Great Spotted Cuckoos Frequently Lay Their Eggs While Their Magpie Host is Incubating

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Abstract

Species that suffer from brood parasitism face a considerable reduction in their fitness which selects for the evolution of host defences. To prevent parasitism, hosts can mob or attack brood parasites when they approach the host nest and block the access to the nest by sitting on the clutch. In turn, as a counter-adaptation, brood parasites evolved secretive behaviours near their host nests. Here, we have studied great spotted cuckoo (Clamator glandarius) egg-laying behaviour and defence by their magpie (Pica pica) hosts inside the nest using continuous video recordings. We have found several surprising results that contradict some general assumptions. The most important is that most (71%) of the parasitic events by cuckoo females are completed while the magpie females are incubating. By staying in the nest, magpies force cuckoo females to lay their egg facing the high risk of being attacked by the incubating magpie (attack occurred in all but one of the events, n = 15). During these attacks, magpies pecked the cuckoo violently, but could never effectively avoid parasitism. These novel observations expand the sequence of adaptations and counter-adaptations in the arms race between brood parasites and their hosts during the pre-laying and laying periods.

Introduction

By laying a parasitic egg in the nest of their host, brood parasites dramatically reduce host fitness, which selects for the evolution of host defences (Davies 2000; Soler & Soler 2000). Egg discrimination is the best studied host defence and has provided textbook examples of coevolutionary interactions (Brooke & Davies 1988; Soler & Möller 1990; Spottiswoode & Stevens 2012). However, in theory, efficient defences and counter-defences can evolve at any phase of the host-breeding cycle, driving the fate of the long-term coevolution between brood parasites and their hosts (Davies 2011; Grim et al. 2011; Soler 2014). In fact, recent studies have emphasized the importance of co-evolved adaptations prior to the deposition of the parasite egg, and these defences are known as the ‘frontline’ of the coevolutionary arms race (reviewed in Feeney et al. 2012).

Once a host species has identified the brood parasite as an enemy (Langmore et al. 2012; Feeney & Langmore 2013), two immediate defences against brood parasite females can evolve. First, hosts might defend their nests by mobbing or attacking brood parasites when they approach the host nest (e.g. Moksnes et al. 1991). This direct nest defence against brood parasites can be considered as a specific adaptation because it has been demonstrated that hosts are able to discriminate between predators and brood parasites (Welbergen & Davies 2008; Feeney et al. 2013) and even between different morphs of the same cuckoo species (Thorogood & Davies 2012; Trnka & Grim 2013). Nest defence against brood parasites also has traditionally been thought to effectively diminish the risk of parasitism (Davies 2000; Welbergen & Davies 2009; Trnka & Grim 2013). In addition, the presence of a brood parasite near the host nest could increase host responsiveness on egg appearance and consequently
improve egg rejection (Davies & Brooke 1988; Moksnes et al. 2000) and even chick rejection (Langmore et al. 2009).

Second, sitting on the nest (Hobson & Sealy 1989; Moksnes et al. 2000; Davies et al. 2003) could also prevent the parasite from laying its egg by blocking the access to the nest (Hobson & Sealy 1989; Canestrari et al. 2009). This defence has also been considered to be a specific adaptation against brood parasites, given that, for instance, yellow warbler females (Setophaga petechia) only perform this behaviour when they detect brown-headed cowbirds (Molothrus ater) or after hearing parasite-specific alarm calls given by other individuals (Gill & Sealy 2004).

Thus, if host detection of brood parasites provokes efficient nest defences, decreasing the likelihood of successful parasitism, selection should favour secretive behaviours in brood parasite females when parasitizing nests to avoid detection by their hosts. Abundant empirical research suggests that this is the case given that the moment of egg-laying by brood parasites usually occurs when hosts are less likely to be at their nests (Davies & Brooke 1988; Moksnes et al. 2000; Gloag et al. 2012) and the act of egg-laying by brood parasites is extremely rapid (Davies & Brooke 1988; Sealy et al. 1995; Moksnes et al. 2000).

Parasitic egg-laying behaviour and host strategies of nest defence have already been intensely studied in the great spotted cuckoo, Clamator glandarius – magpie, Pica pica system. However, up to now, studies were always based on observational data from behaviours outside the nest or on the outcome of parasitism (i.e. eggs) inside the nest. Results of these studies so far suggest that (i) great spotted cuckoo females use host activity at the nest and host nest size (as an indicator of parental ability) to decide which nests to parasitize (Soler et al. 1995; Soler & Pérez-Contreras 2012), (ii) great spotted cuckoos behave secretly in the surroundings of magpie nests (Arias de Reyna 1998; personal observation), (iii) magpies recognize adult great spotted cuckoos as enemies and attack them when detected near their nests (Soler et al. 1999a), (iv) nest defence by magpies is counteracted by the ‘distraction strategy’ of great spotted cuckoos, in which the male attracts the attention of the host away from the nest, providing the great spotted cuckoo female with easy access to the host nest (Álvarez & Arias de Reyna 1974; Soler et al. 1999a), (v) as a response to the distraction strategy, some magpies do not chase the great spotted cuckoo and remain in their nests (Soler et al. 1999a), (vi) the act of egg-laying is extraordinarily rapid (approximately 2–3 s; Arias de Reyna 1998) and (vii) cuckoo eggs have a stronger shell than magpie eggs, and during cuckoo egg-laying, usually some of the magpie eggs are broken (Soler et al. 1997). This is thought to be the result of cuckoo egg-laying from the rim of the nest (Arias de Reyna 1998), cuckoo pothering and pecking host eggs, or a combination of both (Soler et al. 1997).

So far, however, we have no knowledge on what is precisely going on during cuckoo egg-laying inside the nest. Here, we used video recordings that continuously filmed the inside of magpie nests to study cuckoo egg-laying behaviour and magpie defence inside the nest. Our main aim was to test two predictions based on traditional theory presented above (but see Discussion and references therein for relevant exceptions). Our predictions are: (i) great spotted cuckoo females should behave secretly during parasitic events and (ii) nest defence by magpies should be efficient to avoid parasitism mainly given that magpies are larger than cuckoos. Our recordings have provided several surprising results that will improve our understanding of the coevolutionary interactions between brood parasites and their hosts during the pre-laying and laying phases.

**Material and Methods**

This study was carried out during 2010 and 2011 in the Hoya de Guadix (37°25′N, 3°33′W), a high-altitude plateau (approx. 1000 m a.s.l.) with extensive non-cultivated areas, cereal crops (especially barley), almond orchards (Prunus dulcis) and some areas with holm oak trees (Quercus rotundifolia). Brood parasitism rate was 43% (n = 76 nests) in 2010 and 83% (n = 131 nests) in 2011.

Magpie nests were continuously filmed during the magpie egg-laying period using micro-cameras (KPC-S500 or KT&C Co. Ltd.) hidden within the nest dome, camouflaged with material used by magpies to construct the dome of their nests and connected to the video recorder. The recordings were visualized using a USB playback console software. Further details on the filming procedure and visualization of recordings can be found in Soler et al. (2012).

Research was conducted according to national (Real Decreto 1201/2005, de 10 de Octubre) and regional guidelines. All necessary permits (permission provided yearly by the Consejería de Medio Ambiente, Junta de Andalucía, Spain) were obtained for this field study.

The prevalence of cuckoo egg-laying events was analysed with chi-squared tests. To analyse the length of cuckoo egg-laying and of magpie-cuckoo
encounters (seconds), we used a repeated-measures ANOVA (RM-ANOVA), given that both variables fitted a normal distribution after log-transformation (Kolmogorov–Smirnov p > 0.2). Means of raw data are presented for clarity to the reader. All tests are two-tailed and were performed with STATISTICA 7.0 (StatSoft, Inc. 2004, Tulsa, OK, USA). Means ± SE are provided, unless stated otherwise.

Results

The filming equipment was successfully set up in 29 nests, in which we obtained more than 1500 h of recordings. In 11 of these nests, the camera filmed 21 events of cuckoo egg-laying. In 45% of the nests, one egg-laying event was filmed, while the other nests were multi-parasitized with 2.6 ± 0.3 eggs in the same nest [range: 2 (n = 3), 3 (n = 2), 4 (n = 1)].

Great spotted cuckoo females entered the nest more frequently when the magpie female was incubating (71.4%) than when the nest was empty (28.6%). This implies that great spotted cuckoo female behaviour is not secretive at all, which contradicts our first prediction. Cuckoos entering the nest dome elicited magpies to rise from their eggs. Magpies attacked the cuckoo almost always (except for once, i.e. 95.2% of the events). When the nest was empty during parasitism, magpies were most likely in the neighbourhood as they usually stay in their territory, frequently foraging near the nest and often guarding it. The frequency of defence behaviour when magpies were incubating was, however, significantly higher compared with events in which cuckoos entered the nest when the magpie was not incubating [χ²(1) = 6.10, p = 0.013, Fig. 1].

When magpies defended the clutch, they were always harassing and pecking the cuckoo female while she was laying her egg, and the attack continued even after the cuckoo tried to leave the nest. In fact, the total duration of the attack of the magpie was significantly longer than the time the cuckoo was in the nest (RM-ANOVA F₁,15 = 14.74, p = 0.0016, duration of the attack 11.84 ± 2.34 s, length of cuckoo egg-laying inside the nest 4.64 ± 1.15 s) (see Video S1 in Supplementary Material). In spite of the violent attacks by magpies, they never succeeded in preventing the cuckoo female from laying her egg, which contradicts our prediction 2.

In two events (9.5%), two cuckoos were involved. The incubating magpie was elicited by one cuckoo and engaged in an attack. While attacking this first cuckoo, another cuckoo female entered the nest and laid her egg (in one of these cases, the magpie was temporarily caught in the nest dome; see Video S2 in Supplementary Material). We suspect that both cuckoos entering the nest were females because males have been observed facilitating egg-laying by the female via the ‘distraction strategy’, but never entering the nest. Here, it is worth mentioning that during routine monitoring of magpie nests, the female magpie usually leaves the nest when we are climbing the tree. At that moment, sometimes, a female cuckoo could suddenly appear, enter the nest and lay her egg (personal observations from at least 20 breeding seasons during which 100–150 magpie nests were monitored, at least three times per breeding season). In a few of these cases, this occurred even when we almost reached the nest, ready to introduce our hand.

Cuckoo egg-laying events were observed to take place throughout the whole day (range 07:20 am to 16:00 pm, Fig. 2), but did occur most frequently between 10:20 and 12:40 (95% CI, mean 11:29 ± 33 min).

The time the cuckoo was inside the nest (during which she laid her egg) was highly variable (range: 1–41.5 s, median: 2.75 s, 95% CI: 1.83–10.13 s). In 66.7% of the events (n = 14), the cuckoo remained in the nest for less than 4 s. Sometimes the magpie kept hold of the cuckoo inside the nest during the attack and it was not possible to see at which moment the egg was laid (see Video S1 in Supplementary Material), but in one occasion, a cuckoo was not attacked and took 40 s to lay her egg. The length of cuckoo laying did not differ in relation to the presence of the host inside the nest (ANOVA, F₁,19 = 0.053, p = 0.82). Cuckoos never laid their egg from the border of the nest cup, but always completely entered the nest for egg-laying while always pottering (i.e. mix up
and jostle) and sometimes (four events, 19%) pecking the other eggs present in the nest. Cuckoo pecking frequency did not differ in relation to the presence of the magpie in the nest ($\chi^2 (1) = 0.03, p = 0.86$). As a result of cuckoo pottering, pecking and/or magpie attack, some magpie eggs turned out to be pecked, cracked or totally broken. In our sample, this was the case in 47.6% of the events ($n = 21$), and in those cases, the laying of one cuckoo egg caused a mean of 1.3 ± 0.15 eggs to become damaged. Completely broken eggs were always immediately eaten by the magpie ($n = 7$). An example of pottering behaviour can be seen in Video S3 in Supplementary Material.

**Discussion**

We have found that most (71%) of the parasitic events by great spotted cuckoo females are completed while the magpie female is incubating and that magpies were never able to prevent cuckoo females from laying their egg. These surprising results contradict our first and second predictions and so contradict two important generally assumed traditional thoughts: first, that brood parasitic females lay their eggs secretly and second, that mobbing and sitting by hosts are effective strategies to avoid parasitism (see reviews in Davies 2000; Kilner & Langmore 2011; Feeney et al. 2012).

Fig. 2: Frequency of great spotted cuckoo egg-laying throughout the whole day considering periods of 30 min.

However, our results are in agreement with some reports (some of them mentioned in the reviews cited above) showing that sometimes brood parasite females are able to lay their eggs in spite of direct nest defence by hosts (Moksnes et al. 2000; Gloag et al. 2012, 2013), that nest blocking by the host female sitting on the nest sometimes is not always effective (Ellison & Sealy 2007) and also that laying behaviour by brood parasite females is less secretive than traditionally assumed (Moksnes et al. 2000; Gloag et al. 2012). The recent paper by Gloag et al. (2013) deserves a special mention. In it, by filming parasitic behaviour by shiny cowbirds (*Molothrus bonariensis*) at chalk-browed mockingbird (*Mimus saturninus*) nests, the authors have studied the effectiveness of direct nest defence of hosts against the brood parasite. They have shown that cowbirds are attacked by mockingbirds in most of their visits to the nest (82%) and that cowbird females are usually able to lay their eggs while enduring the mockingbird’s attacks. An important difference between this and our study system is that shiny cowbirds almost always enter the nest when it is empty, being attacked by vigilant mockingbirds that follow them into the nest, but great spotted cuckoos, in most cases, enter into magpie nests while the female is incubating.

Parasitic egg-laying while the magpie is incubating is more costly for great spotted cuckoo females than egg-laying when the magpie is absent from the nest, because in the former situation, magpies almost always attacked the cuckoo (see Fig. 1). Thus, if egg-laying is frequently performed in such a difficult situation, this should be because cuckoo females are forced to do so. This implies that many magpies might have evolved the defence behaviour of staying in the nest as a response to the distraction strategy by great spotted cuckoos (Fig. 3). Cuckoos then are forced to adopt the only possible solution: to lay their egg facing the
risk of being attacked by the incubating magpie. These attacks might have the advantage for great spotted cuckoos that some magpie eggs can get crushed or cracked during the fight that takes place inside the nest, while a cuckoo egg was never damaged, which is in agreement with previous experimental results (Soler & Martínez 2000; see below). However, magpie attacks are most likely also costly to the cuckoo because magpies are of a larger size than great spotted cuckoos and aggressive pecking (see videos in Supplementary Material) could inflict injuries of variable severity to cuckoo females. We have not been able to determine these costs to cuckoo females that were attacked by magpies, but, for instance, Trnka & Grim (2013) reported that common cuckoo females can be killed by their great reed warbler (Acrocephalus arundinaceus) host, which is much smaller than the cuckoo.

Magpie attacks against cuckoo females never resulted in effectively avoiding parasitism, but as they are most likely costly for the cuckoo, they should have selected female cuckoos to adopt any strategy to avoid or decrease the costs of being attacked. One of these could be to wait secretly in the neighbourhood of the nest and lay their egg when the magpie is being distracted by another cuckoo (see Video S2 in Supplementary Material) or by a researcher (predator) climbing the tree. Gloag et al. (2013) found that in some cases, shiny cowbird females also lay their eggs taking advantage of a previous cowbird female being engaged in a fight with the mockingbirds. These novel observations expand the list of adaptations and counter-adaptations of brood parasites and their hosts during the pre-laying and laying periods (see Fig. 3). Furthermore, our results on great spotted cuckoos, together with those previously obtained on shiny cowbirds (Gloag et al. 2012, 2013), show that some brood parasite females are able to lay their eggs in spite of direct nest defence by hosts and that they endure attacks by hosts during laying. Curiously, these brood parasites that come into contact with their hosts are also non-evictor species, that is, they do not evict or kill all host chicks upon hatching. We can, however, only speculate about the questions why brood parasitic species in which females endure attacks by hosts during laying are non-evictors and what the coevolutionary implications of this behaviour might be.

Females of most brood parasitic species usually lay their eggs at a concrete time of the day, that is, when the possibility of being detected by their hosts is reduced (see Introduction). For instance, common cuckoos lay during the afternoon and evening (Wyllie 1981; Honza et al. 2002), other parasitic cuculidae species lay in the morning (Brooker et al. 1988;
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Davies 2000) and several species of cowbirds (Molothrus spp.) lay before sunrise (Peer & Sealy 1999). However, if cuckoos have predictable time slots for egg-laying (e.g., always during the morning), this could allow hosts to develop an effective defence strategy by staying on the nest during concrete times of the day. However, great spotted cuckoo females lay throughout the whole day, which probably prevents magpies to improve their nest defence strategy, because it is too costly to stay on the nest during the whole day (i.e., trade-off with foraging, because cuckoos parasitize magpie nests when incubation has not started yet, at the beginning of the magpie egg-laying period).

The duration of egg-laying is highly variable among avian species, but in most species, it usually takes more than 20 min to lay an egg (Sealy et al. 1995). However, in brood parasites, egg-laying is a much quicker process that usually takes no more than a few seconds. For instance, egg-laying lasts on average 41 s in brown-headed cowbirds (Molothrus ater; Sealy et al. 1995), and between 5 and 10 s in bronzed cowbirds (Molothrus aeneus; Peer & Sealy 1999), and in common cuckoos, time spent laying has oscillated between on average 5 s (Andou et al. 2005), 26 s (Honza et al. 2002) and 41 s (Moksnes et al. 2000). Our recordings have shown that the speed of egg-laying by great spotted cuckoo females is even higher than those reported for other brood parasite species (<4 s in 66.6% of the egg-laying bouts). This extremely rapid laying by great spotted cuckoo females cannot be explained by the usual argument that it would decrease the probability of being detected by the hosts given that magpies often are incubating when the cuckoo enters the nest. Perhaps rapid egg-laying evolved first to minimize host detection, but later, after the strategy ‘stay inside the nest instead of mobbing cuckoos’ appeared (see Fig. 3), it is possible that such rapid laying was selected mainly to decrease the duration of the attack by incubating magpies.

Our results support previously reported observations on duration of laying (Arias de Reyna 1998) and on the frequency of broken eggs in parasitized magpie nests (Soler et al. 1997). However, our recordings contradict another previous statement, specifically that great spotted cuckoo females lay from the edge of the nest cup (Arias de Reyna et al. 1982). This cuckoo egg-laying tactic was frequently assumed to be the cause of egg damage in host nests in later studies (Soler et al. 1997, 1999b; Soler & Martínez 2000). Cuckoo parasitism resulted in damaged host eggs in almost 50% of egg-laying events. This recurrent observation of damaged eggs (either pecked, crushed or cracked) in parasitized magpie nests is in accordance with previously reported frequencies (62.2%; Soler et al. 1997). Crushed or cracked eggs represented 55.2% (Soler et al. 1997) of the damaged eggs, and these were considered to be the consequence of the parasite egg crashing into the host eggs (Soler 1990; Soler et al. 1997). However, video recordings of the present study revealed that cuckoo females never lay from the rim of the nest but always completely entered the nest. In addition, it was previously assumed that the parasite pottered the eggs just once when leaving the nest after egg-laying (Soler et al. 1997). Our video recordings also show that pottering the eggs is much more frequent than previously suspected as it was observed in all egg-laying events. Thus, we can conclude that crushed eggs are the consequence of host eggs being jostled against one another and against the parasitic egg by the cuckoo pottering the eggs and/or by the magpie attacking the cuckoo inside the nest. This result could also explain the fact that in an experimental study, when laying behaviour by the great spotted cuckoo female from the rim of the nest was simulated, the number of damaged magpie eggs was significantly lower than in natural parasitized nests (Soler & Martínez 2000).

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**Supporting Information**

Additional supporting information may be found in the online version of this article:

**Video S1**: A magpie female, which is incubating, attack an approaching great spotted cuckoo female. The magpie harasses and pecks the cuckoo while she is laying her egg. The attack continues after the cuckoo leave the nest.

**Video S2**: The incubating magpie is elicited by one cuckoo female and engaged in an attack. While attacking this first cuckoo, the magpie remained caught in the nest dome, and a second cuckoo female entered the nest and lays her egg.

**Video S3**: A great spotted cuckoo female completely enter the nest and lay her egg while pottering and pecking the other eggs present in the nest. This is the only case in which an incubating female did not attack the cuckoo.