Egg-recognition abilities in non-incubating males

Ruiz-Raya, Francisco; Soler, Manuel; Roncalli, Gianluca; Ibanez-Alamo, Juan Diego

ORIGINAL ARTICLE

CrossMark

Egg-recognition abilities in non-incubating males: implications for the evolution of anti-parasitic host defenses

Francisco Ruiz-Raya[1] · Manuel Soler[1] · Gianluca Roncalli[1] · Juan Diego Ibáñez-Álamo[2]

Abstract

In the field of brood parasitism, it has been traditionally assumed that only the incubating sex rejects parasitic eggs, but this assumption has been rarely explored despite its important implications for the evolutionary relationship between brood parasites and hosts. Here, we used information on previous egg-rejection experiments to explore the recognition abilities of both males and females of Eurasian blackbirds *Turdus merula* towards experimental eggs with a variable degree of mimicry. We found that both sexes recognized non-mimetic eggs, supporting the idea that visits to the nest can favor the evolution of rejection abilities. In contrast, only females recognized mimetic eggs, indicating that although recognition abilities can evolve in both sexes, they are subsequently refined in females probably due to their more frequent interaction with parasitic eggs. Clutch size affected nest attendance since females, but not males, spent more time at the nest and visited it more frequently in larger clutches. Finally, our recordings showed that blackbird males are able not only to recognize, but also to eject parasitic eggs. Our results provide new insights into the main anti-parasitic defense in birds, egg rejection, and highlight the need of considering the role of the non-incubating sex in egg-rejection studies.

Significance statement

Given the high costs associated to avian brood parasitism, both sexes are expected to evolve anti-parasitic defenses. However, in those species in which only females incubate, females have traditionally been assumed to be the responsible for egg rejection. Here, using the Eurasian blackbird (*Turdus merula*), we investigated the existence of egg-rejection abilities in non-incubating males and compared them to those exhibited by females. We found that males can recognize non-mimetic eggs, although their recognition abilities were less fine-tuned compared to females, who also recognized mimetic eggs. Even though females were the responsible for most documented egg-ejection events, recordings confirmed that males could also be involved in egg ejection, which could have important implication for the evolution of anti-parasitic defenses in host populations.

Keywords Avian brood parasitism · Egg recognition · Egg ejection · Nest attendance

✉ Francisco Ruiz-Raya
   fraruiz@correo.ugr.es

[1] Departamento de Zoología, Facultad de Ciencias, Universidad de Granada, E-18071 Granada, Spain

[2] Groningen Institute for Evolutionary Life Sciences, University of Groningen, 9700 CC Groningen, The Netherlands

Introduction

Birds exploited by obligate brood parasites usually suffer significant fitness costs because parasitic chicks frequently kill or evict all host's offspring or they are better competing for food (Rothstein 1990; Davies 2000). In response, many host species have evolved defenses at all stages of the breeding cycle to reduce or avoid such costs, including active nest defense (Feeney 2017), rejection of parasitic eggs (Rothstein 1982; Davies and Brooke 1989; Soler 1990; Moksnes et al. 1991) and chicks (Grim 2017), or parent reluctance to feed parasitic fledglings (De Mársico et al. 2012; Soler et al. 2014). Among these lines of defense, egg rejection is the most effective and widespread strategy to minimize the fitness costs associated to

rearing a parasitic chick (Davies 2000). Given the high selective pressure imposed by brood parasitism, both parents would be expected to invest in egg rejection. However, despite the significant advances in the study of the co-evolutionary relationship between brood parasites and their hosts over the last three decades, the role played by each sex in egg rejection remains poorly studied.

Traditionally, females are assumed to be the main responsible for anti-parasitic defenses towards parasitic eggs as they carry out egg incubation in most bird species (e.g., Davies and Brooke 1988; Lotem et al. 1992). This assumption has been confirmed by experimental studies showing that in those species in which only females incubate, females were responsible for egg rejection (Rohwer et al. 1989; Soler et al. 2002; Požgayová et al. 2009). Instead, in host species where both parents incubate, both males and females have been found to be able to reject parasitic eggs (Soler et al. 2002; Honza et al. 2007). There is evidence, however, of egg recognition and rejection by males even though they are not involved in incubation, as is the case of northern orioles *Icterus galbula*, a host species of the brown-headed cowbird *Molothrus ater* (Sealy and Neudorf 1995). According to the authors, rejection behavior could also evolve in males even when they play no role in incubation, but frequently visit the nest; however, this prediction has not been confirmed in any other host species (Požgayová et al. 2009).

The question of which sex is responsible for the host response against parasitic eggs has important implications for the evolution of anti-parasitic defenses in host populations. If both mates rather than only females can respond to parasites, defensive traits are expected to spread faster within the population (Rothstein 1975a; Sealy and Neudorf 1995). Therefore, the study of sex roles in the rejection behavior could be crucial to understand the long-term outcome of the co-evolution between brood parasites and their hosts. In this study, we explore the role of non-incubating males in the host response against parasitic eggs. To do so, we use the Eurasian blackbird *Turdus merula* (blackbird hereafter) as model species, a potential but rarely exploited host species of the common cuckoo *Cuculus canorus* whose egg-rejection behavior is well known. Blackbird females are able to recognize and eject foreign eggs at high rates (Grim et al. 2011; Samas et al. 2011; Ruiz-Raya et al. 2015, 2016; Soler et al. 2017). Regarding the sex roles in the blackbirds' response towards parasitic eggs, Soler et al. (2002) found that all ejection events ($n = 5$) were performed by females whereas no male approached the nests during the filming period ($n = 9$). However, the sample size of their study was very small, and most importantly, the existence of different stages in the egg-rejection process was not considered. Egg rejection is a complex response involving three different stages (judgment, decision, and action), so recognition abilities should not be inferred from ejection rates alone given that it could exist acceptance decisions (Soler et al. 2012; Ruiz-Raya and Soler 2017, 2018). Recent studies have experimentally

demonstrated the existence of acceptance decisions in blackbird females (Ruiz-Raya et al. 2015; Soler et al. 2017), which highlight the importance of assessing recognition and ejection abilities of non-incubating males separately. Here, using a dataset from egg-recognition experiments in which the behavior of both parents was video-monitored, we assessed the recognition abilities of both blackbird males and females towards several types of experimental eggs showing a variable degree of mimicry. We predict that as females are the responsible for egg incubation in blackbirds, blackbird males will not show recognition abilities and therefore will not participate in the host's response towards parasitic eggs (Soler et al. 2002; Honza et al. 2007). Alternatively, it could be predicted that non-incubating blackbird males could show recognition abilities if they frequently visit the nest during egg incubation (Sealy and Neudorf 1995).

Methods

General field procedure

We combined both unpublished and published data from previous experiments on the egg-rejection abilities of the common blackbird carried out in a population located in the Valley of Lecrín, Southern Spain (Ruiz-Raya et al. 2015, 2016; Soler et al. 2017). As a general procedure, natural blackbird nests were artificially parasitized with experimental eggs during the egg laying (minimum of two eggs laid) or incubation stage (never after the sixth day of incubation). Previous studies have found that the day of incubation does not affect the response of blackbirds towards experimental eggs (e.g., Davies and Brooke 1989; Polačiková and Grim 2010; Grim et al. 2011; Ruiz-Raya and Soler 2018). Blackbird nests used in this study contained two or three eggs. Our dataset includes information on the parents' response to four different types of experimental eggs showing a decreasing degree of mimicry: (1) *natural blackbird eggs*, real blackbird eggs collected from deserted clutches and used to simulate conspecific brood parasitism; (2) *mimetic experimental eggs*, real blackbird eggs that were painted mimetic (to obtain experimental eggs less mimetic than conspecific eggs); (3) *cuckoo-sized non-mimetic eggs*, real house sparrow *Passer domesticus* eggs collected from deserted nests (for additional information, see Ruiz-Raya et al. 2016), whose size is similar to the cuckoo eggs of southern Spain (Martín-Vivaldi et al. 2002); (4) *non-mimetic experimental eggs*, real blackbird eggs that were painted red. We used real blackbird eggs painted red based on previous egg-rejection studies supporting their use as non-mimetic eggs (e.g., Soler et al. 1999; Avilés et al. 2004; Martín-Vivaldi et al. 2012). Furthermore, an additional group of non-parasitized blackbird nests was used as *control*. Some types of experimental eggs, specifically mimetic and red-type eggs,

included eggs that differed in size (small, medium, and large eggs; for detailed information, see Soler et al. 2017). However, we did not consider the effect of egg size in egg recognition since it has been previously proven that egg size does not affect egg recognition in blackbirds, but exerts its effect on egg rejection by hindering the ejection itself once the parasitic egg is recognized (Soler et al. 2017). All nests were checked every 24 h to determine whether the model egg was ejected. We consider the experimental egg was accepted if it remained in an active nest for 5 days. Just after the experimental parasitism, a video camera (Panasonic HDC-SD40) was placed near the nest (1.5–2.5 m) to film the blackbird response towards the experimental egg for the following 1.5–2 h. We followed a standardized procedure previously used to study the incubation behavior of this species (Ibáñez-Álamo and Soler 2012). When possible, we filmed the behavior of both males and females. The clear sexual dimorphism showed by this species was used to differentiate males and females: blackbird males exhibit black plumage and a distinctive yellow eye ring, while females are brownish occasionally exhibiting a lighter mottling on the throat and chest. From recordings, we extracted information on (i) nest attendance and (ii) egg recognition (see below for a more detailed description of variables) from those cases where information of both male and female was available (63 nests). Data on the females' response to experimental eggs were previously published (see references above). However, information regarding nest attendance of adults and the egg-recognition abilities of blackbird males remain unpublished. It was not possible to record data blind because our study involved focal animals in the field.

Variables and statistical analysis

Sex differences in nest attendance were analyzed using two different variables: (i) number of visits to the nest per hour and (ii) time spent by blackbirds at the nest per hour. We used the *lme4* R package (Bates et al. 2015) to perform generalized linear mixed models (GLMM) with gamma error and inverse-link function including nest identity as a random factor (to control for the non-independence of parents belonging to the same nest) and the following fixed factors: type of parasitic egg, sex, their interaction, clutch size (two or three blackbird eggs), and its interaction with sex. Egg-recognition abilities of parents were assessed according to egg-touching behavior (i.e., number of times that individuals touched the eggs with its bill during the first visit) (Ruiz-Raya et al. 2015, 2016; Soler et al. 2017). Egg-pecking or egg-touching behavior is considered reliable proxies for egg recognition (Soler et al. 2002, 2012; Underwood and Sealy 2006; Antonov et al. 2008, 2009), even when acceptance decisions occurs (Ruiz-Raya et al. 2015; Soler et al. 2017). The relationship between egg touches and egg recognition is based on two

main pieces of evidences: first, egg touches occur more frequently in experimentally parasitized nests, and most importantly, egg touches are more frequent in clutches parasitized with non-mimetic eggs than those containing mimetic eggs (Soler et al. 2017). Egg-recognition abilities of males and females were analyzed separately because we mainly intended to assess the egg-touching behavior of each sex regarding the different types of experimental eggs, as well as control nests. Thus, we did not include sex in the egg-recognition models since it makes them more complex and provides little information about recognition abilities of each sex. We performed negative binomial generalized linear models (GLM) including the type of parasitic egg and clutch size as predictors. All analyses and graphics were performed using R version 3.4.0 (R Core Team 2017).

Data availability The datasets used in the current study are available upon request to the corresponding author.

Results

Blackbird males visited 24.3% of all nests ($N = 263$), checking inside and occasionally feeding the female during incubation. As expected, in those nests in which the behavior of both sexes was recorded ($N = 63$), blackbird females visited more frequently ($\chi^2 = 6.47$; $p = 0.01$) and spent more time in the nest than males ($\chi^2 = 23.25$; $p < 0.001$). Clutch size partially affected nest attendance as blackbird females, but not males, visited more frequently ($\chi^2 = 5.49$; $p = 0.02$) and spent more time ($\chi^2 = 9.07$; $p < 0.01$) at those nests containing a higher number of eggs (Fig. 1). Egg mimicry did not affect nest attendance (all cases $p > 0.19$).

Egg mimicry significantly affected egg recognition in both males ($\chi^2 = 40.94$; $p < 0.0001$) and females ($\chi^2 = 23.80$; $p < 0.0001$). Both sexes recognized non-mimetic eggs (cuckoo-type and red-type eggs; Table 1; Fig. 2); however, unlike females, blackbird males did not recognize mimetic eggs (Table 1; Fig. 2). Natural blackbird eggs were not recognized by either males or females (Table 1; Fig. 2). Clutch size did not affect recognition neither in males nor in females (both cases $p > 0.70$).

We filmed one case in which a blackbird male ejected a non-mimetic egg (red type) by grasping it with its bill (see Video 1 in ESM). We filmed a total of 43 ejection events (41.2% of egg ejections; $N = 102$), of which 2.3% were carried out by males and 97.7% by females.

Discussion

In this study, we investigated the existence of sex differences in the egg-rejection behavior in blackbirds to shed light on the
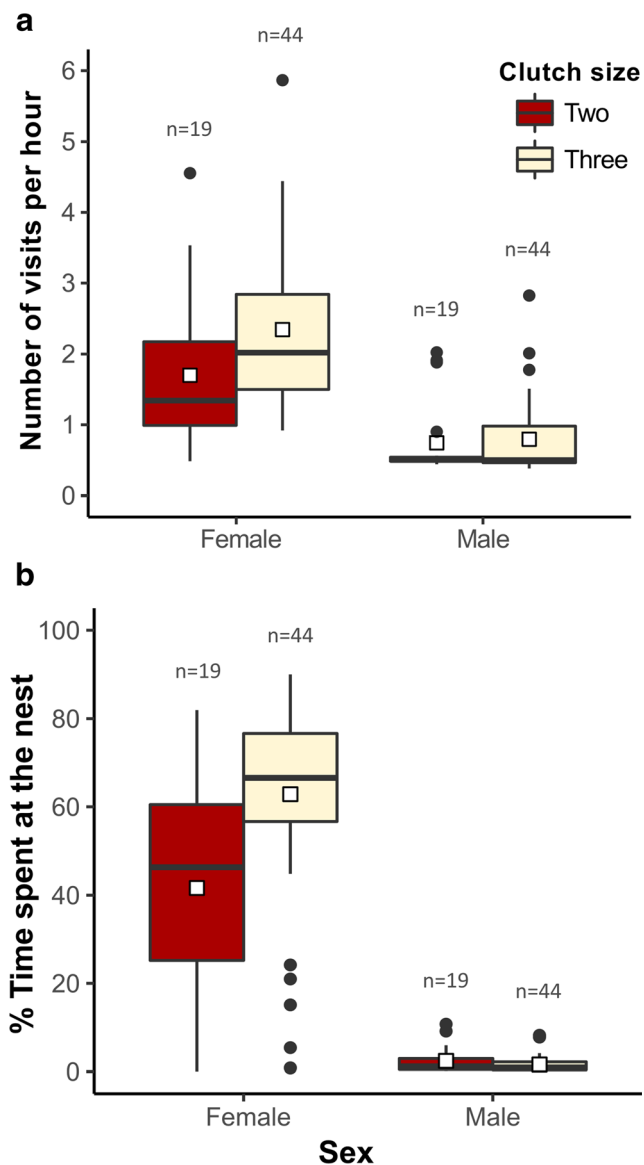
a

b

Fig. 1 **a** Number of visits to the nest per hour and **b** percentage of time spent by the blackbirds at the nest regarding the clutch size. Box plots show the median (black line), the mean (white box), and 25th and 75th percentiles (colored boxes), with whiskers denoting the 5th and 95th percentiles. Black points indicate outliers

relationship between egg incubation and the evolution of anti-parasitic defenses. We found that blackbird males do recognize parasitic eggs even though they are not actively involved in egg incubation, which contradicts the general hypothesis stating that incubation is a prerequisite for the evolution of the egg-rejection behavior (Davies and Brooke 1988; Lotem et al. 1992; Soler et al. 2002). Instead, our results show that in single-sex incubator species, non-incubating individuals (males) can also evolve recognition abilities, which supports the hypothesis that visits to the nests could favor the evolution of anti-parasitic host responses during the egg stage (Sealy and Neudorf 1995). During the egg stage, parental care of blackbirds relies mainly on females, who visited the nest more

frequently and stayed at it for longer than males (Fig. 1). However, despite this preponderant role of females, our recordings showed that blackbird males occasionally visited and inspected the clutch too. Male visits to the nest during the incubation stage have been previously described in blackbirds (Ibáñez-Álamo and Soler 2012). On the other hand, we found that females increased their nest visits and attendance in nests with larger clutches (Fig. 1), which could be related to higher incubation requirements of larger clutches (Moreno and Carlson 1989; Dobbs et al. 2006). Previous studies have shown that in other single-sex incubator species such as swallows *Hirundo rustica*, females increased their percentage of time spent incubating in response to artificially enlarged clutches (Jones 1987).

Both egg-recognition and egg-ejection abilities of blackbird females have been well documented in previous studies that used egg-touching behavior as a proxy of egg recognition (Ruiz-Raya et al. 2015, 2016; Roncalli 2017; Soler et al. 2017). Nevertheless, little is known on the recognition abilities of non-incubating males. Blackbird males touched more frequently non-mimetic eggs (i.e., cuckoo and red experimental eggs) than mimetic ones (Fig. 2), which suggest that egg-touching behavior is a good proxy of egg-recognition abilities also in non-incubating males (see "Methods"; Soler et al. 2017). Males were able to recognize non-mimetic parasitic eggs but, unlike blackbird females, they did not recognize mimetic experimental eggs. These results show that recognition abilities are less fine-tuned in blackbird males compared to those in females (Fig. 2). From an overall perspective, the most likely explanation for the better egg-recognition abilities shown by females is that the evolution of fine-tuned recognition abilities could be restricted in males because they have fewer opportunities than females to inspect the clutch and thus learn the appearance of their own eggs. This argument assumes that both sexes rely on learning mechanisms for egg recognition, which seems to be the most widespread egg-recognition mechanism among the cuckoo's hosts (Rothstein 1974, 1975b; Lotem et al. 1995; Lahti and Lahti 2002; Lyon 2007; Lang et al. 2014). Furthermore, the evolution of learning-based mechanisms for egg recognition could be limited in blackbird males as they usually mate with multiple females throughout their life. Given that learning mechanisms could be disadvantageous in some situations (Lotem 1993; Liang et al. 2012), males of some host species could rely on discordance mechanisms, thus avoiding the potential costs linked to learning mechanisms for egg recognition (Liang et al. 2012). As far as we know, little is known about sex differences in current host species in terms of cognitive decision rules for egg rejection. Finally, our results support that blackbirds mainly rely on visual cues, instead of tactile cues (e.g., the coating of painted eggs), for egg recognition (Ruiz-Raya et al. 2015), as it happens in most open-nesting hosts (Langmore et al. 2005).

Table 1 Summary of GLMs for the effect of egg mimicry on recognition touches in both males and females. Significant values are set in italics

	Female				Male			
	Estimate	SE	z	p	Estimate	SE	z	p
Intercept	− 2.341	1.122	− 2.087	0.037	− 1.355	0.705	− 1.921	0.055
Blackbird egg	2.099	1.167	1.806	0.071	0.124	0.838	0.148	0.882
Mimetic egg	3.334	1.154	2.891	*0.004*	0.865	0.799	1.082	0.279
Cuckoo-type egg	3.659	1.135	3.225	*0.001*	2.363	0.695	3.399	*< 0.001*
Red-type egg	3.461	1.113	3.109	*0.002*	2.544	0.671	3.792	*< 0.001*
Clutch size (3)	− 0.171	0.456	− 0.376	0.707	− 0.041	0.398	− 0.102	0.919
R^2	0.297				0.407			

Even though blackbird males can recognize experimental non-mimetic eggs added to their nests, the evolution of anti-parasitic defenses in males would require that they are involved in egg ejection, thus imposing selection pressures on brood parasites. In our study, most of the filmed ejections were carried out by females, although a small percentage (2.3%) were accomplished by males (see Video 1 in ESM). Our information about the sex responsible for egg ejection is restricted to 2 h after the experimental parasitism, but these results suggest that blackbird males are able to eject experimental eggs and could therefore be responsible for some egg-ejection events not filmed (58.2% of ejection events were not filmed; $N = 102$). Even so, in those cases when ejection events were filmed, egg ejection by males was rare when compared to that by females, which could have different non-mutually exclusive

Fig. 2 Number of touches to the eggs by both males and females in relation to the degree of mimicry of the parasitic egg. Different letters indicate significant differences at $p < 0.05$. Sample sizes for each treatment are shown next to each value. Values are presented as means ± SE

explanations. One possibility would be that as females visit the nest more frequently than males do and they show more fine-tuned recognition abilities, they have more opportunities to reject the parasitic egg, which therefore decreases the probability of ejection by males. On the other hand, in those cases in which males arrive at the nest before females do, the less precise recognition abilities shown by males could lead to a delay in their ejection decisions, which would facilitate the ejection being carried out by the female. This delay in the ejection decision would also make difficult for the ejection event to take place within the filming period and to be documented. Although our results show that non-incubating blackbird males have the cognitive abilities necessary to recognize non-mimetic eggs and are able to eject foreign eggs added to their nests, more information is needed to clarify the role of non-incubating males in egg ejection and therefore in the evolution of anti-parasitic defenses. Even though birds do not usually remove intact eggs from their nests (Guigueno and Sealy 2012), egg ejection by males might be thought to occur as part of nest sanitation tasks. However, in that case, they would be expected to participate more actively in removing such clearly odd object from their nests, especially considering that blackbird males significantly contribute to nest sanitation during incubation and nestling stage (Ibáñez-Álamo et al. 2013). The most likely explanation is therefore that egg ejection by blackbird males reflects a specific response towards parasitic eggs.

The evolution of egg-rejection abilities in non-incubating males is intriguing and probably requires very strong selective pressures, with a long duration of sympatry with the brood parasite. But were blackbirds so heavily exploited by interspecific brood parasites in the past? Egg-recognition abilities exhibited by some potential host species which are currently not exploited by interspecific brood parasites, as is the case of the common blackbird, have been proposed to be the result of past parasitism by an interspecific brood parasite (Soler 2014a; Ruiz-Raya et al. 2016). Alternatively, conspecific brood parasitism has also been proposed as an explanation for the evolution of egg-recognition abilities in this species (Samas et al. 2014; but see Soler 2014b). However, two pieces of evidence support the interspecific-origin hypothesis: first, our results
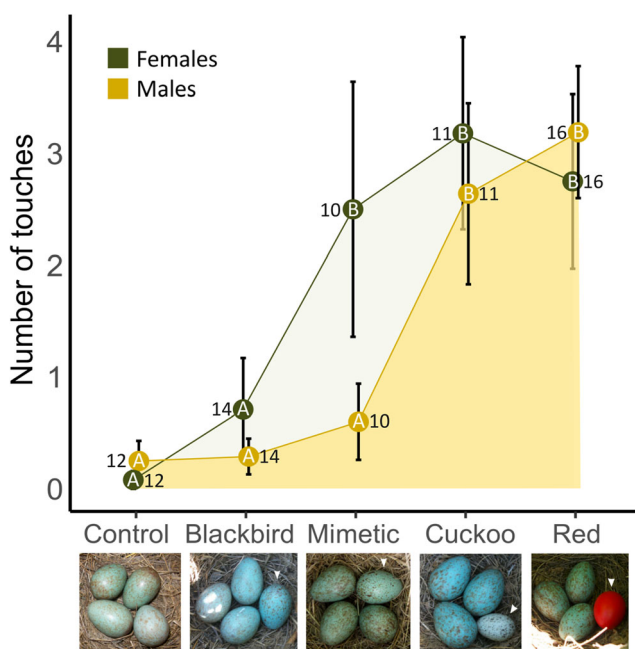
showing the ability of blackbird males to recognize non-mimetic but not mimetic eggs, and second, that neither males nor females were able to recognize natural blackbird eggs (i.e., conspecific eggs), which would be expected if the recognition abilities were the result of parasitism by conspecifics (Liang et al. 2016; Ruiz-Raya et al. 2016). Certain ecological factors linked to the biology of blackbirds, such as their main habitat or the characteristics of their nests, could have facilitated cuckoos to parasite blackbirds in the past. If we assume that the habitats preferred by cuckoos are open forests where caterpillars are abundant and that species nesting in this habitat and with conspicuous nests would be preferentially exploited (Soler 2014a), it seems fair to conclude that blackbirds, or their ancestors, were likely heavily parasitized in the past. Non-incubating males of current host species, such as males of the great reed warbler *Acrocephalus arundinaceus*, have been found to play a crucial role in cuckoo mobbing and nest defense (Požgayová et al. 2009). In this context, an intense brood parasitism in the past would have selected for blackbird males actively participating in nest defense against parasites, and this relationship of males with brood parasites, together with the visits of males to the nest, could have facilitated the initiation of the evolution of egg recognition in males.

To sum up, we found support for the hypothesis that non-incubating males that occasionally visit the nest can evolve egg-recognition abilities, so they could be involved in the host response against parasitic eggs. Our results also reinforce the importance of studying egg-recognition and egg-rejection abilities separately so that the former are not underestimated (Soler et al. 2012; Ruiz-Raya et al. 2015). Egg-recognition abilities in non-incubating males entail important consequences for the evolution of anti-parasitic responses within host populations, so additional studies addressing the sex role on anti-parasitic host defenses are required to advance in our understanding on avian brood parasitism.

Compliance with ethical standards

Ethical statement We performed the study following all relevant Spanish national (Decreto 105/2011, 19 de Abril) and regional guidelines. Ethical approval for this study was not required. During this study, nest desertion rate of the blackbird population was not affected by experimental parasitism.

Competing interests The authors declare that they have no conflict of interest.

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

References

Antonov A, Stokke BG, Moksnes A, Røskaft E (2008) Getting rid of the cuckoo *Cuculus canorus* egg: why do hosts delay rejection? Behav Ecol 19:100–107. https://doi.org/10.1093/beheco/arm102

Antonov A, Stokke BG, Moksnes A, Røskaft E (2009) Evidence for egg discrimination preceding failed rejection attempts in a small cuckoo host. Biol Lett 5:169–171. https://doi.org/10.1098/rsbl.2008.0645

Avilés JM, Soler JJ, Soler M, Møller AP (2004) Rejection of parasitic eggs in relation to egg appearance in magpies. Anim Behav 67:951–958. https://doi.org/10.1016/j.anbehav.2003.08.022

Bates D, Maechler M, Bolker BM, Walker S (2015) Fitting linear mixed-effects models using lme4. J Stat Softw 67:1–48

Davies NB (2000) Cuckoos, cowbirds and other cheats. Poyser, London

Davies NB, Brooke MDL (1988) Cuckoos versus reed warblers: adaptations and counteradaptations. Anim Behav 36:262–284. https://doi.org/10.1016/S0003-3472(88)80269-0

Davies NB, Brooke MDL (1989) An experimental study of co-evolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. J Anim Ecol 58:207–224

De Mársico MC, Gantchoff MG, Reboreda JC (2012) Host-parasite co-evolution beyond the nestling stage? Mimicry of host fledglings by the specialist screaming cowbird. Proc R Soc Lond B 279:3401–3408. https://doi.org/10.1098/rspb.2012.0612

Dobbs RC, Styrsky JD, Thompson CF (2006) Clutch size and the costs of incubation in the house wren. Behav Ecol 17:849–856. https://doi.org/10.1093/beheco/arl019

Feeney WE (2017) Evidence of adaptations and counter-adaptations before the parasite lays its egg: the frontline of the arms race. In: Soler M (ed) Avian brood parasitism behaviour, ecology, evolution and coevolution. Springer, Cham, pp 307–324

Grim T (2017) Host defences against brood parasite nestlings: theoretical expectations and empirical evidence. In: Soler M (ed) Avian brood parasitism behaviour, ecology, evolution and coevolution. Springer, Cham, pp 539–556

Grim T, Samas P, Moskát C, Kleven O, Honza M, Moksnes A, Røskaft E, Stokke B (2011) Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts? J Anim Ecol 80:508–518. https://doi.org/10.1111/j.1365-2656.2010.01798.x

Guigueno MF, Sealy SG (2012) Nest sanitation in passerine birds: implications for egg rejection in hosts of brood parasites. J Ornithol 153:35–52. https://doi.org/10.1007/s10336-011-0731-0

Honza M, Požgayová M, Procházka P, Tkadlec E (2007) Consistency in egg rejection behaviour: responses to repeated brood parasitism in the blackcap (*Sylvia atricapilla*). Ethology 113:344–351. https://doi.org/10.1111/j.1439-0310.2007.01340.x

Ibáñez-Álamo JD, Sanllorente O, Arco L, Soler M (2013) Does nest predation risk induce parent birds to eat nestlings' fecal sacs? An experimental study. Ann Zool Fenn 50:71–78. https://doi.org/10.5735/086.050.0106

Ibáñez-Álamo JD, Soler M (2012) Predator-induced female behavior in the absence of male incubation feeding: an experimental study. Behav Ecol Sociobiol 66:1067–1073. https://doi.org/10.1007/s00265-012-1357-9

Jones G (1987) Time and energy constraints during incubation in free-living swallows (*Hirundo rustica*): an experimental study using precision electronic balances. J Anim Ecol 56:229–245. https://doi.org/10.2307/4812

Lahti DC, Lahti AR (2002) How precise is egg discrimination in weaverbirds? Anim Behav 63:1135–1142. https://doi.org/10.1006/anbe.2002.3009

Lang AK, Bollinger EK, Peer BD (2014) Effect of parasite-to-host egg ratio on egg rejection by a brown-headed cowbird host. Auk 131: 694–701. https://doi.org/10.1642/AUK-14-28.1

Langmore NE, Kilner RM, Butchart SHM, Maurer G, Davies NB, Cockburn A, Macgregor NA, Peters A, Magrath MJL, Dowling DK (2005) The evolution of egg rejection by cuckoo hosts in Australia and Europe. Behav Ecol 16:686–692. https://doi.org/10.1093/beheco/ari041

Liang W, Møller AP, Stokke BG et al (2016) Geographic variation in egg ejection rate by great tits across 2 continents. Behav Ecol 27:1405–1412. https://doi.org/10.1093/beheco/arw061

Liang W, Yang C, Antonov A, Fossøy F, Stokke B, Moksnes A, Røskaft E, Shykoff JA, Møller AP, Takasu F (2012) Sex roles in egg recognition and egg polymorphism in avian brood parasitism. Behav Ecol 23:397–402. https://doi.org/10.1093/beheco/arr203

Lotem A (1993) Learning to recognize nestlings is maladaptive for cuckoo Cuculus canorus hosts. Nature 362:743–745

Lotem A, Nakamura H, Zahavi A (1992) Rejection of cuckoo eggs in relation to host age: a possible evolutionary equilibrium. Behav Ecol 3:128–132. https://doi.org/10.1093/beheco/3.2.128

Lotem A, Nakamura H, Zahavi A (1995) Constraints on egg discrimination and cuckoo-host co-evolution. Anim Behav 49:1185–1209. https://doi.org/10.1006/anbe.1995.0152

Lyon B (2007) Mechanism of egg recognition in defenses against conspecific brood parasitism: American coots (Fulica americana) know their own eggs. Behav Ecol Sociobiol 61:455–463. https://doi.org/10.1007/s00265-006-0273-2

Martín-Vivaldi M, Soler M, Møller AP (2002) Unrealistically high costs of rejecting artificial model eggs in cuckoo Cuculus canorus hosts. J Avian Biol 33:295–301. https://doi.org/10.1034/j.1600-048X.2002.330311.x

Martín-Vivaldi M, Soler JJ, Møller AP, Pérez-Contreras T, Soler M (2012) The importance of nest-site and habitat in egg recognition ability of potential hosts of the common cuckoo Cuculus canorus. Ibis 155:140–155. https://doi.org/10.1111/ibi.12000

Moksnes A, Røskaft E, Braa AT (1991) Rejection behavior by common cuckoo hosts towards artificial brood parasite eggs. Auk 108:348–354. https://doi.org/10.2307/4087959

Moreno J, Carlson A (1989) Clutch size and the costs of incubation in the pied flycatcher Ficedula hypoleuca. Ornis Scand 20:123–128. https://doi.org/10.2307/3676879

Polačiková L, Grim T (2010) Blunt egg pole holds cues for alien egg discrimination: experimental evidence. J Avian Biol 41:111–116. https://doi.org/10.1111/j.1600-048X.2010.04983.x

Požgayová M, Procházka P, Honza M (2009) Sex-specific defence behaviour against brood parasitism in a host with female-only incubation. Behav Process 81:34–38. https://doi.org/10.1016/j.beproc.2008.12.019

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria, https://www.R-project.org/

Rohwer S, Spaw CD, Røskaft E (1989) Costs to northern orioles of puncture-ejecting parasitic cowbird eggs from their nests. Auk 106:734–738

Roncalli G (2017) Behavioral and physiological responses to brood parasitism and nest predation in two passerine species. Doctoral dissertation, University of Granada

Rothstein SI (1974) Mechanism of avian egg recognition: possible learned and innate factors. Auk 91:796–807

Rothstein SI (1975a) Evolutionary rates and host defenses against avian brood parasitism. Am Nat 109:161–176. https://doi.org/10.1086/282984

Rothstein SI (1975b) Mechanisms of avian egg-recognition: do birds know their own eggs? Anim Behav 23:268–278. https://doi.org/10.1016/0003-3472(75)90075-5

Rothstein SI (1982) Mechanisms of avian egg recognition: which egg parameters elicit responses by rejecter species? Behav Ecol Sociobiol 11:229–239. https://doi.org/10.1007/BF00299299

Rothstein SI (1990) A model system for coevolution: avian brood parasitism. Annu Rev Ecol Syst 21:481–508

Ruiz-Raya F, Soler M (2017) Phenotypic plasticity in egg rejection: evidence and evolutionary consequences. In: Soler M (ed) Avian brood parasitism - behaviour, ecology, evolution and coevolution. Springer, Cham, pp 449–471

Ruiz-Raya F, Soler M (2018) Rejection of parasitic eggs: an updated terminology for a complex process. J Avian Biol 46(3). https://doi.org/10.1111/jav.01484

Ruiz-Raya F, Soler M, Roncalli G, Abaurrea T, Ibáñez-Álamo JD (2016) Egg rejection in blackbirds Turdus merula: a by-product of conspecific parasitism or successful resistance against interspecific brood parasites? Front Zool 13:16. https://doi.org/10.1186/s12983-016-0148-y

Ruiz-Raya F, Soler M, Sánchez-Pérez LL, Ibáñez-Álamo JD (2015) Could a factor that does not affect egg recognition influence the decision of rejection? PLoS One 10:e0135624. https://doi.org/10.1371/journal.pone.0135624

Samas P, Hauber ME, Cassey P, Grim T (2011) Repeatability of foreign egg rejection: testing the assumptions of co-evolutionary theory. Ethology 117:606–619. https://doi.org/10.1111/j.1439-0310.2011.01917.x

Samas P, Hauber ME, Cassey P, Grim T (2014) Host responses to interspecific brood parasitism : a by-product of adaptations to conspecific parasitism ? Front Zool 11:34. https://doi.org/10.1186/1742-9994-11-34

Sealy SG, Neudorf DL (1995) Male northern orioles eject cowbird eggs: implications for the evolution of rejection behavior. Condor 97:369–375

Soler JJ, Martínez JG, Soler M, Møller AP (1999) Genetic and geographic variation in rejection behavior of cuckoo eggs by European magpie populations: an experimental test of rejecter-gene flow. Evolution 53:947–956

Soler M (1990) Relationships between the great spotted cuckoo Clamator glandarius and its corvid hosts in a recently colonized area. Ornis Scand 21:212. https://doi.org/10.2307/3676781

Soler M (2014a) Long-term coevolution between avian brood parasites and their hosts. Biol Rev 89:688–704. https://doi.org/10.1111/brv.12075

Soler M (2014b) No evidence of conspecific brood parasitism provoking egg rejection in thrushes. Front Zool 11:68. https://doi.org/10.1186/s12983-014-0068-7

Soler M, de Neve L, Roncalli G, Macías-Sánchez E, Ibáñez-Álamo JD, Pérez-Contreras T (2014) Great spotted cuckoo fledglings are disadvantaged by magpie host parents when reared together with magpie nestlings. Behav Ecol Sociobiol 68:333–342. https://doi.org/10.1007/s00265-013-1648-9

Soler M, Fernández-Morante J, Espinosa F, Martín-Vivaldi M (2012) Pecking but accepting the parasitic eggs may not reflect ejection failure: the role of motivation. Ethology 118:662–672. https://doi.org/10.1111/j.1439-0310.2012.02058.x

Soler M, Martín-Vivaldi M, Pérez-Contreras T (2002) Identification of the sex responsible for recognition and the method of ejection of parasitic eggs in some potential common cuckoo hosts. Ethology 108:1093–1101. https://doi.org/10.1046/j.1439-0310.2002.00841.x

Soler M, Ruiz-Raya F, Roncalli G, Ibáñez-Álamo JD (2017) Relationships between egg-recognition and egg-ejection in a grasp-ejector species. PLoS One 12:e0166283. https://doi.org/10.1371/journal.pone.0166283

Underwood TJ, Sealy SG (2006) Grasp-ejection in two small ejecters of cowbird eggs: a test of bill-size constraints and the evolutionary equilibrium hypothesis. Anim Behav 71:409–416. https://doi.org/10.1016/j.anbehav.2005.06.004