gapes in the nest (Tanaka et al. 2005; Tanaka and Ueda 2005). The exaggeration of begging signals is expected since parasitic chicks are only constrained by the direct costs of begging (Godfray 1995). This has raised the question of whether parasite's begging displays are honest signals of need or not. There is growing evidence for a positive relationship between hunger level and begging intensity of parasitic chicks, supporting the view that despite their exaggeration begging displays convey reliable information to host parents, as predicted by models of honest signalling (Kilner and Davies 1999; Lichtenstein 2001; Hauber and Ramsey 2003; Tanaka and Ueda 2005; Soler et al. 2012; but see Rivers 2007).

The ubiquity of intense begging behaviours among brood parasites has led to the assumption that this is an adaptation for brood parasitism. However, few studies have tested this hypothesis taking evolutionary history into account. Rivers et al. (2013) quantified nestling begging intensity in the brown-headed cowbird and a close non-parasitic relative, the red-winged blackbird (*Agelaius phoeniceus*) under similar conditions. Contrary to the expectation, they found that begging intensity of nestling cowbirds was similar or lower than that of blackbirds (Rivers et al. 2013). By contrast, Lichtenstein (2001) showed that screaming cowbird (*Molothrus rufoaxillaris*) nestlings beg more intensely than those of its phylogenetically related host, the baywing (*Agelaioides badius*), after controlling for short-term need. Given

Fig. 30.1 Shiny cowbird (*Molothrus bonariensis*) chick exhibiting its begging display in a nest of a common host, the chalk-browed mockingbird (*Mimus saturninus*), which contains two host chicks. Photo credit: Vanina D. Fiorini



such mixed evidence, it is too early to either conclude or dismiss that increased begging intensity is a tuning adaptation of parasite young.

30.2.5 Host Chick Mimicry

Active host defences against parasitism at the chick stage are either less common or less commonly documented than those at the egg stage (see Chap. 29). Direct evidence of host parents rejecting cuckoo nestlings comes from hosts of the Australasian bronze cuckoos (*Chalcites* spp.), which either drag newly hatched cuckoo nestlings out of the nest (*Gerygone* sp.; Sato et al. 2010; Tokue and Ueda 2010) or abandon lone cuckoo chicks (superb fairy wrens, *Malurus cyaneus*; Langmore et al. 2003). Bronze cuckoos are thus expected to have evolved counter-adaptations to evade host rejection. Consistent with visual mimicry as one such counter-defence, bronze cuckoo nestlings are more similar in skin colour, flange colour and feather colour to their respective hosts than they are to congener cuckoos (Langmore et al. 2011; Fig. 30.2). However, experimental evidence is needed to confirm that hosts use visual cues to recognize and reject parasite chicks and thus that the evolution of visual similarities with hosts is driven by host defences (Grim 2005). Indeed, Langmore et al. (2003) found that superb fairy wrens reject shining bronze cuckoo chicks (*C. lucidus*) more consistently than Horsfield's bronze cuckoo chicks (*C. basalis*), despite the two being similarly close visual matches for the fairy wren's young (Langmore et al. 2003, 2011). Thus visual mimicry in this case must be, at best, only one of several cues used to identify cuckoos. Horsfield's bronze cuckoos may benefit from mimicry of additional cues used by fairy wrens to make rejection decisions, such as rictal flange colour or begging call structure (Langmore et al. 2011; Colombelli-Négrel et al. 2012).

Vidua finches closely resemble their hosts in the colours and patterns of their gapes, but whether similarity in this case derives from counter-defences by parasites remains unresolved (Payne et al. 2001). In experimental manipulations, red-billed

Fig. 30.2 Little bronze cuckoo (*Chrysococcyx minutillus*) chick (top) showing striking visual similarity to the chicks of its host, the large-billed gerygone (*Gerygone magnirostris*). Photo credit: Hee-Jin Noh



firefinches (*Lagonosticta senegala*) were more likely to abandon the nestlings of non-parasitic estrildid finches, which look unlike their own young, than they were the nestlings of the parasitic village indigobird (*V. chalybeata*), which closely resemble their own young (Payne et al. 2001). However, common waxbills (*Estrilda astrild*) parasitized by another gape-mimicking *Vidua* (*V. macroura*) showed no active defence against parasitic nestlings in the field (Schuetz 2005a) nor were they more likely to abandon waxbill young with modified gape colour than those with unmanipulated gapes (Schuetz 2005b). Other explanations for the visual similarity of *Vidua* sp. and their host nestlings do not require an assumption of active host defence at the nestling stage. For example, gape mimicry may be driven by increased exploitation of host's sensory biases during provisioning, or a coevolutionary arm's race in which intrabrood conflict has led host young to converge on parasite morphology (Hauber and Kilner 2007).

30.3 Proposed Parasite Adaptations During the Fledgling Stage

The post-fledging period represents a critical yet understudied life stage. In many species, fledglings are flightless by the time they leave the nest, and post-fledging parental care becomes crucial to enhance their survival (Naef-Daenzer and Gruebler 2016). Therefore, it is expected that fledgling brood parasites deploy tactics to secure parental care (Table 30.2).

30.3.1 Tuning Adaptations

Fledglings of the brown-headed cowbird exhibit loud and persistent begging calls even after being able to forage for themselves (Woodward 1983). Most notably, they can engage individuals other than their foster parents to provision them (reviewed in Sealy and Lorenzana 1997). These so-called ‘auxiliary feedings’ of parasitic fledglings have been reported for another 12 parasite species and involved provisioning adults of either the same or a different species than the original hosts, suggesting that some parasites may be adapted to ‘tune’ into a broad range of parent-offspring communication systems (Sealy and Lorenzana 1997).

Auxiliary feedings seem to occur more frequently among parasitic than non-parasitic fledglings (Shy 1982; Sealy and Lorenzana 1997) and could enhance the survival of parasitic fledglings when hosts cease to feed them prematurely or provide inadequate amounts of food (Sealy and Lorenzana 1997). Yet, whether parasitic fledglings are adapted to look for auxiliary feedings or exploit them opportunistically is not clear. So far, the only parasite species believed to regularly use this tactic are the pallid cuckoo (*Cuculus pallidus*; Sealy and Lorenzana 1997) and the great spotted cuckoo (Soler et al. 1995b, 2014c). The latter may abandon their natal group and join other conspecific fledglings to find new caregivers (Soler et al. 1995b, 2014a, c). Looking for auxiliary feedings could be an adaptive response of great spotted cuckoo fledglings that fail to tune into host’s sensory preferences and become undernourished when reared in mixed broods (Soler et al. 2014a, c). Consistent with this idea, cuckoo fledglings were more likely to elicit alloparental feedings from adult magpies that have reared only cuckoo chicks than from those that have cared for mixed broods (Soler et al. 2014c).

30.3.2 Trickery Adaptations

Just as in the nestling stage, fledgling parasites may outcompete host young if they are able to monopolize parental feedings after leaving the nest. Rasmussen and Sealy (2006) compiled 102 reports of post-fledging parental feedings in hosts of the brown-headed cowbird that cared for mixed broods and found that hosts fed only the cowbird fledglings in 95% of these cases. Although most of these reports were anecdotal and likely subjected to biases, it is possible that reproductive losses caused by cowbird parasitism just before or after fledging are higher than previously thought.

If high enough, post-fledging fitness costs could drive the evolution of host defences against fledgling parasites, which may potentially lead to a coevolutionary arms race at this last stage of the nesting cycle. The most compelling evidence of coevolution at the fledgling stage comes from the host specialist screaming cowbird and its primary host, the baywing. Fledgling screaming cowbirds match closely the plumage coloration and begging calls of baywing fledglings (Fraga 1998; De Marsico et al. 2012). This resemblance seems to be a case of true mimicry evolved in response to host discrimination because baywing parents provide prolonged parental care to screaming cowbird fledglings but refuse to feed non-mimetic fledglings of the closely related shiny cowbird (Fraga 1998; De Marsico et al. 2012). Why baywings have evolved rejection of parasitic fledglings instead of parasitic eggs or chicks is intriguing. Delaying discrimination could be adaptive if it makes recognition of alien young easier and allows hosts to save energy for future reproduction. Similar trickery adaptations could occur in other parasite species (e.g. the Jacobin cuckoo, *Clamator jacobinus*) (reviewed in Grim 2006a; Feeney et al. 2014), but those reports require confirmation.

30.3.3 Adaptations for Conspecific Recognition

Juveniles of obligate brood parasites must also solve the problem of meeting their conspecifics after having been reared by heterospecific hosts (Table 30.2). In birds, conspecific recognition templates are shaped through social experience with individuals (e.g. parents or siblings) from whom developing young can reliably learn species-specific phenotypes (ten Cate and Voss 1999; Slagsvold and Hansen 2001). So, how do young parasites avoid sexually misimprinting and develop the appropriate species-recognition templates?

Hauber et al. (2001) suggested that brood parasites may use ‘passwords’ for species recognition. Young parasites would be able to innately recognize certain phenotypic traits that reliable signals conspecific identity, which in turn would trigger learning of additional cues for species recognition from the password-giver’s phenotype (Soler and Soler 1999; Hauber et al. 2001). In the brown-headed cowbird, the ‘chatter’ call of adult males and females has been proposed as such a password (Hauber et al. 2001). A similar mechanism could be at play in parasitic whydahs and indigobirds (*Vidua* spp.). Male indigobirds exhibit ‘mimicry songs’ that are common to conspecific males that share the same host species and ‘non-mimicry songs’ that are common to conspecific males from the same local neighbourhood but vary over larger geographic scales (Payne et al. 1998; DaCosta and Sorenson 2014). Young males that disperse outside their local ‘dialect neighbourhood’ may use mimicry songs to identify conspecifics, from which they can subsequently learn new repertoires of non-mimicry songs (DaCosta and Sorenson 2014).

A second mechanism for species recognition could be self-referencing, which is developing a conspecific recognition template based on the individual’s own phenotype (the ‘armpit effect’; Dawkins 1982). This idea has found some support in a choice experiment performed with brown-headed cowbird juveniles that were dyed

to manipulate their phenotype (Hauber et al. 2000). Juveniles approached more quickly and associated preferentially with cowbird females coloured like themselves (Hauber et al. 2000), indicating that they could use salient features of their own phenotype to identify conspecifics in the absence of, or in addition to, other recognition cues.

Another possibility is that adult parasites themselves facilitate conspecific recognition by providing opportunities for social learning of species-specific cues to juveniles. This idea arose from studies showing social interactions between adult females and juveniles in the brown-headed cowbird (Woodward 1983; Hahn and Fleischer 1995; Hauber 2002) and the great spotted cuckoo (Soler and Soler 1999). Such interactions could facilitate an early socialization if parasitic juveniles follow conspecific females to foraging flocks or communal roosting sites. However, a recent study based on intensive monitoring of radio-tagged cowbirds failed to find temporal correlation in the departures of females and juveniles out of the juveniles' natal area (Louder et al. 2015). The authors suggest that cowbird juveniles may use their solitary excursions outside the natal area to locate conspecifics and gradually segregate from hosts before sexual misimprinting can occur (Louder et al. 2015).

Adult great spotted cuckoos had been observed approaching parasitic fledglings (Soler and Soler 1999). These observations indirectly support the facilitation hypothesis, but the role of adult parasites in the socialization of juvenile cuckoos remains to be determined. Contrary to non-parasitic birds, adult and juvenile cuckoos migrate separately, with adults leaving the breeding areas earlier than juveniles (Soler et al. 1994). This suggests that cuckoo juveniles are able to locate wintering grounds without the assistance of conspecific adults (Soler et al. 1994).

Concluding Remarks and Future Directions

Testing of putative adaptations for brood parasitism requires comparison of parasites not to their hosts but to their non-parasitic relatives. Comparative studies that take into account the parasite's evolutionary history would help to understand if seemingly beneficial traits (e.g. early hatching) are true adaptations or 'pre-adaptations'. Some traits such as growth patterns and begging behaviour can vary widely within parasite species according to environmental factors. To study whether such flexibility reflects ecological constraints or adaptive phenotypic plasticity would be a fruitful subject for future research. Also, additional studies that quantify the fitness costs and benefits of nestmate-killing *versus* nestmate acceptance may help to better understand the evolution of these strategies.

The unexpected discovery of chick rejection by some hosts has led to renewed focus on host–parasite coevolution during the nestling and fledgling stages. Some recent studies suggest the evolution of visual or vocal mimicry in parasitic chicks, but more research is needed into how hosts integrate perceptual cues in rejection decisions. This will help to determine whether host

(continued)

resemblance in parasite chicks is a tricky adaptation or not. Understanding how phylogenetically widespread is chick rejection behaviour and how parasitism drives selection on host young would further shed light on the matter.

The post-fledgling stage is perhaps the most neglected topic in the study of brood parasitism. As new technologies to track juvenile parasites in the wild become increasingly available, we can expect to increase our knowledge of the brood parasitic life cycle beyond the nestling stage. Further experimental studies on social interactions during the post-fledgling stage and the development of species-recognition templates in young parasites may uncover additional key adaptations to brood parasitism.

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