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# Predation risk affects egg-ejection but not recognition in blackbirds

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## Abstract

Predation and brood parasitism have critical effects on the fitness of animals, but few studies have focused on the potential interactions between these two important selective forces. For instance, the egg-rejection process, one of the most important defensive responses of hosts against brood parasites, may be affected by variation in predation risk, which might divert their focus from the nest (present reproduction) to self-maintenance (future reproduction). In this study we explore the effect of predation risk on the first two stages of the egg-rejection process (judgment and decision) and if this potential effect changes according to the target of predation (adults vs offspring). To do so, we experimentally parasitized nests of common blackbirds (*Turdus merula*) with mimetic model eggs simultaneously exposing them to different predation-risk situations: adult predator, egg predator, and control. We found that predation risk did not affect egg recognition. Nevertheless, blackbirds exposed to the adult predation risk showed a significant reduction in the ejection rate, particularly at the end of the breeding season. We discuss our results in relation to the egg-rejection process and life-history theory. Our findings suggest that a predation risk directed to adults of parasitized nests, but not to their offspring, can play an important role in the blackbirds' decision-making influencing the ejection of parasitic eggs, consequently affecting the outcome of the evolutionary relationship between brood parasites and their hosts.

## Significance statement

Brood parasitism and predation are two important selective forces in nature, which play a crucial role in the evolutionary process in birds. Despite this, few studies have explored the possible relationships between these two selective pressures. In particular, the possibility that predation risk affects host defenses against brood parasites has usually been neglected. Predation risk could influence the egg-rejection process, which is the main defensive measure adopted by hosts once they have been parasitized. In this study we showed that predation risk seems to modulate host defenses against brood parasites in common blackbirds, but depending on the threat posed by predators. In particular, adult predation risk affects the second stage of the egg-rejection process reducing the ejection rate of parasitic eggs. Our results open a new line of research in brood parasitism studies, demonstrating that external stimuli to brood parasite-host systems can influence egg-rejection decisions.

**Keywords** Adult predation · Brood parasitism · Egg ejection · Life-history · Nest predation

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## Introduction

Brood parasitism and predation are two important biological interactions representing decisive selective forces in nature, capable of evolutionarily shaping morphological, behavioral, and physiological traits (Lima 2009; Soler 2014; Ibáñez-Álamo et al. 2015). During the breeding period, individuals invest the majority of resources in reproduction and offspring care (Harshman and Zera 2007). Both brood parasitism and predation are particularly important during the breeding period as they can exert a big influence in relation to the nest environment. Consequently, they have been described as paramount selective pressures modulating the trade-offs between

self-maintenance and the production of viable offspring (Roff 2002; Cox et al. 2010).

Avian brood parasites impose high costs on their hosts (Rothstein 1990; Davies 2010; Soler 2014, 2017), which favored the evolution of several defensive mechanisms in the latter. These defenses can evolve before the parasitic event (i.e., frontline defenses; Feeney et al. 2012) and once the brood parasite has laid its egg (Davies 2010; Kilner and Langmore 2011; Soler 2014). One of the most important of such defensive mechanisms is the rejection of the parasitic egg (Davies 2010; Soler 2014), which is a complex behavioral process composed of three different stages: first, hosts should recognize the parasitic eggs (recognition: judgment according to the new terminology suggested by Ruiz-Raya and Soler 2018); second, they have to evaluate the situation to decide whether to eject or not the foreign egg (decision); and third, the action of ejection itself (Soler et al. 2012; Ruiz-Raya and Soler 2018). Interspecific variation in host resistance to brood parasitism seems to be genetically fixed (Stokke et al. 2008), while the differences within species suggest that in addition to the genetic component, there is a certain degree of phenotypic plasticity (Hauber et al. 2006; Stokke et al. 2008; Soler et al. 2012) deriving from trade-offs between costs and benefits associated with the decision to eject under different ecological conditions (Ruiz-Raya and Soler 2017). Hosts must evaluate the possibility of incurring recognition errors (ejecting one of their own eggs instead of the parasitic one; Davies 2010), and rejection costs (the risk of damaging one or more of their own eggs while trying to eject the parasitic egg; Davies 2010). Likewise, the risk of parasitism is another important factor that influences the egg rejection, because the presence of the brood parasite in the proximity of the nest increases the probability of rejecting the parasitic egg (Moksnes et al. 1993; Lindholm and Thomas 2000). Therefore, although hosts show the cognitive abilities to recognize the odd egg as a parasitic egg, they can finally decide not to eject it depending on different external stimuli and their internal state of motivation (Underwood and Sealy 2006; Moskát and Hauber 2007; Antonov et al. 2008; Soler et al. 2012; Ruiz-Raya et al. 2015). For example, Eastern olivaceous warblers though strongly pecking parasitic eggs (indicating recognition) did not eject them because of the difficulties in performing puncture ejection (Antonov et al. 2009). In blackbirds, 20% of recognized parasitic eggs were finally not ejected (Soler et al. 2017a). In these circumstances, the acceptance of the parasitic egg is a host decision (i.e., second phase) and not a consequence of recognition failures (i.e., first phase; Soler et al. 2017a).

Predation could act as one of such external stimuli that affects the egg-rejection process. Predation can profoundly modulate several components of the birds' biology (Caro 2005; Lima 2009), particularly those associated with the nest (Martin 1995; Martin and Briskie 2009; Ibáñez-Álamo et al.

2015). An elevated predation risk alters nest vigilance (Morosinotto et al. 2013), reduces nest visits (Eggers et al. 2008; Ibáñez-Álamo and Soler 2012), and increases on- and/or off-bout durations (Kleindorfer 2007; Massaro et al. 2008) and nest attentiveness (Ghalambor and Martin 2002; Fontaine and Martin 2006). Furthermore, nest defense is a factor known to affect egg rejection (Moksnes et al. 1991; Soler et al. 1999; Campobello and Sealy 2018).

It is possible therefore that predation and brood parasitism may interact in relation to the nest environment. Despite these possible scenarios, few studies have investigated the possible relationship between predation and brood parasitism, most of them by exploring whether brood parasitism affects predation. These studies have been mainly focused on the possibility that the activity of brood parasites could increase the probability of detection of host nests by predators (Hannon et al. 2009). The causes for such increase in nest predation seem to rely on the higher frequency of foster parents' feeding visits (Hoover and Retz 2006) and the loud begging calls produced by parasitic nestlings (Ibáñez-Álamo et al. 2012). Some studies have also investigated a protective effect of parasites on host nests which seems to be related to the use of repellent secretions emanated by parasitic chicks (Canestrari et al. 2014), although they do not seem to be effective in all host populations (Soler et al. 2017b). In contrast to these studies, very few papers have investigated the opposite direction of the interaction, that is, whether predation can affect brood parasitism. This aspect was recently explored in two host species, the yellow warbler (*Setophaga petechia*) and the reed warbler (*Acrocephalus scierpaceus*), where the authors showed that nest predation risk can influence nest defense towards brood parasites (Campobello and Sealy 2018). This was also indirectly considered by studying the physical resemblance between adult common cuckoos (*Cuculus canorus*; hereafter cuckoo) and Eurasian sparrowhawks (*Accipiter nisus*; hereafter sparrowhawks; Welbergen and Davies 2011), demonstrating that cuckoos mimic hawks in order to frighten adult hosts so that they can safely parasitize their nests. Another possibility, which has been nearly unexplored (but see York and Davies 2017), is that predation risk could influence host defenses against brood parasites during the egg-rejection process, specifically at the judgment and decision stages. This potential influence could change depending on the kind of threat that the predator poses for the parents as it happens for other behaviors. It was observed, for example, that different types of predator alter incubation behavior differently (Basso and Richner 2015), probably due to changes in the trade-offs between current and future reproduction (Ghalambor and Martin 2001). In a brood parasitism context, predation risk may act as an important stimulus affecting the cognitive processes which are the basis for the decision outcomes. For example, the presence of a predator may alter the cognitive abilities used by hosts to discriminate and recognize the foreign egg. An

increased adult predation risk may distract parents' attention from their clutches to self-protection making it more difficult to inspect and therefore to possibly recognize parasitic eggs since parents would be more watchful of the direct threat posed by the predator. If an adult individual fails to detect and respond to a predator signal, it may lose its life and therefore all the future reproductive events (Ghalambor and Martin 2001). In a recent study, incubating females of reed warblers showed a lower rejection rate of the experimental parasitic egg when they were exposed to sparrowhawk calls, a typical predator of adult reed warblers (York and Davies 2017). Alternatively, an elevated nest predation risk might affect the cognitive processes which determine the recognition of the egg and result in a higher probability to detect foreign eggs since the presence of a potential nest predator can increase the duration of on-bouts (Conway and Martin 2000; Fontaine and Martin 2006). Thus, it could be expected that parents, by spending more time at the nest, might increase the rate at which they check their clutch to detect potentially missing eggs. In case of a parasitized nest, the perception of a nest predator may increase the possibility of recognizing the foreign eggs. In addition to these possible effects during the judgment stage, predation could also affect the second stage of the egg-ejection process (i.e., decision) by acting as an external stimulus which alters the trade-off between the costs and benefits associated with the choice of ejecting the parasitic egg. In fact, even after the recognition of a foreign egg in the clutch, adults might be deterred to eject it in case of adult predation risk, since the ejection could reveal its location to the predator and expose them to a predator attack. Furthermore, carrying an egg in the bill will reduce the maneuverability of ejectors making them more prone to be preyed upon. Adults, by not ejecting, would therefore evict this potential (deadly) cost of ejection, sacrificing their present rather than their future reproduction, which may lead to an increase in fitness.

In this study, we explore these hypotheses by means of experimentally parasitizing common blackbird (*Turdus merula*; hereafter blackbird) nests with mimetic model eggs while simultaneously exposing adults to three different predation-risk situations: (1) an exclusive threat for the parents, (2) a threat only directed towards offspring, and (3) a control situation with no increased predation risk. We make several predictions based on the above-mentioned hypotheses (Table 1). In particular, we can predict (1a) that blackbirds exposed to an adult predator should recognize foreign eggs less often because their attention will be mainly placed in protecting themselves from predation. On the other hand, (1b) parents exposed to a nest predator should recognize a higher proportion of foreign eggs because they will increase the checking of the clutch in order to look for potentially predated eggs. We also expect (2a) a reduction in egg-rejection rate under the adult predator treatment given the

**Table 1** Summary of predictions according to “sparrowhawk” and “magpie” treatments. The up arrow indicates an increase, the down arrow indicates a decrease

Predictions	Sparrowhawk	Magpie
Recognition	↓ (1a)	↑ (1b)
Ejection rate	↓ (2a)	↑ (2b)
Incubation activity		
Mean nest attendance duration	↑ (3a)	↓ (3b)
Proportion of time incubating	↑ (3a)	↓ (3b)

lower motivation to eject caused by the important cost of being preyed upon. In contrast, (2b) egg-rejection rate should increase in the nest-predator treatment as a consequence of the predicted increase in egg recognition and the absence of the direct costs associated with the ejection. Finally, given the strong influence of predation on incubation (Fontaine and Martin 2006; Kleindorfer 2007; Massaro et al. 2008), we expect that (3a) females facing a risk to adult predation risk should have longer nest attendance duration to avoid being detected (Martin and Briskie 2009). In this scenario, the proportion of time incubating should increase because females should spend more time hidden in the nest and sitting on the clutch. Regarding females exposed to nest predation risk, we can hypothesize (3b) a reduction both in mean nest attendance duration, as parents will probably spend more time looking for the nest predator in order to expel it from the area (Ibáñez-Álamo and Soler 2012), and in the proportion of time incubating because of the increased time spent by females inspecting the clutch.

## Materials and methods

The study was conducted in a population of common blackbirds located in the Valley of Lecrín (Southern Spain, 36°56' N, 3° 33' W) during the breeding season of 2014. This area is dominated by orange groves in which blackbirds build their nests. The density of blackbird nests is 2.9 ha<sup>-1</sup> and nest predation rate is 48.9% (Ibáñez-Álamo and Soler 2010). The site presents both typical adult predators such as sparrowhawks or booted eagles (*Hieraetus pennatus*) and offspring predators such as mammals (stone marten *Martes foina*, genet *Genetta*, weasel *Mustela nivalis*, domestic cats *Felis catus*, and rats *Rattus* spp.), birds (principally corvids), and snakes (ladder snake *Elephe escalearis*, Montpellier snake *Malpolon monspessulanus*). The blackbird is considered a medium-sized potential host of the common cuckoo and has been frequently used in egg-recognition experiments (Polačiková and Grim 2010; Samaš et al. 2011; Ruiz-Raya et al. 2015, 2016; Soler et al. 2015, 2017a) because it exhibits the cognitive capacities to recognize and eject the experimental eggs by

grasping ejection (Ruiz-Raya et al. 2015), despite the fact that it is not currently parasitized. We actively searched for blackbird nests throughout the breeding period; once a nest was located we visited it every 2 days to determine the exact laying date and clutch size. The experiment was initiated only when the clutch size was completed, that is when we found the same number of eggs in the nest for two consecutive days. We used only nests with a complete clutch of three eggs, which represents the median in our population (Ibáñez-Álamo and Soler 2010), to standardize our study in this respect.

### Experimental procedure

We experimentally manipulated both predation risk and brood parasitism in blackbird nests. To do this, we introduced a parasitic model egg into the nest while exposing blackbirds to different predation-risk situations using different playbacks (see below). We did not remove any blackbird eggs (as cuckoos do in natural conditions) because the experimental removal of one host egg does not change rejection rate (Davies and Brooke 1989; Grim and Honza 2001) and due to ethical reasons. We started our experimental protocol once the clutch was completed.

To investigate the potential effects of predation risk on egg recognition, we placed a video camera (Panasonic HDS-SD40) near the nest (approximately 2 m) and filmed female behavior prior (“pre-manipulation session”) and after (“manipulation session”) the experimental parasitic event. In our population, blackbird nests were video-monitored in several previous studies showing that their behavior was not affected by the presence of cameras (Ibáñez-Álamo and Soler 2012; Ruiz-Raya et al. 2015, 2016; Soler et al. 2015, 2017a). “Pre-manipulation session” lasted during 1.5 h and allowed us to check the usual female behavior at the nest, without the experimental egg. “Manipulation session” started immediately after “pre-manipulation session,” when we simulated simultaneously, both the parasitic event by introducing the foreign egg, and the increase of predation risk by playing the speakers. We finished this session after 2 h of recording, when we removed the camera. All video recordings were carried out in the morning, between 08:30 to 13:00.

To parasitize nests, we used blackbird mimetic model eggs, obtained by collecting fresh natural blackbird eggs from abandoned nests of the same population (Soler et al. 2015). Eggs were stored in the fridge at 4 °C temperature until their use (no more than 5 days from their collection). We painted the eggs by using two different acrylic paints: blue-green (background) and light brown (spots; Fig. 1; see Soler et al. 2015 for a more detailed description). We decided to use mimetic eggs because they elicit intermediate ejection responses (Soler et al. 2015), thus allowing blackbirds to increase or reduce their responses depending on the predation-risk situation. Each egg was used only once.



**Fig. 1** Picture of the experimental treatment. The arrow marks the model egg used

Predation risk was manipulated by exposing incubating females to the calls of two different diurnal predators: the sparrowhawk, a typical predator of adult blackbirds (Newton 1986) that is known to affect blackbird’s anti-predator behavior (Møller and Ibáñez-Álamo 2012); and the Eurasian magpie (*Pica*; hereafter magpie), which is an important nest predator for blackbirds (Collar 2005) that alters different behaviors related to the nest in this species including incubation patterns (Ibáñez-Álamo and Soler 2012). As a control group, we used calls of the turtle dove (*Streptopelia turtur*), which is also present in the area but does not present a threat to either adults or offspring. We randomly assigned the nest to each group to evenly balance the treatments throughout the season. We used calls from 8 to 10 individuals belonging to 7–10 individuals per species collected from an online database ([www.xeno-canto.org](http://www.xeno-canto.org)). Recordings in mp3 format were modified by using the software Audacity in order to cut only higher-quality elements from the original ones and to set up longer audio files composed by several calls belonging to different individuals. Each playback consisted of a 4-min presence period (20 s of calls interspersed with 40 s of silence) followed by an 8-min absence period (silence). The playbacks were joined together in a single 3-h-long audio file. We composed different long audio files. Each of the long audio files per treatment (6–7) was broadcasted near the nest (8 m) at a mean of 70 dB (at 1 m from the nest; Magrath et al. 2007, 2009) using speakers (JVC CS-V428, 70 Hz, 200 W) connected to an mp3 player (MP3 Zipy Lion 4 gb) and hidden under a camouflage cloth.

To explore the potential role of predation risk on ejection behavior, we broadcasted the audio files for the following 5 days from dawn until dusk. This 5 days interval is frequently used in other egg-rejection experiments to assess host responses towards foreign eggs (e.g., Davies and Brooke 1988; Grim et al. 2011; Soler et al. 2015). We considered the model egg to have been accepted when it remained warm in the nest for this period. In this case, on the fifth day, we removed it and considered the trial finished. We considered the model egg to be ejected if it disappeared from the nest during this 5-day interval but hosts' eggs were still warm in the nest. On the other hand, we noted nest desertion when we found the clutch, including the model egg, cold for two consecutive visits. In accordance with Soler et al. (2015), nest desertion was not considered in the analysis as a rejection response to brood parasitism. Nest desertion has reported to be used as a response to predator presence or partial predation (Ackerman et al. 2003), but, since we recovered only one deserted nest over 52 used in the experiment, we are confident that there was no differences in the desertion probability among the three predation risk treatments. We followed previous recommendations to prevent the habituation of birds to our manipulation (Forsman and Martin 2009; Zanette et al. 2011): (i) we avoided the laying period, (ii) we changed the position and the direction of the speakers every day of this 5-day period; and (iii) a different audio file was used every day for each nest (assigned following a structured random design).

### Video recording variables

To obtain information on female behavior in relation to egg recognition, we compiled different variables from the video recordings, in particular by analyzing both the number of touches to the eggs and the time spent looking inside the nest and touching the eggs (see ESM videos S1, S2): (1) "initial number of egg touches" (the number of times that females touched the eggs since their first arrival to the nest until they sat to incubate divided by the time between the arrival at the nest and the start of the incubation) and (2) "initial time spent inspecting eggs," as the time spent by females looking at and touching the eggs during the first visit. Moreover, we quantify (3) "egg touch rate," as the number of times that females touched the eggs during the incubation divided by the time spent at the nest, and (4) "time spent inspecting eggs," considering the sum of the time spent by females checking and touching the eggs divided by the time spent at the nest. Previous studies on several host species suggest that egg-touching behavior performed by females at the nest can be considered a clear indicator of foreign egg recognition, even if ejection does not occur (Soler et al. 2002, 2012; Underwood and Sealy 2006; Antonov et al. 2008, 2009), which has also been evidenced in blackbirds (Ruiz-Raya et al. 2015; Soler et al. 2017a). For example, Olivaceous warbler *Iduna pallida*,

a small cuckoo host, clearly demonstrate recognition of foreign eggs by its egg-pecking behavior documented during the video recordings (Antonov et al. 2009). The egg-touching behavior has been proposed as a mechanism for obtaining additional information on the parasitic egg, especially in grasp-ejector hosts (Ruiz-Raya and Soler 2018). In blackbirds, two main pieces of evidence support this assumption. First, females touch more frequently the eggs in experimentally parasitized nests compared to control nests. Second, these touches are more frequent in nest parasitized with non-mimetic than mimetic eggs (Ruiz-Raya et al. 2015, 2016, 2019; Soler et al. 2017a).

To assess the incubation behavior at the nest, we quantified two variables (Martin and Briskie 2009): (1) "mean nest attendance duration" (the mean time that females spend at their nests) and (2) "proportion of time incubating," measured as the time spent incubating divided by all the time at the nest.

To minimize observer bias, blinded methods were used when all behavioral data were analyzed.

### Statistical analyses

We first analyzed variables related to egg recognition using linear models (*lm* function in the "stats" package). After inspecting the normal distribution of the residuals and the homogeneity of their variance (Zuur et al. 2010), we decided to use the square root transformation for the variables "egg touch rate" and "time spent inspecting eggs" since they did not fit these assumptions. Because of the presence of many zeros in the variable "initial number of egg touches," we used hurdle zero models with a truncated negative binomial distribution (Zuur et al. 2009) and analyzed the data with the *hurdle* function in the "pscl" package (Zeileis et al. 2008). Secondly, we analyzed incubation behavior. We ran a linear model for the variable "mean nest attendance," whereas, following the indications of Warton and Hui (2011) on the correct methods to use for analyzing proportional data, we fit a generalized linear model with binomial error (*glm* function in the "stats" package) for the variable "proportion of time incubating." All models referred to the video recording variables included the predation-risk treatment ("sparrowhawk," "magpie," or "dove"), "pre-manipulation session," and laying date as predictors. "Pre-manipulation session" allowed us to control for the baseline behavior for each variable before our manipulation. We included laying date, a suitable estimator of the seasonal variability of the environment during the reproductive period (Dubiec and Cichon 2005), because it is known that both predation risk (Newton 1986) and brood parasitism (Molina-Morales et al. 2012) may change along the breeding season.

We ran a generalized linear model with binomial error to assess the effect of our treatment on ejection rate. The model included the predation-risk treatment as factor, the laying date

as covariate, and their interaction. The differences among the levels of significant factors were compared by the *interactionMeans* function in the “phia” package (De Rosario-Martinez et al. 2015). This function creates a data frame with the adjusted means of a fitted model, or the slopes associated to its covariates, plus the standard error of those values for all the interactions of given factors. These interactions are plotted by pairs of factors (De Rosario-Martinez et al. 2015).

Finally, we used generalized linear models with binomial error to examine the association between egg ejection (response variable) and egg recognition (predictors). We ran a model for each egg-recognition variable (four in total).

Values provided in the manuscript are means  $\pm$  SE. All analyses were performed using R version 3.3.2 (R Core Team 2016).

## Data availability

The datasets used in the current study are available from the corresponding author on reasonable request.

## Results

### Egg recognition and incubation behavior

We obtained video recordings from 52 nests, but we experienced some logistical problems (e.g., cameras malfunction, damaged recording files, or the impossibility to observe female’s behavior at the nest) that reduced our sample size to 44 nests: 14, 15, and 15 nests for “dove,” “magpie,” and “sparrowhawk” treatment, respectively.

Neither adult- or nest-predator risk affected egg recognition (Table 2; Fig. 2a–d). Three of the four egg-recognition variables were positively associated with “pre-manipulation session” (Table 2), which indicates that the common females’ behavior during the incubation period (i.e., “pre-manipulation session”) predicted the females’ behavior once we manipulated them. Laying date was not significant for any of the variables either (Table 2).

The exposure to two different types of predation risk did not induce significant changes in females’ incubation behavior (Fig. 2e, f). Both “mean nest attendance” and “proportion of time incubating” were positively associated with “pre-manipulation session” (Table 2), whereas we found no effect of laying date on incubation behavior (Table 2).

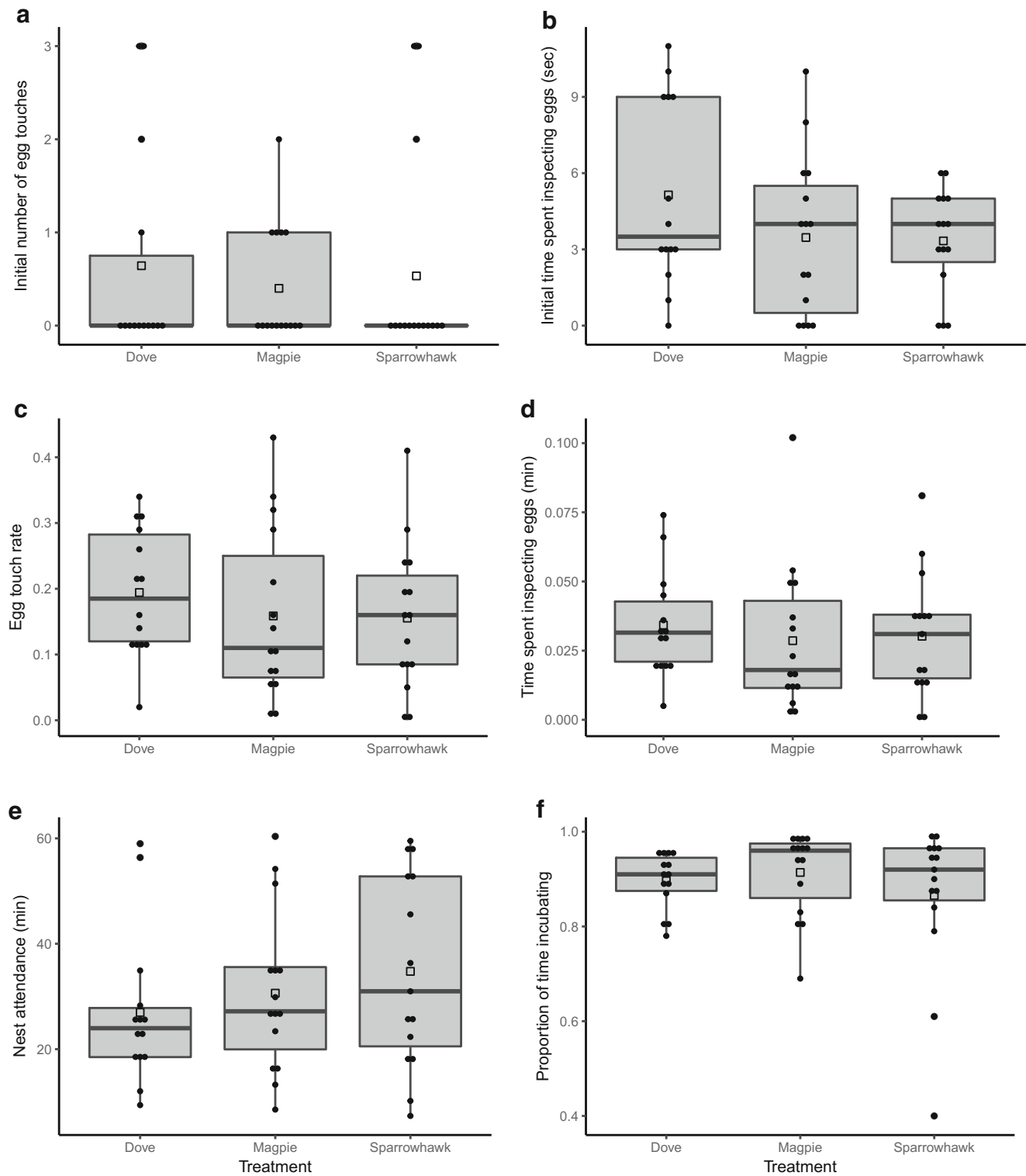
### Egg ejection

We completed the 5-day-experimental manipulation in 45 nests: 16, 16, and 13 nests for “dove,” “magpie,” and “sparrowhawk” treatment, respectively. We could not use data

**Table 2** Linear, generalized, and hurdle zero models used for video-recording variables. All the models included treatment (“sparrowhawk,” “magpie,” and “dove”), pre-manipulation session, and laying date as predictors. Estimates are shown for significant predictor (in italics)

Egg recognition	$\beta \pm$ SE	F, Z, $\chi^2$	df	P
Initial number of egg touches (Z) *Hurdle model				
Zero hurdle model				
Pre-manipulation session		0.004		0.99
Treatment magpie		0.62		0.53
Treatment sparrowhawk		−0.41		0.68
Laying date		−0.95		0.94
Count model				
Pre-manipulation session		0.07		0.94
Treatment magpie		−1.61		0.11
Treatment sparrowhawk		0.15		0.88
Laying date		144		0.15
Initial time spent inspecting eggs (F)				
<i>Pre-manipulation session</i>	<i>0.49 <math>\pm</math> 0.18</i>	7.91	1, 39	0.01
Treatment		1.86	2, 39	0.17
Laying date		1.08	1, 39	0.30
Egg touch rate (F)				
<i>Pre-manipulation session</i>	<i>0.79 <math>\pm</math> 0.25</i>	11.94	1, 39	0.001
Treatment		0.99	2, 39	0.38
Laying date		0.18	1, 39	0.67
Time spent inspecting eggs (F)				
<i>Pre-manipulation session</i>	<i>2.24 <math>\pm</math> 0.49</i>	21.21	1, 39	< 0.001
Treatment		0.80	2, 39	0.45
Laying date		0.66	1, 39	0.41
Egg Recognition				
	$\beta \pm$ SE	F, Z, $\chi^2$	df	P
Mean nest attendance duration (F)				
<i>Pre-manipulation session</i>	<i>0.52 <math>\pm</math> 0.14</i>	12.59	1, 39	0.001
Treatment		1.11	2, 39	0.34
Laying date		2.30	1, 39	0.14
Proportion of time incubating ( $\chi^2$ )				
<i>Pre-manipulation session</i>	<i>11.43 <math>\pm</math> 2.47</i>	1.63	1, 39	< 0.001
Treatment		0.18	2, 41	0.28
Laying date		0.001	1, 39	0.95

of seven nests because in six of them chicks hatched before the end of the trial (i.e., the fifth day after the egg introduction) and in one case the female deserted the nest. Blackbird females exposed to “sparrowhawk” significantly reduced their ejection rate by more than a half while those under the “magpie” treatment did not modify their ejection rate (Fig. 3a). However, this effect was associated with date (treatment  $\times$  laying date;  $\chi^2 = 47.15$ ,  $P = 0.02$ ; Fig. 3b). The ejection rate for females of the “sparrowhawk” treatment was reduced as the breeding season advanced ( $\beta = -0.37$ ,  $P = 0.03$ ) while those exposed to “magpie” or “dove” maintained



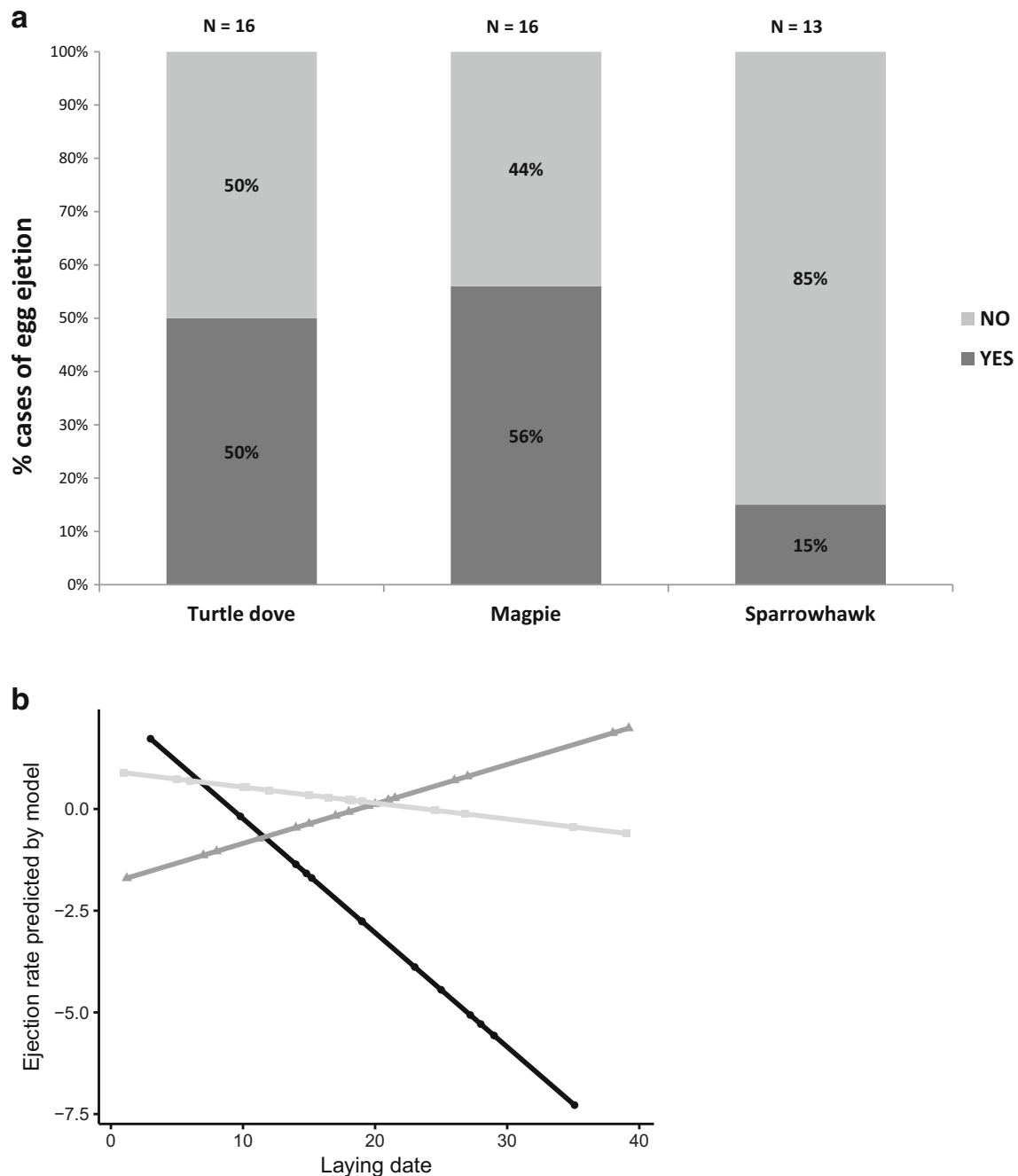
**Fig. 2** Recognition of mimetic eggs and incubation behavior according to the predation risk treatment. The thick black lines and the squares represent the medians and the means respectively. The black points represent our data points. The boxes encompass the interquartile ranges and the whiskers extend to the variability outside the quartiles.

their ejection rate constant during all the breeding period ( $\beta = +0.15$ ,  $P = 0.14$  and  $\beta = -0.21$ ,  $P = 0.14$ , respectively).

Differences regarding: **a** initial number of egg touches, **b** initial time spent inspecting eggs, **c** egg touch rate, **d** time spent inspecting eggs, **e** mean nest attendance duration, and **f** proportion of time incubating. For more detailed explanation of each variable, see “Material and methods” section

We found no difference in the ejection time ( $F_{2,20} = 0.59$ ,  $P = 0.56$ ): females of “sparrowhawk,” “magpie,” and “dove”





**Fig. 3** **a** Percentages of ejection according to the predation risk treatment. Light gray represents when ejection occurred, while dark gray represents when ejection did not occur. Sample sizes for each treatment are shown at the top of each column. **b** Variation of ejection rate (i.e., predicted values

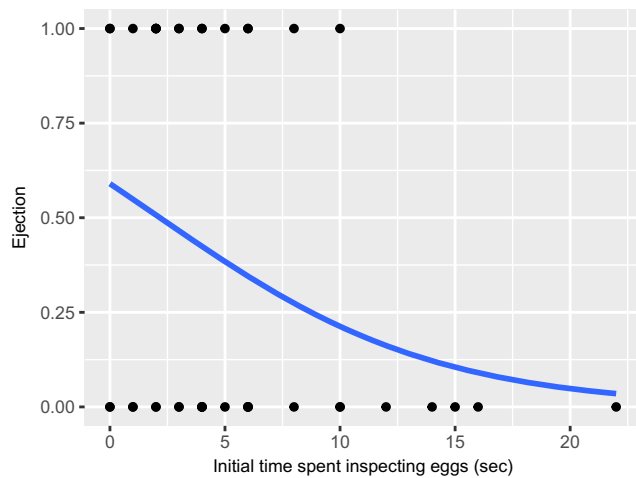
derived from generalized linear model) according to the laying period. Dark, light, and intermediate grays represent sparrowhawk, magpie, and turtle dove treatments, respectively

groups ejected on average at 38.4, 55.5, and 54 h after the introduction of the egg, respectively.

Only the variable “initial time spent inspecting eggs” was related with egg-rejection response ( $\chi^2 = 4.21$ ,  $P = 0.04$ ), showing that females which spent more time inspecting the clutch during the first visit are less likely to eject the parasitic egg (Fig. 4).

## Discussion

The egg-rejection process is the main defense adopted by hosts once they have been parasitized (Soler 2017). This complex and multifaceted mechanism can be affected by multiple factors, which can condition the plasticity of this defensive behavior (Ruiz-Raya and Soler 2017). Our study shows for



**Fig. 4** Ejection rate according to initial time that females spent inspecting eggs. Y-axis refers to ejection variable: 1 indicates the ejection event, while 0 indicates no ejection

the first time that predation risk constitutes an external conditional stimulus of brood parasite-host interactions that does condition the egg-rejection process. This influence seems to be mainly accomplished by its effect on the host decision-making that ultimately leads to changes in ejection outcomes. Females exposed to an adult predatory threat eject fewer eggs indicating that they seem to divert their attention from the clutch (present reproduction) to self-maintenance (future reproduction).

### Predation risk and the egg-rejection process

Contrary to our first predictions (predictions 1a, b), the first stage of the egg-rejection process (egg judgment) was not affected by the type of predatory threat (Fig. 2a–d). This finding suggests that the recognition of the putative parasitic egg depends on the cognitive process of hosts and is not affected by predation risk. This result is not so unexpected since the judgment stage is more likely to be affected by additional factors linked to the characteristic of the eggs, such as the mimicry of the parasitic egg or intraclutch variation (Cherry et al. 2007). The “initial number of egg touches” was the only variable that was not associated with the “pre-manipulation session”. In blackbirds, the experimental egg is recognized immediately after females come back to the nest (Soler et al. 2017a). So, our result is indicating that the egg-recognition behavior is not associated with the common activities that occur during the incubation, but because of a cognitive process of rejection occurring once females visit the nest.

Despite the fact that predation risk did not affect the first stage of egg-rejection process (i.e., judgment), the exposure to adult predation risk seemed to condition the motivational

process, which led to the decision of ejecting or accepting the egg (second phase). Females exposed to the sparrowhawk calls showed lower egg-rejection rate, fitting with prediction 2a, whereas the “magpie” treatment did not provoke any effect, contrasting with prediction 2b (Fig. 3). As already demonstrated in several studies (Antonov et al. 2008, 2009; Soler et al. 2012, 2017a; Ruiz-Raya et al. 2015), egg recognition is not always followed by egg rejection. This is also supported by our data because three of the four egg-recognition variables were not significantly associated with ejection. And the only variables that did show a significant association (“time inspecting the nest during the first visit”) highlighted the opposite effect (i.e., longer time inspecting, less likely to eject the parasitic egg; Fig. 4). This seems to suggest that the females that spent more time in inspecting should be those that are less likely to eject because of the potential costs associated with the ejection, which affect the final decision (Davies et al. 1996). Low ejection rates under a predation risk imply that the pressure derived from the potential presence of a predator would induce a decrease in the motivation to eject in parasitized females. Recently, it was reported that a factor that does not affect egg recognition (egg mass) influences the decision of ejection because an increased egg mass may imply higher rejection costs and hamper ejection (Ruiz-Raya et al. 2015). Similarly, we found that another factor (predation risk), which does not affect egg recognition but may increase ejection costs, decreases the probability of a parasitic egg previously recognized to be ejected. In addition, it worth considering that in this case the potential cost of ejection imposed by a high predation risk is extremely high. Females risk their life and therefore, all their future reproductive events because the predator could detect them when they fly away from the nest, and further, the extra weight represented by the egg can reduce females’ flight capacity and their possibility to evict the predator attack (Ercit et al. 2014). By contrast, the potential loss of a single reproductive event in the case that the accepted cuckoo egg would hatch should be less costly than losing all future reproduction. Actually, the blackbird can be considered as a medium-lived species since its longevity is the highest in the Order Passeriformes, after the Family Corvidae (Wasser and Sherman 2010). Long- and medium-lived species are known to rarely favor a high investment in the current reproduction as a small decrease in the probability of future survival for the parents will mean a reduction of the number of the future reproduction (Sæther et al. 1993). In addition, the blackbird populations of the Iberian Peninsula are able to raise up to three broods per season (Aparicio 2008) and therefore, they generally have many opportunities of breeding during their lifetime.

The decrease in egg-ejection rates depended on the timing of the breeding season, since the probability of ejecting was lower as the breeding season advanced (Fig. 3b). This suggests that the effect on egg ejection associated with the potential presence of the sparrowhawk was more intense during late spring, which is actually, the period in which it is more likely to encounter sparrowhawks. In fact, the reproductive period of several hawk species seems to have evolved to coincide with the end of the blackbird's breeding period (Newton 1976), when the maximum abundance of passerine fledglings satisfy the higher food demands of breeding (Newton 1986).

Interestingly, the results obtained for the magpie group contrast with those obtained for another blackbird population, in which females exposed to the same nest predator changed their breeding activities (Ibáñez-Álamo and Soler 2012, 2017). These contrasting results might be explained by the important differences in predation risk and life-history strategies between these two blackbird populations, which reinforce the existence of an important trade-off between current and future reproductions in this species. Blackbirds in our population invest less in a single reproductive event than those in the population used by Ibáñez-Álamo and Soler (2012), probably due to the higher nest predation pressure in the former, which was double compared with that of our study area (Ibáñez-Álamo and Soler 2010). These differences would suggest that the nest predation pressure in our study area (contrary to sparrowhawk pressure) might not be intense enough to provoke consistent changes, since blackbirds of our population can invest in multiple-breeding attempts through the years.

## Concluding remarks

To sum up, predation risk can modulate host responses to brood parasitism indicating that it can act as an important environmental factor shaping some anti-parasitic responses. Adult predators seem to exert an important impact on the decision to eject the parasitic egg. In an evolutionary context, the observed changes in anti-parasitic defenses associated with the presence of adult predators could be the result of the trade-off between current and future reproduction.

The effect of predation risk on hosts' defenses against brood parasitism offers a new fascinating insight into the interplay between these two selective forces and opens a new research line in the study of brood parasitism. Since our results indicate that the presence of sparrowhawk discourages egg ejection, we could predict that, when parasites select their potential hosts, they could evaluate to choose those species or populations that suffer high levels of adult predation risk. In this way, the parasitic offspring should have more opportunities to avoid the rejection and survive until their fledging. This hypothesis however could only be accepted if the benefits obtained due to the reduction in egg rejection outweigh with the higher probability of predation of parasitic fledglings.

However, host adults in such areas might also be more predated and parasites should also compensate for this fact, for example, by selecting high quality foster parents (Soler et al. 1995) with a lower probability of being predated (Bortolotti et al. 2002; Møller et al. 2009).

Our results also offer an additional benefit associated with the coloration of the cuckoos mimicking sparrowhawks. It is assumed that this adaptation has been evolved to scare the hosts and help the parasite to lay their egg undisturbed (Welbergen and Davies 2011). However, our findings imply that this adaptation may also favor the cuckoo by reducing the probability of ejection of their eggs (York and Davies 2017). More studies are needed to test if the patterns observed here using acoustic cues and long periods of increased adult predation risk could also be applied to visual cues and punctual encounters.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** We conducted the study following all relevant Spanish national (Decreto 105/2011, 19 de Abril) and regional guidelines. Ethical approval for this study was not required.

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