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ORIGINAL ARTICLE

Intraspecific avian brood parasites avoid host nests infested by ectoparasites

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Abstract Intraspecific brood parasitism is widespread among birds and provides clues for elucidating the evolutionary origin of interspecific brood parasitism. Studies suggest that brood parasitism does not occur at random, but that parasitic females select nests with advantages such as higher physical stability, reduced predation risk, or lower ectoparasite infestations. However, this evidence is sparse and mainly correlative. By experimentally increasing the abundance of *Carnus hemapterus* (a common, generalist and widespread ectoparasitic nest fly of a multitude of bird species) in half of the nests, we show that parasitic Spotless Starlings (*Sturnus unicolor*) avoid conspecific nests infested by ectoparasites. Since *Carnus* ectoparasites impinge costs on their avian nestling hosts, this avoidance response would be adaptive for parasitic Starlings. Further, we suggest a mechanism by which parasitic females may assess the level of ectoparasite infestation to select host nests accordingly: by using parasite cues such as faeces and blood remains. Additionally, these cues may be used by parasitic females for synchronization with the reproductive cycle of host females because ectoparasite cues also indicate that incubation has already commenced. Whatever the functionality, the mechanism suggested here may be employed by intra- and interspecific brood parasites, so it might represent a widespread strategy in nature.

Keywords Conspecific brood parasitism · Host-selection mechanisms · Ectoparasitism risk · Host-parasite synchronization · Eggshell spottiness · Intraspecific nest parasitism

Zusammenfassung

Intraspezifisch brutparasitäre Vögel meiden Wirtsnester mit Ektoparasitenbefall

Innerartlicher Brutparasitismus ist in der Vogelwelt weit verbreitet und liefert Hinweise zur Klärung des evolutionären Ursprungs zwischenartlichen Brutparasitismus. Untersuchungen legen nahe, dass sich Brutparasitismus nicht zufällig ereignet, sondern dass parasitische Weibchen Nester mit Vorzügen wie zum Beispiel höherer Stabilität, verringertem Prädationsrisiko oder niedrigerem Ektoparasitenbefall auswählen. Allerdings sind solche Belege spärlich und überwiegend korrelativ. Indem wir die Anzahl von *Carnus hemapterus* (einer häufigen, generalistischen und weit verbreiteten Gefiederfliegenart, die bei einer Vielzahl von Vogelarten vorkommt) in der Hälfte der Nester experimentell erhöhten, konnten wir zeigen, dass parasitische Einfarbstare (*Sturnus unicolor*) arteigene Nester mit Ektoparasitenbefall meiden. Da Ektoparasiten der

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Gattung *Carnus* ihren Wirtsnestlingen Kosten verursachen, wäre diese Vermeidungsreaktion für parasitische Stare adaptiv. Weiterhin postulieren wir einen Mechanismus, mittels dessen parasitische Weibchen den Grad des Ektoparasitenbefalls einschätzen können, um die Wirtsnester entsprechend auszuwählen: indem sie Parasitenspuren wie Kot oder Blutreste hinzuziehen. Zusätzlich können diese Anhaltspunkte den parasitischen Weibchen zur Synchronisierung mit dem Fortpflanzungszyklus der Wirtsweibchen dienen, da Ektoparasitenspuren auch ein Zeichen dafür sind, dass die Brut bereits begonnen hat. Ganz gleich, welche Funktion er hat, der hier vorgeschlagene Mechanismus könnte von inner- und zwischenartlichen Brutparasiten genutzt werden und somit eine in der Natur weit verbreitete Strategie darstellen.

Introduction

Intraspecific brood parasitism is widespread among birds (Yom-Tov 2001). It has received much less attention than interspecific parasitism (Lyon and Eadie 2008), although it may provide clues for elucidating the evolutionary origin of the latter (Payne 1977; Davies 2000). Identifying possible host cues used by brood parasites for host selection that maximize reproductive success is central to understanding the evolution of intra- (Lyon and Eadie 2008) and interspecific brood parasitism (Parejo and Avilés 2007; Soler et al. 2014).

In the case of intraspecific brood parasitism, some stimulating evidence indicates that birds do not parasitize nests randomly but use cues associated with breeding success (Pöysä et al. 2014). At least six such cues have been suggested, though some may just be breeding outcomes of potential host nest sites, and the putative cues have yet to be identified. First, parasitic females select host nests at the appropriate time of the host reproductive cycle [e.g. during egg laying (Brown and Brown 1989; Schielzeth and Bolund 2010)]. Second, Cliff Swallows (*Petrochelidon pyrrhonota*) prefer to parasitize old rather than new nests, which may be a guarantee of their structural stability (Brown and Brown 1991). Third, the probability of parasitism in nests increases with the number of previous nesting attempts and occupation rate in Common Goldeneyes (*Bucephala clangula*) (Paasivaara et al. 2010). Fourth, Common Goldeneyes select host nests with reduced predation risk (Pöysä 2006; Pöysä et al. 2010). Fifth, Wood Ducks *Aix sponsa* preferentially parasitize nests with smaller clutch sizes, which may increase hatching success (Odell and Eadie 2010). Finally, intraspecific brood parasitism in Cliff Swallows was mainly detected in nests that were most successful at producing fledglings (Brown and Brown 1991). Interestingly, this nest-selection bias of parasitic Cliff Swallows was associated with a low probability of infestation by bloodsucking ectoparasites (fleas and bugs), a major source of nestling mortality in this species (Brown and Brown 1991). Nevertheless, mechanisms for the assessment of ectoparasite loads of conspecific host nests were unknown (Brown and Brown 1991; Pöysä et al. 2014). In addition, most of this evidence is correlational and experimental manipulation of host nest features is necessary to understand the detected non-random selection of conspecific host nests (Pöysä et al. 2014).

We took advantage of a study closely monitoring egg laying and incubation in Spotless Starlings (*Sturnus unicolor*) to detect events of intraspecific parasitism once incubation has commenced. We aimed to test whether ectoparasite infestation of a nest predicts its probability of being parasitized by conspecific females, for which purpose we experimentally increased abundance of the ectoparasitic nest fly *Carnus hemapterus* in half of the nests. The abundance of this ectoparasite is revealed by conspicuous spots on eggs, which are the product of parasite faeces and blood remains (López-Rull et al. 2007; Avilés et al. 2009; Tomás et al. 2016). We expected that parasitic females would avoid experimental nests with an increased load of *C. hemapterus* flies. Additionally, ectoparasite cues may be used also by parasitic females for a better synchronization with the reproductive cycle of host females. Parasitic females would avoid nests with ectoparasite cues because these would indicate that incubation has already commenced.

Methods

The Spotless Starling is a hole-nesting passerine that mostly breeds in colonies, where intraspecific parasitism is a common phenomenon occurring in around 25% of nests (Calvo et al. 2000). Overall, 17% of nests are parasitized during the host's egg-laying stage and 9% during incubation, with the latter representing 32–53% of parasitism depending on year (Calvo et al. 2000). Our study was carried out in 2011 in a Starling colony breeding in nest-boxes in Guadix, Spain (37°18′N, 3°11′W). Typical clutch sizes are four to five eggs in the population, laid one per day. The incubation lasts 12–13 days and usually starts before clutch completion, resulting in asynchronous hatching (Soler et al. 2008). Soon after the onset of incubation, immaculate blue eggs sometimes become brownish spotted as a result of the viscous faeces (and blood remains) that adults of the ectoparasite *C. hemapterus* (hereafter *Carnus* sp.) deposit, which attach to substrates,

Fig. 1 Representative Spotless Starling clutches uninfested (*left*) and infested (*right*) by *Carnus hemapterus* flies. Note that no *Carnus* sp. fly is seen on the photographs, giving support to our suggestion that spottiness is a likely cue used by parasitic females to infer ectoparasite infestation level

including the birds' skin, feathers, and eggs (López-Rull et al. 2007; Avilés et al. 2009; Tomás et al. 2016; Fig. 1). *Carnus* sp. is a 2-mm blood-sucking fly found in nests of an extremely wide diversity of birds. It has been found parasitizing 64 host species from 24 avian families, from raptors to passerines (Grimaldi 1997; Brake 2011; Calero-Torralbo 2011). It has been recorded throughout most of North America and Europe, with scarcer records for Asia and North Africa (Grimaldi 1997; Brake 2011). After emergence from overwintering pupae inside nests, winged adults may disperse, and lose their wings once a suitable nest is found (Mercier 1928; Grimaldi 1997; Calero-Torralbo 2011). *Carnus* sp. feeds exclusively on birds while in the nest, mainly on nestlings, but also on incubating birds (López-Rull et al. 2007; Avilés et al. 2009; Tomás et al. 2016). *Carnus* sp. flies are hardly visible in nests as they dwell within the nest matrix. Infestation at the incubation stage can therefore be cued almost exclusively from egg spottiness and is positively correlated with infestation at the nestling stage (López-Rull et al. 2007).

Nest boxes were inspected every 4 days to detect the initiation of egg laying, and eggs were individually marked. Five days after the first egg had been laid, we measured length and breadth of all eggs with a digital calliper (±0.01 mm) and estimated eggshell spottiness (see below). Eggshell surface area was estimated according to Narushin (2005). Then, nests were alternately assigned to experimental or control treatments (33 nests each). In experimental nests, ten wingless *Carnus* sp. flies collected from nearby nests were added [which is within the natural infestation level at the beginning of incubation (López-Rull et al. 2007; Avilés et al. 2009)], while no flies were added to control nests. Ectoparasite cues were already visible on eggs within 24 h after experimental infestation (G. Tomás et al., personal observation).

Nests were visited 4 and 7 days after manipulation to estimate eggshell spottiness and to ascertain whether parasitic eggs were present. Estimations of eggshell spottiness were performed three times during the incubation period: (1) when incubation had already commenced (day 5 after the first egg had been laid, immediately before treatment assignment); (2) in the middle (day 9); and (3) late (day 12) incubation period. Egg spots, as an indication of ectoparasite abundance, were counted on every egg of each nest at the three visits. In some nests where egg spots were so abundant that counting them became unreliable, we counted spots within 1 cm^2 at a random position along the shortest axis of the egg (López-Rull et al. 2007), which was extrapolated to eggshell surface. Both estimates were correlated on a subsample of eggs ($r^2 = 0.25$, $P < 0.0001$, $n = 53$). On each visit, a randomly selected egg was cleaned of spots with a sterile swab to sample bacterial loads for other purposes (Tomás et al. 2016). The eggs cleaned on previous visits were not included in the data when calculating within-nest mean eggshell spottiness per egg for analyses.

Although intraspecific parasitism may occur earlier, we specifically focused on events occurring after the experimental treatment. Since eggs were individually marked, parasitic eggs were recognized when new eggs appeared in nests after clutch completion [no eggs laid in 2 days and incubation started (Yom-Tov 1980; McRae 1997)]. Events of intraspecific parasitism were always visually confirmed by differential colour and morphology between parasitic and host eggs (Yom-Tov 1980; Evans 1988; McRae 1997). Laying dates of the parasitic eggs used in this study were spread over a period of 17 days and distance between host nests ranged from 50 to 200 m. Parasitism in colonial birds usually occurs among close neighbours (Møller 1987; Brown and Brown 1989), so we are confident that parasitic eggs were laid by different females.

To explore the effectiveness of the experiment in increasing ectoparasite abundance (and ectoparasite cues), a repeated-measures ANOVA (rmANOVA) was carried out with values of eggshell spottiness (log10 transformed) at early, middle and late incubation as a dependent repeated-measures variable, with treatment as factor. The probability of nests being parasitized was compared between treatments with a *G*-test with Williams' correction, indicated for contingency tables with empty cells (Sokal and Rohlf 1995). A value of 0.1 was added to all cells to eliminate zeros (e.g. Fallon and Ricklefs 2008). Analyses were performed with Statistica 8.0 (StatSoft 2007).

Results

Nests under different treatments did not differ in laying date ($F_{1,64} = 0.40$, $P = 0.53$), clutch size ($F_{1,64} = 0.10$, $P = 0.76$), or eggshell spottiness before the experiment ($F_{1,64} = 0.10$, $P = 0.76$). Later on, as expected, eggshell spottiness was higher in *Carnus* sp.-infested than in control nests (rmANOVA, $F_{1,63} = 279.32$, $P < 0.0001$). Eggshell spottiness increased during incubation ($F_{2,126} = 268.03$, $P < 0.0001$), with this increase being pronounced in *Carnus* sp.-infested (post hoc LSD tests, all $P < 0.0001$) but not in control nests (all $P > 0.05$) (time × treatment interaction, $F_{2,126} = 196.77$, $P < 0.0001$) (Fig. 2). Ectoparasitism, and therefore egg spottiness, varied greatly among study areas and years (unpublished data), and the non-significant detected increase in eggshell spottiness of control nests indicates a relatively low incidence of ectoparasitism during the study year.

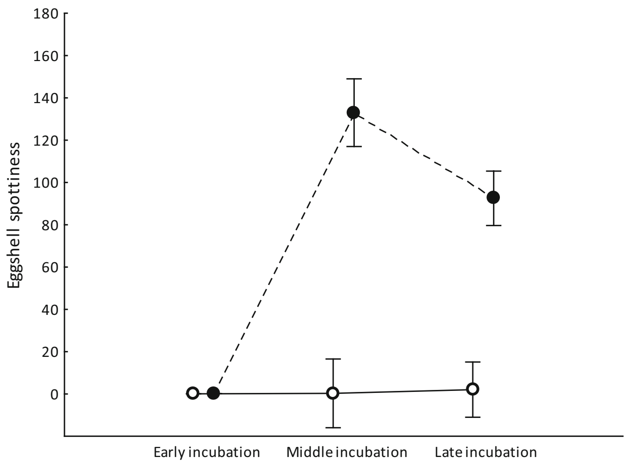

Fig. 2 Effect of experimental addition of *Carnus hemapterus* flies on spottiness (mean number of spots per egg) of Spotless Starling eggs during the incubation period. Mean ± SE values at early (before treatment), middle, and late incubation, for *Carnus* sp.-infested ($n = 33$; *filled circles*) and control nests ($n = 33$; *open circles*) are shown

During incubation, none of the 33 experimental *Carnus* sp.-infested nests were parasitized by Starlings, while four out of 33 control nests (12.1%) received a parasite egg. Thus, the probability that nests were parasitized was lower in experimental *Carnus* sp.-infested nests (*G* adjusted = 4.59, *df* = 1, $P = 0.0322$).

Discussion

A quarter of a century ago, Brown and Brown (1991) first suggested that conspecific parasite birds may actively select host nests with lower ectoparasite loads and higher overall success. Their study was, however, correlative, and the mechanism(s) employed by birds to assess parasitic loads, if any, were unknown. We present one of the first experimental evidence for the non-random selection of conspecific host nests by brood parasitic females and the first one regarding the risk of ectoparasitism. By manipulating the abundance of a common, generalist and widespread ectoparasite of a multitude of bird species, we have shown that parasitic birds avoid conspecific nests which have been experimentally infested. Because *Carnus* sp. ectoparasites impinge costs on their avian hosts (Avilés et al. 2009), this avoidance response would be adaptive for parasitic Starlings. Furthermore, we suggest one mechanism by which parasitic females may assess the level of ectoparasite infestation to perform an active selection of host nests: by using parasite cues such as faeces and blood remains. Ectoparasite cues may also be used by parasitic females for a better synchronization with the reproductive cycle of host females. The most evident cue of *Carnus* sp.

parasitism available to an external observer is egg spottiness (see Fig. 1; Online Resource 1), as *Carnus* sp. parasites remain hidden within the nest materials. In fact, researchers have long been intrigued by egg spottiness in many bird species, ignoring which parasite, if any, may be the causative agent (Jackson 1970; Feare and Constantine 1980; Hornsby et al. 2013). Utilization of these cues may be widespread in brood parasitism systems during the incubation stage, as other nest-dwelling ectoparasites also develop within the nest matrix in close contact with eggs, thereby producing similar cues [e.g. fleas (McNeil and Clark 1987); bugs (Krinsky 2002); or mites (G. Tomás, personal observation)]. An experimental manipulation of egg spottiness in the absence of parasites would be necessary to demonstrate that brood parasites cue mostly, if not solely, on egg spottiness rather than something else related to the ectoparasite.

We consider three scenarios in which this non-random choice of host nests would be adaptive for conspecific and interspecific brood parasites. First, by selecting nests with lower ectoparasite infestation, parasitic birds would increase the survival prospects of their offspring (Brown and Brown 1991), as nest ectoparasites are deleterious for nestling birds (Møller et al. 2009). Furthermore, nests with a high level of ectoparasitism may indicate females and/or nest sites of overall inferior quality, which influence the quality of parental care received by developing offspring (Avilés et al. 2009).

Second, by selecting nests with no or few spots on eggs, females may better synchronize parasitism with host egg laying or with the beginning of incubation, because egg spottiness is low at the beginning of incubation and increases as incubation progresses (this study; López-Rull et al. 2007). The success of parasitic eggs is higher when they are laid during the egg-laying period of the host or at early incubation, but it declines gradually with advancing incubation because of an increased mismatch with the host hatching time (Calvo et al. 2000). It is likely that parasitic females do make use of egg spottiness not only to avoid nests infested by ectoparasites, but also to avoid nests where incubation is much advanced. It should be noted that dependence on egg spottiness to infer reproductive timing of hosts would not be effective in years or populations with a low level of ectoparasite infestation.

Third, parasitic females may preferentially lay eggs in nests with no or less egg spottiness to make foreign egg recognition by host birds more difficult because newly laid parasitic eggs would appear conspicuous in nests with more egg spottiness. However, several studies with related Starling species have shown that Starlings do not eject parasitic eggs once they have begun egg laying (Stouffer et al. 1987; Pinxten et al. 1991; Yamaguchi 1997). In accordance with this, we found that Starlings never evicted eggs cleaned of spots (see “Methods”), despite having the appearance of newly laid eggs. In addition, we know from another experiment that Spotless Starlings do not eject red-painted model eggs when placed in nests during incubation (Soler et al., unpublished data). Therefore, this third possibility is not likely to explain our results.

We can consider several shortcomings in the interpretation of our results. It could be argued that we only detect parasitic eggs in control nests because any parasite egg laid in an experimental nest is quickly recognized and evicted by host females. However, as stated above, Starlings do not evict parasitic eggs during egg laying and incubation. On the other hand, it could be questioned whether the mechanism employed by parasitic females to assess ectoparasite load is egg spottiness or any other cue, such as direct observation of ectoparasites or differential behaviour of females from parasitized nests. We are confident that egg spottiness is the most patent and plausible cue because, as stated above, *Carnus* sp. flies are hardly observed in nests and the only apparent cue is egg spottiness (see Fig. 1; Online Resource). In addition, because *Carnus* sp. flies do not crawl onto birds when out of the nest (Grimaldi 1997), it is unlikely that female birds from parasitized nests behave differently. Additionally, it could be argued that the manipulation of ectoparasites may have affected the overall health of incubating females and consequently their nest defence capabilities against conspecific parasites. Nevertheless, if females from experimental nests were less efficient in defending their nests against brood parasites, we should have found that *Carnus* sp.-infested nests were more parasitized than control nests, which is the opposite of what we did find.

It should be noted that the rate of intraspecific parasitism in our Starling population is likely larger than reported here, as we did not record parasitic eggs laid before or during the laying period of the host because this was beyond the scope of the present study. Our specific purpose was to record intraspecific parasitism in relation to experimental ectoparasite infestation and, in order to resemble natural ectoparasitism timing, this manipulation was carried out at the beginning of incubation and not before. Therefore, we exclusively focused on intraspecific parasitism occurring during the incubation period. Parasitism during the incubation stage of the host is a common phenomenon for this (see “Methods”) and many other species (Pöysä et al. 2014). It should be noted that the mechanism for host selection that we suggest here is applicable to parasitic females parasitizing nests during the host incubation stage, but there might be other cues that parasitic birds use for nest selection during the host egg-laying stage, when ectoparasite cues are not present. Nevertheless, egg laying and incubation stages overlap for many avian species, which usually start incubation before clutch completion. This provides a time frame when the suggested mechanism for host selection may be effective. Although incurring costs, parasitism during incubation may be advantageous in giving the parasite more time for the assessment and appropriate choice of better hosts (Brown and Brown 1991). The appropriate timing of parasitism to match the host reproductive cycle may therefore be, to some extent, traded off against waiting to gather more cues to select better host nests.

In our study, none of the parasitic eggs produced fledglings. However, it is likely that the success of parasitic eggs laid during incubation shows strong geographical and seasonal variability. In another Spotless Starling population, 9% of the eggs laid during incubation produced fledglings (Calvo et al. 2000). Similarly, in the closely related European Starling, 22% of parasitic eggs laid after the host's laying stage succeeded in hatching and, of these, 40% produced fledglings (Evans 1988).

To conclude, we have experimentally shown that conspecific brood parasites avoid host nests infested by ectoparasites. We further suggest that parasitic females may use ectoparasite cues such as faeces and blood remains to assess the level of ectoparasitism and/or to time egg laying with the laying period of the host. Both instances would be adaptive for parasitic females by increasing survival prospects for their offspring. This suggested mechanism may be commonly employed not only by conspecific but also by interspecific brood parasites, so it might represent a widespread strategy in nature and merits further research.

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Compliance with ethical standards

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Ethics statement All procedures were conducted under licence from the Environmental Department of the Regional Government of Andalusía, Spain (reference SGYB/FOA/AFR). All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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