



Parasitic Behaviour of Interspecific Brood Parasitic Females

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Abstract

Interspecific avian brood parasites have to solve unique problems associated with their reproductive habit: they need to recognize potential hosts, search for and locate their nests, monitor nests progress and return to them at the appropriate time for egg laying. In addition, parasitic females may improve the survival of their own eggs and chicks by removing or destroying part of the clutch content. Lastly, they should remember the nests in which they have laid eggs to avoid laying two or more eggs in the same nest to prevent harming their own previously laid eggs and generating competition between their own offspring. In this chapter, we summarize information on the behaviour of parasitic females from the moment they start searching for host nests until they parasitize them. We review the different hypotheses for explaining the recognition of hosts and the cues used to search for and locate their nests. We also review the different adaptive explanations for the removal or destruction of eggs as well as the information on competition among females for host nests and repeat parasitism.

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18.1 Introduction

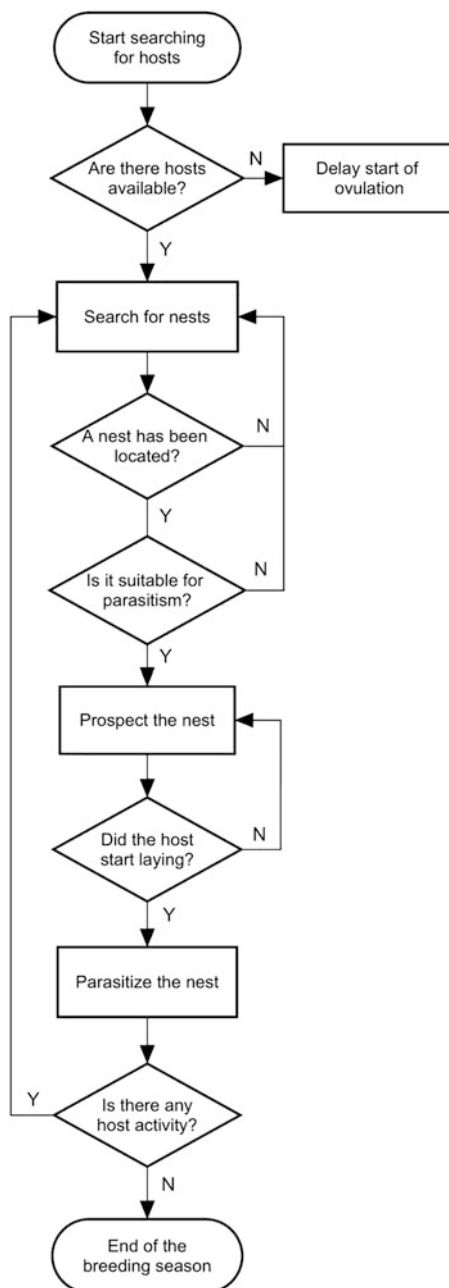
Unlike other birds, avian brood parasites must locate host nests where to lay their eggs and then decide whether to parasitize them. They should also synchronize parasitism with host laying, as this reduces the probability of rejection and increases the hatching success of parasite eggs and the survival of parasite chicks. Besides, although brood parasites do not provide parental care, they could increase the survival of their eggs and chicks by removing or destroying part of the host clutch. Thus, during the breeding season, parasitic females must take several hierarchical decisions since they start searching for host nests until they parasitize them (Fig. 18.1). To do that they should be capable of recognizing potential hosts (Brooke and Davies 1991; Slagsvold and Hansen 2001), locate and prospect their nests (Wyllie 1981; Clotfelter 1998; Moksnes et al. 2000; Soler and Pérez-Contreras 2012), return to them at the time nests are suitable for parasitism (Scardamaglia et al. 2017) and, at that time, circumvent host frontline defences to gain access to the nest (Feeney et al. 2012). During nest visits they should decide whether to remove or destroy part of the clutch (Davies and Brooke 1988; Sealy 1992; Soler et al. 1997; Peer 2006). They also should avoid parasitizing a nest repeatedly to prevent harm to their own previously laid eggs and competition among their offspring (Hahn et al. 1999; Ellison et al. 2006; Gloag et al. 2014a). All these behaviours affect directly the fitness of parasitic females, and therefore we expect they have been shaped by natural selection.

In this chapter, we review different hypotheses to explain how parasite females recognize their hosts, their spatial behaviour during the breeding season, the cues they use to find host nests, whether they prospect nests before parasitism and the timing of parasitism. We also review the different adaptive explanations for the removal or destruction of eggs and analyse whether parasitic females avoid competition with other females (i.e. multiparasitism) or competition between their own offspring (i.e. repeat parasitism). Finally we discuss future directions of research on parasitic behaviour of brood parasitic females.

18.2 Recognizing Hosts

The most accepted hypothesis to explain host recognition by brood parasites is that females imprint on their foster parents and, once mature, search for nests of the same species in which they were reared (“host preference hypothesis”; Brooke and Davies 1991; Slagsvold and Hansen 2001). This hypothesis predicts that even in generalist parasites (i.e. species that parasitize many hosts), individual females should parasitize preferentially one host (i.e. they should be specialists at individual level). This hypothesis has been directly supported by experiments with village indigobirds, *Vidua chalybeata*, bred in captivity and foster-reared by their normal host or by an experimental foster species and tested as adults for host choice (Payne et al. 2000). Indirect evidence in support of this hypothesis includes the association between host species and parasite’s mitochondrial but not nuclear DNA in common cuckoos, *Cuculus canorus* (Gibbs et al. 2000), and greater honeyguides, *Indicator indicator*

Fig. 18.1 Flow chart showing some of the decisions parasitic females take during the breeding season from the moment they start searching for host nests until they parasitize them. The chart does not include decisions related to the removal or destruction of eggs when they visit host nests



(Spottiswoode et al. 2011). Similarly, Mahler et al. (2007, 2009) have shown an association between host species and parasite's mitochondrial DNA in the shiny, *Molothrus bonariensis*, and the screaming, *M. rufoaxillaris*, cowbirds, which indicates non-random laying behaviour of these parasites.

Host preferences by parasitic females have been directly assessed by parentage analysis using microsatellite DNA markers. Marchetti et al. (1998) and Skjelseth et al. (2004) found that most common cuckoo females were specialized in parasitizing one single host. However, Martínez et al. (1998) found that great spotted cuckoo, *Clamator glandarius*, females use nests of two hosts in the same season and genetic data ruled out the presence of different host-specific races in this species (Baglione et al. 2017). Similarly, studies in the brown-headed cowbird, *M. ater*, showed contrasting results, with females of the same population using both specialist and generalist laying strategies (Alderson et al. 1999; Woolfenden et al. 2003; Strausberger and Ashley 2005), and studies in the shiny cowbird (de la Colina et al. 2016) found that females were mostly faithful to one particular host species throughout a reproductive season but that a few females parasitized more than one host. Thus, parentage analysis indicates that host preferences are not absolute and parasitic females may use more than one host in the same season.

Other hypotheses proposed to explain how parasitic females (mainly common cuckoos) find host nests are “natal philopatry” (females return to where they were born and choose hosts randomly; Brooke and Davies 1991), “nest site choice” (females choose host species with similar eggs and nest sites; Moksnes and Røskaft 1995) and “habitat imprinting” (females learn the characteristics of the habitat in which they grow up by an imprinting-like process and establish their reproductive home ranges in areas that resemble the habitat they had experienced as nestlings; Teuschl et al. 1998; Vogl et al. 2002).

18.3 Searching for Host Nests

The study of spatial behaviour by brood parasitic females during the reproductive season may help to understand how they search for hosts' nests. Unfortunately, data on space use and home ranges of radio-tagged females during the breeding season are only available for cuckoos and cowbirds.

Female common cuckoos spent significantly more time at areas of high host density on laying days than on non-laying days, and reproductive activities were observed predominantly in these areas, with individuals commuting to other areas for foraging (Vogl et al. 2002, 2004). Home ranges of female common cuckoos overlapped, and territories boundaries were not well defined when parasitism frequency was high (Nakamura and Miyazawa 1997). Besides, females seemed to know the location of every nest in their range but laid selectively in some of them (Nakamura et al. 2005). Similarly, in the great spotted cuckoo, territoriality is absent (Martínez et al. 1998), and there is a substantial overlap among home ranges of breeding females (Bolopo et al. 2017).

Female brown-headed cowbirds usually spend the morning in host-rich breeding areas and commute several kilometres to feeding areas for the rest of the day (Rothstein et al. 1984; Thompson 1994; Gates and Evans 1998). Home ranges for this species have generally been estimated by recording one location per animal per day during several days (Dufty 1982; Rothstein et al. 1984; Teather and Robertson 1985; Thompson 1994; Gates and Evans 1998; Hahn et al. 1999), and therefore it

has not been possible to evaluate if females maintain stable daily ranges throughout the breeding season. However, females were more closely related to young cowbirds in nests inside than outside their home ranges, which would indicate that they lay eggs within stable home ranges (Hahn et al. 1999).

Shiny and screaming cowbirds showed considerable overlap in the female morning ranges during consecutive days, and the addition of new area to their ranges decreased over time indicating that the size of home ranges tends to an asymptotic value (Scardamaglia and Reboreda 2014). Shiny cowbirds showed sex differences in home ranges, with greater daily and cumulative ranges for males than for females, while these sex differences were not present in screaming cowbirds (Scardamaglia and Reboreda 2014). These data are consistent with the nest-searching behaviour of these species, as female shiny cowbirds search for nests alone while female screaming cowbirds search for host nests together with the male (Mason 1987). In addition to home range fidelity within the breeding season, studies in the brown-headed (Hahn et al. 1999) and the shiny (Scardamaglia and Reboreda 2014) cowbirds have shown range fidelity over successive breeding seasons.

18.4 Locating Host Nests

Various nonmutually exclusive mechanisms of nest location have been proposed (Table 18.1). These mechanisms have received varying support from observational and experimental studies conducted primarily in cuckoos and cowbirds. For instance, whereas the proximity of vantage points was positively related to parasitism risk in some host–parasite systems (i.e. Álvarez 1993; Øien et al. 1996; Clotfelter 1998; Hauber and Russo 2000; Begum et al. 2011), other studies failed to find such effect (i.e. Avilés et al. 2009; Fiorini et al. 2009a; Jelínek et al. 2014). Similarly, the level of host aggression towards parasitic females at the nest was

Table 18.1 Different hypotheses proposed to explain how brood parasitic females locate host nests

Hypothesis	Proposed mechanism	Parasite species
Perch proximity	Parasitic females scan their habitats from vantage points to spot suitable host nests	Common cuckoo (<i>Cuculus canorus</i>) ^{a,b,c}
		Brown-headed cowbird (<i>Molothrus ater</i>) ^{d,e}
		Asian koel (<i>Eudynamis scolopacea</i>) ^f
Host activity	Parasitic females cue on the level of host activity near the nest	Brown-headed cowbird ^g
		Great spotted cuckoo (<i>Clamator glandarius</i>) ^h
Nest exposure	Nest location is driven by the extent of visual conspicuousness of host nests to parasites	Common cuckoo ^{b,c,g,i,j,k,l}

References: ^aÁlvarez (1993); ^bØien et al. (1996); ^cAntonov et al. (2007); ^dHauber and Russo (2000); ^eClotfelter (1998); ^fBegum et al. (2011); ^gBanks and Martin (2001); ^hSoler and Pérez-Contreras (2012); ⁱMoskát and Honza (2000); ^jClarke et al. (2001); ^kAvilés et al. (2009); ^lJelínek et al. (2014)

positively related (Robertson and Norman 1977; Smith et al. 1984), negatively related (Briskie et al. 1990) or unrelated (Gill et al. 1997; Clotfelter 1998) to the likelihood of parasitism. These conflicting results suggest that locating appropriate host nests in which to lay may be a complex and hierarchical process and that the mechanisms and cues employed by parasitic females can be influenced by many ecological factors such as host species, habitat structure, nest density and/or time of the breeding season (Martínez et al. 1996; Burhans 1997; Langmore and Kilner 2007; Patten et al. 2011; Jelínek et al. 2014).

In parasite species other than cuckoos and cowbirds, nest-searching strategies are poorly known. Anecdotal observations of captive and free-living individuals of the only precocial obligate brood parasite, the black-headed duck, *Heteronetta atricapilla*, indicate that this species searches for host nests in pairs and monitors host's nesting activities either by passing close to the nests or by sitting quietly in the surrounding vegetation (Rees and Hillgarth 1984; Lyon and Eadie 2013).

Females of the common cuckoo have been observed monitoring host's nesting activity from nearby trees (i.e. Chance 1922; Wyllie 1981). The effect of perch proximity on parasitism risk by cuckoos has received considerable attention (Álvarez 1993; Øien et al. 1996; Moskát and Honza 2000; Antonov et al. 2007), but fewer studies have examined the effect of host activity on cuckoo parasitism. Soler and Pérez-Contreras (2012) tested the effect of host activity on the risk of parasitism of magpie, *Pica pica*, nests by the great spotted cuckoo. They found that cuckoo parasitism was significantly more frequent in natural, active magpie nests during the pre-laying stage than in nests with no eggs and parental activity, whereas nest exposure had no clear effect on the likelihood of parasitism (Soler and Pérez-Contreras 2012). By contrast, the probability of host nests being parasitized by common cuckoos increases with nest exposure (Øien et al. 1996; Moskát and Honza 2000; Clarke et al. 2001; Antonov et al. 2007; Avilés et al. 2009; Jelínek et al. 2014). It is possible that common cuckoo females are first attracted by host activity and then find suitable nests by closer visual inspection or, conversely, they detect more exposed nests first and then cue on host activity to decide where to lay their eggs (Moksnes et al. 2000). Interestingly, the effect of nest exposure on the risk of parasitism may depend on the availability of host nests (Jelínek et al. 2014). More concealed nests of the great reed warbler were less likely to escape parasitism when host pairs breed at lower densities, which indicates that cuckoo females would search for host nests more intensively when suitable nests are in short supply (Jelínek et al. 2014).

Brood parasitic cowbirds exhibit similar nest-searching behaviours with both nest site characteristics and host activity influencing parasitism risk. The perch proximity hypothesis is relatively well supported in the brown-headed cowbird (Clotfelter 1998; Hauber and Russo 2000; Patten et al. 2011). The host activity hypothesis also received support in the brown-headed cowbird (Clotfelter 1998; Banks and Martin 2001; Robinson and Robinson 2001) and the shiny cowbird (Fiorini and Reboreda 2006; Svagelj et al. 2009). However, the effect of host activity arose more clearly in experimental studies that compared parasitism rates between active and inactive host nests (Robinson and Robinson 2001; Fiorini and Reboreda 2006; Svagelj et al. 2009) than in observational studies analysing the relationship between

the level of host activity at the nest and the likelihood of parasitism (e.g. McLaren and Sealy 2003; Fiorini et al. 2009a). This would indicate that whereas host activity is key to elicit parasitism, parasitic females might rely primarily on habitat or nest characteristics for host nest detection (i.e. Fiorini and Reboresda 2006). The role of host's nest defensive behaviours towards visiting cowbirds as a cue for nest location is even more controversial (i.e. Gill et al. 1997).

Intriguingly, the social behaviour of some parasite species suggests other potential mechanism of nest location, namely, that individual females eavesdrop on each other's nest-searching activities or follow conspecific females to host nests from communal roosting sites (De Mársico et al. 2010; Gloag et al. 2013). This possibility has some indirect support from studies on the shiny cowbird showing that females overlap extensively in territory use (Scardamaglia and Reboresda 2014), and multiparasitism on a single day often involves a second laying female that tails closely a preceding conspecific on her arrival to the nest (Gloag et al. 2013). Nevertheless, whether eavesdropping provides an alternative nest-searching strategy to brood parasitic females awaits further research.

18.5 Prospecting Host Nests

After searching for and locating a host nest, parasitic females should monitor its progress to ensure they synchronize parasitism with host laying, as this increases the success of the parasite's egg and chick. Some studies have used the observation of the removal or destruction of host eggs before the event of parasitism as indirect evidence of prospecting behaviour by the parasitic female (e.g. Massoni and Reboresda 1999). However, to assume that the same female was responsible for both nest visits could be an important source of error in species at which there are no territories and multiparasitism is common. On the other hand, the use of video records in nest-centred studies (e.g. Moksnes et al. 2000; Gloag et al. 2013) cannot assess the activity of parasitic females around the nest, which increases the likelihood of false negatives (i.e. prospecting visits not recorded). Lastly, traditional tracking of radio-tagged individuals (e.g. Honza et al. 2002) has the drawback that it is quite difficult to continuously monitor the activity of the female, also giving an underestimate of the amount of prospecting behaviour.

Even with these limitations, there is some evidence that common cuckoo females prospect host nests before parasitism. In a study based on continuous video recordings made at nests of reed warblers, *Acrocephalus scirpaceus*, Moksnes et al. (2000) found that there were cases at which the female visited the nest prior to laying one or several times. Honza et al. (2002) examined the behaviour of radio-tagged cuckoo females in the area surrounding host nests during the pre-laying and laying periods and showed that only half of cuckoo nest visits resulted in laying, suggesting that cuckoo females visited host nests before parasitizing them.

Scardamaglia et al. (2017) studied visits to potential host nests by shiny and screaming cowbirds in the periods preceding and overlapping the laying period of their hosts. They recorded the presence of radio-tagged females within a 20 m area

around nests of chalked-browed mockingbirds, *Mimus saturninus* (a common host of shiny cowbirds), and baywings, *Agelaioides badius* (the main host of screaming cowbirds), using proximity data loggers placed at host nests. They found that in all cases, females of both species visited potential host nests prior to laying. The number of prospecting visits was higher in screaming than in shiny cowbirds, likely because the host of this parasite begins laying at a less predictable interval after completion of the nest (De Mársico and Reboreda 2008), creating a need for more prospecting visits.

18.6 Timing of Parasitism

In addition to coinciding with the laying period of their hosts, two other aspects of the timing of parasitism can influence a parasite's success: the time of the day that parasitism occurs and the speed of egg laying itself.

Many hosts will actively attack female parasites at their nests, and by doing so may thwart a parasite's attempt to lay (Welbergen and Davies 2009; Gloag et al. 2013). The likelihood that parasites encounter host parents at the nest depends in part on the time of day that parasitism occurs. Cuckoos lay eggs anytime within a broad window of daylight hours (common cuckoo, afternoon-evening, Chance 1940; bronze-cuckoos, morning to early afternoon, *Chrysococcyx sp.*, Brooker et al. 1988; *Chalcites minutillus*, Gloag et al. 2014b; great spotted cuckoo, morning to afternoon, Soler et al. 2014). As hosts must periodically leave the nest during the day for feeding and other activities, female cuckoos thus have opportunities to approach an unoccupied nest. While such large laying windows do not guarantee that egg laying occurs by stealth (e.g. great spotted cuckoos regularly encounter hosts at the nest; Soler et al. 2014, and have behavioural strategies to evade host attention when laying; Álvarez and Arias de Reyna 1974), the unpredictable timing of cuckoo egg laying presumably makes the task of nest guarding against parasitism more difficult for hosts.

Cowbirds, in contrast, lay during a narrow interval of the 30 min or so before sunrise (Peer and Sealy 1999; Ellison and Sealy 2007; Gloag et al. 2013; Scardamaglia et al. 2017). Such a short, predictable time frame for parasitism favours a corresponding short bout of nest vigilance by hosts. For example, chalk-browed mockingbirds assume sentinel positions near their nests prior to sunrise and strive to intercept shiny cowbirds approaching their nests, such that almost all cowbirds at or near nests are aggressively mobbed (Gloag et al. 2013). Yellow warblers, *Dendroica petechia* (Tewksbury et al. 2002), and some orioles (Ellison and Sealy 2007) instead sit tight on their nests during the "parasitism hour" to deter brown-headed cowbird laying or egg removal. Similarly, baywings sit tight on the nest before sunrise, the time at which screaming cowbirds parasitize (De Mársico et al. 2013). At the same time, the low light levels prior to sunrise may provide some advantage to cowbirds, by making them hard for hosts to detect until they are already in the nest. The time of day of egg laying typical in other brood parasitic lineages is not well reported, but it is likely that in all cases this aspect of timing influences the

probability that parasites evade host frontline defences and in turn the defensive strategies adopted by hosts.

For all parasites where the act of parasitism has been observed, egg laying occurs exceptionally rapid. Most bird species require 20 min or more to lay an egg (Sealy et al. 1995), but typical times among parasites vary from 5 to 41 s in common cuckoos (Moksnes et al. 2000; Honza et al. 2002; Andou et al. 2005), 4–40 s in great spotted cuckoos (Soler et al. 2014), 41s in brown-headed cowbirds (Sealy et al. 1995), 5–10 s in bronzed cowbirds, *M. aeneus* (Peer and Sealy 1999), and 2–16 s in shiny cowbirds (Gloag et al. 2013). While the actual time the parasite spends at the host nest may be prolonged by the clutch-reduction behaviours that precede laying or by interactions with hosts, the total visit time of these parasites to host nests rarely exceeds 1 min. Such rapid egg laying both reduces the time that a female parasite must endure host attack if detected and increases the chances that she evades host detection entirely.

18.7 Removing and Puncturing Eggs

Many brood parasites reduce host clutch by removing or by pecking and puncturing their eggs (Davies and Brooke 1988; Sealy 1992; Soler et al. 1997; Peer 2006). The host, as part of its nest sanitation behaviour, then removes the punctured egg (Kemal and Rothstein 1988; Soler et al. 1999). These egg removal or egg damaging behaviours can occur at the time the nest is parasitized, in a visit not associated with parasitism or after the nest has been parasitized (Sealy 1992; Gloag et al. 2014a). Different adaptive hypotheses have been proposed for explaining these behaviours including direct benefits for the parasitic female or benefits for the parasitic egg or chick (i.e. higher survival) (Table 18.2).

The first group (direct benefits) include the hypothesis that there are nutritional benefits to parasitic females from eating the removed egg (Davies and Brooke 1988; Scott et al. 1992; Sealy 1992). This hypothesis predicts that egg removal will occur in visits both associated and not associated with parasitism. Scott et al. (1992) found that less than half of the eggs removed by the brown-headed cowbird were eaten, and according to Sealy (1992) evidence supporting this hypothesis is scarce and equivocal.

An alternative direct benefit of egg destruction is the “farming hypothesis” (Arcese et al. 1996; Swan et al. 2015), which states that when a parasitic female finds a nest late in the nesting cycle, by destroying or removing most of the nest content, she may induce hosts to renest, creating new opportunities for parasitism. In this case, egg destruction should occur only in nests that have not been parasitized by the “farming” female (see Chap. 15).

Egg destruction might also confer indirect benefits to female parasites (i.e. to increase the survival of the parasite egg or chick). The “test incubation hypothesis” (Livesey 1936; Massoni and Reboreda 1999) states that by puncturing host eggs, the parasitic female may assess the degree of development of the embryo and decide whether to parasitize the nest or not (i.e. avoid nests at which incubation is advanced).

Table 18.2 Different adaptive hypotheses to explain the removal or puncture of eggs when brood parasitic females visit host nests

Hypotheses	Proposed benefits	Potential costs	Timing of removal or punctures	Occurrence of parasitism	# of eggs removed or punctured
Nutritional benefits ^{1,2,3}	Direct. Nutritional resources for the female	None	Before and after ^a	Yes or no	One or few
Farming ⁴	Direct. New opportunities for parasitism	None	Before	No	Most
Test incubation ^{5,6}	Indirect. Higher egg and chick survival	None, or nest abandonment	Before	Yes or no	One or few
Incubation efficiency ⁷⁻¹²	Indirect. Higher hatching success	Nest abandonment	Before	Yes	One or few
Deception ¹³	Indirect. Lower probability of egg rejection	None	Before	Yes	One
Reduction of competition ¹⁴	Indirect. Higher chick growth rate and survival	Nest abandonment	Before	Yes	One or few
Mafia ^{15,16}	Indirect. To enforce the acceptance of parasite eggs	None	After	Yes	Most

Direct benefits are those received by the female, while indirect benefits are those that increase the survival of the parasitic eggs and chicks. Each hypothesis makes different predictions regarding the timing of egg removal or egg punctures (before or after parasitism), whether the nests at which egg removal or egg punctures occur should be parasitized at any time and if clutch destruction should affect one egg, few eggs or most eggs

^aThis would require that parasites recognize and avoid eating their own eggs

References: ¹Davies and Brooke (1988); ²Scott et al. (1992); ³Sealy (1992); ⁴Arcese et al. (1996); ⁵Livesey (1936); ⁶Massoni and Reboreda (1999); ⁷Davies and Brooke (1988); ⁸Lerkelund et al. (1993); ⁹McMaster and Sealy (1997); ¹⁰Peer and Bollinger (1997); ¹¹Peer and Bollinger (2000); ¹²Soler et al. (1997); ¹³Sealy (1992); ¹⁴Sealy (1992); ¹⁵Zahavi (1979); ¹⁶Soler et al. (1995)

This hypothesis predicts that egg punctures should occur always before the event of parasitism, either in the same visit or in previous visits. It also predicts the occurrence of punctures in unparasitized nests, if such nests contained eggs at an advanced stage of development. Correlational support for this hypothesis has been found in nests of yellow-winged blackbirds, *Agelasticus thilius*, where punctures by shiny cowbirds occurred in advance or simultaneously with parasitism and nests were more frequently parasitized when host eggs were punctured during egg laying or early incubation than during mid or late incubation, when embryos were more developed (Massoni and Reboreda 1999). A similar correlational result was found in nests of creamy-bellied thrushes parasitized by shiny cowbirds (Astié and Reboreda 2009).

The “incubation limit” or “incubation efficiency hypothesis” (Davies and Brooke 1988; Lerkelund et al. 1993; McMaster and Sealy 1997; Peer and Bollinger 1997; Soler et al. 1997) states that by removing or destroying host eggs, the parasitic female increases the efficiency of incubation of its egg. This hypothesis predicts the removal or destruction of host eggs in parasitized nests and applies mainly to hosts larger than the parasite, as the removal of host eggs in these cases improves the contact of smaller parasitic eggs with the brood patch of the host and increases its hatching success. Peer and Bollinger (1997) found that the hatching success of brown-headed cowbird eggs was higher in nests of a large host, the common grackle (*Quiscalus quiscula*), when host eggs were removed. This benefit was reduced or absent when the cowbird egg was larger than host eggs as in the case of the yellow warbler (McMaster and Sealy 1997). Correlational studies conducted in hosts of the shiny cowbird larger than the parasite did not find an effect of the puncture of host eggs on the incubation efficiency of the parasite egg (Astié and Reboresda 2009; Fiorini et al. 2009b).

The “host deception hypothesis” (Sealy 1992) states that egg removal may dupe a host, reducing the likelihood that it detects parasitism and abandons the nest or ejects the parasitic egg. This hypothesis predicts that egg removal should occur in association with parasitism and assumes that some hosts may have the cognitive ability to assess the number of eggs (Hamilton and Orians 1965; Lyon 2003). Although some correlational evidence seems consistent with this hypothesis (Hamilton and Orians 1965; Moksnes and Røskaft 1987), other studies have failed to find supporting evidence (Sealy 1992; Moksnes and Røskaft 1989).

Another hypothesis for explaining the destruction of host eggs in parasitized nests is the “reduction of competition hypothesis” which states that by removing or puncturing host eggs, parasite females can improve the survival of their offspring as a result of the reduction of competition for food with nestmates (Sealy 1992). This hypothesis applies to parasites that do not eject nestmates, and it is most relevant to parasites whose chicks are smaller than host chicks and therefore have to compete for food with larger nestmates. In agreement with this hypothesis, Soler et al. (1997) showed that by damaging magpie eggs, great spotted cuckoos increase the likelihood that late-laid cuckoo eggs hatch. In greater honeyguides, although parasite chicks kill host chicks and therefore they do not have to compete for food with their nestmates, females puncture host eggs. Because chick killing has high energetic costs for the parasitic chick, egg puncture behaviour may benefit the parasitic chick through decreasing the number of nestlings it has to kill (Spottiswoode and Koorevaar 2012). The reduction of competition hypothesis was also proposed as an explanation of egg puncture behaviour in the bronzed cowbird (Carter 1986) and egg removal behaviour in the brown-headed cowbird (Sealy 1992).

Experimental work carried out in hosts of shiny cowbirds found that the reduction of host clutch size benefits the parasitic chick in nests of chalk-browed mockingbird (a host larger than the parasite) by increasing growth rate and chick survival (Fiorini et al. 2009b; Gloag et al. 2012). On the contrary, brown-headed cowbirds chicks reared in nests of eastern phoebes, *Sayornis phoebe*, and shiny cowbirds reared in nests of house wrens, *Troglodytes aedon*, both cases where the host chicks are

smaller than the parasite chicks, benefit from the presence of host chicks by increasing their food intake and growth rate (Kilner et al. 2004; Gloag et al. 2012). Thus, nestling parasites may face a “provisions trade-off”, whereby the presence of host nestlings can increase or decrease a parasite’s food intake depending on whether host young cause parents to supply more extra food than they consume and the ability of the parasitic chick to monopolize those extra feedings (Kilner et al. 2004; Gloag et al. 2012). This hypothesis predicts that generalist brood parasites should adjust the removal or destruction of host eggs according to host characteristics, for example, destroying host eggs when parasitizing large hosts but not when parasitizing small hosts. Tuero et al. (2012) found correlational evidence in support of this hypothesis. Also, experimental work showed that pecking behaviour of shiny and screaming cowbird females is flexible as they adjust the number (and likely also the intensity) of pecks according to the number and eggshell strength of eggs present in the nest (Fiorini et al. 2014; Cossa et al. 2017).

18.8 Competing with Other Females for Host Nests and Avoiding Repeat Parasitism

Multiparasitism, whereby two or more females lay eggs in the same host nest, is common however in those brood parasitic systems where females’ territories or home ranges overlap (Moskát and Honza 2002; Spottiswoode 2013; Gloag et al. 2014a; Scardamaglia and Reboreda 2014; Zölei et al. 2015; Bolopo et al. 2017). In such cases, competitive behaviours between females may take place indirectly at host nests themselves. For example, the evolution of thicker eggshells in shiny and screaming cowbirds (Hudson 1874), egg mimicry in honeyguides (Spottiswoode 2013) and egg crypsis in little bronze-cuckoos (Gloag et al. 2014b) have likely been driven by female-female competition in multiply parasitized nests, where second-to-arrive parasites preferentially destroy eggs of previous parasites, in turn selecting for parasite egg traits that evade their competitor’s detection. How female parasites adjust other behaviours associated with parasitism to account for female-female competition remains poorly studied.

In addition to avoiding competition with other females for host nests, parasitic females should avoid laying more than one egg in the same host nest (i.e. repeat parasitism). This serves to prevent removing or destroying their own previously laid eggs and to reduce competition among a female’s own offspring. The latter is particularly important in evictor parasitic species. To avoid repeat parasitism females should remember the location and status of host nests within their home ranges, which implies special cognitive capabilities (see Chap. 11).

Hahn et al. (1999) and Ellison et al. (2006) found that brown-headed and bronzed cowbirds avoided laying more than one egg in a particular host nest. On the contrary, McLaren et al. (2003) found that repeat parasitism by brown-headed cowbirds was frequent, and Rivers et al. (2012) found, in a heavily parasitized host community, that the likelihood that an individual cowbird in a multiparasitized nest shared the nest with a full sibling was 40%. Likewise, studies in shiny cowbirds produced

contrasting results. Gloag et al. (2014a) found that repeat parasitism could have occurred in less than 5% of all recorded events of parasitism, and Scardamaglia et al. (2017) found that shiny cowbird females rarely revisit host nests after parasitism, yet de la Colina et al. (2016) showed that in sites with low host nest density, some shiny cowbird females parasitize the same nest repeatedly. Screaming cowbirds also occasionally show repeat parasitism and revisit a nest repeatedly after laying (Scardamaglia et al. 2017). These results suggest that the incidence of repeat parasitism in non-evictor parasitic species may depend on the density of hosts and that parasitic females may face a trade-off between avoiding laying eggs in nests they have already parasitized and finding new nests.

Concluding Remarks and Future Directions

In this review we summarized information on the behaviour of parasitic females from the moment they start searching for nests until they parasitize them. Most available data comes from two species of cuckoos (common and great spotted) and three species of cowbirds (brown-headed, shiny and screaming). For the remaining parasitic species (most Old World and New World cuckoos, *Vidua* finches, honeyguides, giant and bronzed cowbirds and the black-headed duck), there is almost no information about their behaviour. The study of female parasitic behaviour in these less studied interspecific brood parasites will help us to identify different evolutionary solutions to similar biological problems. For example, how do most brood parasites recognize potential hosts? Is the proposed mechanism of host imprinting a “universal” solution that evolved independently in most species, or are there numerous species-specific solutions? It would be particularly interesting to study how a precocial obligate brood parasite, the black-headed duck, has solved the problem of host recognition.

The development of new technologies (e.g. miniaturized global positioning system loggers) will allow us to study the spatial behaviour of brood parasites with high spatial and temporal resolution. This will help us to better understand how females gather information on nest sites and nest status before laying their eggs and to understand social interactions between females. For example, to what extent do females use the information of conspecifics to find nests? How does competition between females modify parasitic strategies?

In summary, the behaviour of parasitic females from the moment they start searching for host nests until they parasitize them includes a sequence of hierarchical decisions that affects the fitness of the female: Which host species to parasitize? How to find their nests? When to parasitize them? How many eggs to remove or destroy at the time of parasitism? How to avoid competition with other females or competition between their own offspring? Further observational and experimental studies on the behaviour of brood parasitic females may help us to understand how they have solved these unique problems associated with this reproductive habit.

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