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ORIGINAL ARTICLE

Experimental evidence for an antipredatory function of egg rejection behaviour in a common host of the brood-parasitic shiny cowbird

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Abstract

The rejection of foreign eggs is the most effective adaptation against brood parasitism in birds. Many hosts, however, show suboptimal responses towards parasitic eggs, which could reflect a compromise between the benefits and costs of egg rejection. Some large-sized hosts of the shiny cowbird (*Molothrus bonariensis*) accept any spotted parasite egg but reject a rarer pure white egg morph that occurs only in some parts of the parasite's distribution. This behaviour is intriguing because it is not an effective defence against parasitism and recent evidences suggest that large-sized hosts could benefit from accepting cowbird eggs as this may dilute the risk of host egg losses at multiply parasitized nests. We studied whether rejection of pure white cowbird eggs can be driven by the increased predation risk of host nests parasitized with this conspicuous egg morph. We conducted a nest predation experiment using artificial clutches placed in natural, inactive nests of a large-sized host, the chalk-browed mockingbird (*Mimus saturninus*). Clutches consisted of two eggs resembling either one host plus one pure white cowbird egg, one host plus one spotted cowbird egg or two host eggs. Clutches with pure white eggs were more likely to be predated than those having either two host eggs or one host and one spotted cowbird egg, supporting an antipredatory function of egg rejection behaviour in mockingbirds. These results suggest that nest predation could operate as part of larger fitness trade-offs shaping host responses towards foreign eggs. Considering the role of nest predation in the studies of host rejection decisions would help to better understand the evolution and expression of antiparasite defences, especially when the hosts seem to behave suboptimally against costly brood parasitism.

Significance statement

One major goal in avian brood parasitism research is to explain the evolution of host defences against parasite eggs and young. Some large-sized hosts of the shiny cowbird (*Molothrus bonariensis*) show an intriguing behaviour: they accept spotted cowbird eggs but reject a rare pure white egg morph that occurs only in some parts of the parasite's distribution. Such behaviour provides little protection against parasitism, but it may serve as an antipredatory defence if conspicuous pure white eggs facilitate the detection of host nests to potential predators. Our study supports this idea by showing that pure white eggs increase the risk of nest predation compared to spotted host and cowbird eggs in a common large-sized host, the chalk-browed mockingbird (*Mimus saturninus*). These findings highlight the importance of considering the role of nest predation in the expression of hosts' strategies against parasitism.

Keywords Brood parasitism · Cowbird · Egg rejection · *Molothrus* · Nest predation

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Introduction

Rejection of foreign eggs is a primary defence against interspecific avian brood parasitism common to many host species (Payne 1977; Rothstein 1990; Davies 2000). Hosts can reject parasite eggs by ejecting them from the nest (Rothstein 1975; Davies and Brooke 1989; Moksnes et al. 1991, Langmore et al. 2005) or less commonly, by burying the eggs or deserting the parasitized clutch (Moksnes et al. 1991; Sealy 1995; Strausberger and Burhans 2001). This behaviour allows hosts to avoid parental investment in unrelated offspring and prevents later reproductive losses when parasitic nestlings attack or outcompete host young (Lotem et al. 1995; Øien et al. 1998; Lorenzana and Sealy 2001). The selective advantages of egg rejection, however, may come at the cost of incurring in recognition errors (i.e. rejection of host own eggs at unparasitized nests; Davies and Brooke 1988; Marchetti 1992; Lotem et al. 1995; but see Røskaft et al. 2002) or rejection costs (i.e. rejection or damage of host eggs at parasitized nests; Davies and Brooke 1988; Marchetti 1992; Røskaft et al. 1993; Lotem et al. 1995; Antonov et al. 2006). Given that egg rejection can be costly, it is expected that host's behaviour towards foreign eggs reflects the fitness pay-offs of accepting versus rejecting parasitic eggs. From this perspective, seemingly maladaptive or suboptimal responses against parasitism could be the result of hosts being subjected to opposing selective pressures that influence the fitness outcomes of alternative egg rejection strategies (Lotem et al. 1995; Davies et al. 1996; Soler et al. 1999; Avilés et al. 2005; Hoover and Robinson 2007). To identify the fitness trade-offs shaping host's responses to parasitism, it is therefore crucial to understand egg rejection decisions and, more generally, the expression of antiparasite defences in host populations (Røskaft et al. 1990; Røskaft and Moksnes 1998).

It has recently been suggested that hosts may benefit from accepting parasitism when they are multiply parasitized because the presence of parasite eggs in the clutch can reduce the risk of host eggs being removed or punctured by parasite females that subsequently visit the nest ('dilution effect' hypothesis; Sato et al. 2010; Gloag et al. 2012). If the benefits of increased host's egg survival in multiply parasitized nests outweigh the fitness costs of accepting parasitism, then egg acceptance can be an evolutionary stable strategy (Sato et al. 2010; Gloag et al. 2012). These conditions are likely to be met in some large-sized hosts of the brood-parasitic shiny cowbird (*Molothrus bonariensis*; hereafter, cowbird), in which host nestling survival is little affected by the presence of parasitic nestmates but egg losses due to punctures inflicted by cowbird females can be severe (Mermoz and Reboreda 1994; Sackmann and Reboreda 2003; Astié and Reboreda 2006; Gloag et al. 2012). Intriguingly, however, many of these hosts that are expected to benefit from accepting parasitism through a 'dilution effect' do show partial rejection of cowbird eggs. In eastern Argentina and neighbouring areas of Brazil and Uruguay, cowbird eggs are highly polymorphic in colour and spotting pattern, ranging from pure white to heavily spotted or blotched on a white, pale grey or pale blue background (Ortega 1998). Large-sized hosts like the chalk-browed mockingbird (*Mimus saturninus*), brown-and-yellow marshbird (*Pseudoleistes virescens*), rufous-bellied thrush (*Turdus rufiventris*) and creamy-bellied thrush (*Turdus amaurochalinus*) usually accept spotted cowbird eggs but reject the pure white eggs soon after being laid (Fraga 1985; Mason 1986; Mermoz and Reboreda 1994; Lichtenstein 1998; Sackmann and Reboreda, 2003; Astié and Reboreda 2005; de la Colina et al. 2012).

The differential rejection of pure white eggs is of very limited effectiveness as an antiparasite defence because this egg morph represents a small proportion of all cowbird eggs laid and it is completely absent in some parts of the hosts' distribution where parasitism rates are high (Salvador 1984; Fraga 1985; Ortega 1998; Astié and Reboreda 2005). Such suboptimal rejection behaviour may simply reflects host's perceptual or cognitive constraints to spot parasitic eggs that are more similar to their own (e.g. Antonov et al. 2008) or an evolutionary lag in which hosts have not yet evolved defences against more mimetic, spotted parasitic eggs (Rothstein 1975). Alternatively, the balance between the benefits and costs of egg rejection may differ between spotted and pure white eggs, thus making it adaptive for hosts to respond differentially to each egg morph. Pure white cowbird eggs can be more costly to accept than spotted ones if they facilitate nest detection to visually oriented predators via making the clutch more conspicuous against the nest background (Tinbergen et al. 1962; Westmoreland and Best 1986; Underwood and Sealy 2002; Kilner 2006; Gillis et al. 2012). Following this idea, if predation costs offset the benefits associated to egg acceptance in nests parasitized with pure white, but not spotted cowbird eggs, it would be adaptive for hosts to selectively reject the pure white egg morph. A critical prediction of this hypothesis is that host nests with pure white eggs should suffer higher predation rates than those having host or spotted cowbird eggs. Our aim in this study was to test this prediction in the primary large-sized host of the shiny cowbird in southern South America, the chalk-browed mockingbird (hereafter mockingbird). Mockingbirds lay eggs that are spotted or blotched with brown on a blue-green background and differ from cowbird eggs in size (mean length × width, 28.3 × 20.4 and 23.5 × 18.3 mm, respectively; Tuero et al. 2012), colour and maculation. The pure white egg morph contrasts markedly with mockingbird eggs and is more conspicuous against the nest background (Fig 1a). If the differential rejection of pure white eggs in mockingbirds is favoured as an antipredatory strategy, then we expect that pure white eggs increased the likelihood of predation of mockingbird nests relative to the spotted (host and cowbird) eggs.

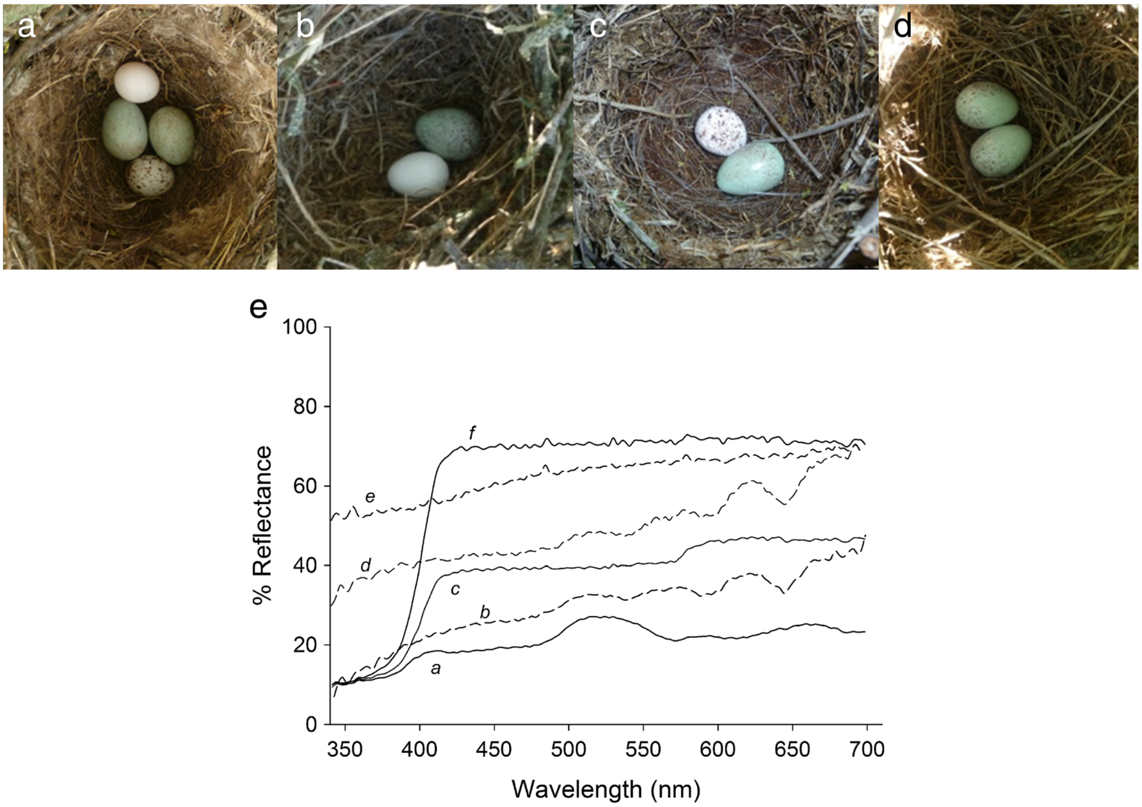

Fig. 1 **a** Active chalk-browed mockingbird nest naturally parasitized with two shiny cowbird eggs of the spotted (*bottom*) and pure white (*top*) morphs. **b**–**d** Experimental mockingbird nests showing the three artificial clutch treatments. From *left* to *right*, 'pure white' (one pure white cowbird egg plus one host egg), 'spotted' (one spotted cowbird egg plus one host egg) and 'unparasitized' (two host eggs). **e** Average reflectance spectra of experimental (*solid lines*) and natural (*dashed lines*) host and cowbird eggs: *a, b* mockingbird eggs (*n* = 13 experimental and 6 natural eggs); *c, d* spotted cowbird eggs (*n* = 8 experimental and 7 natural eggs), *e, f* pure white cowbird eggs (*n* = 12 experimental and 3 natural eggs)

Materials and methods

Study area and species

The study was conducted at Reserve El Destino, near the town of Magdalena in the Province of Buenos Aires, Argentina (35° 08′ S, 57° 23′ W), during the southern breeding season 2011–2012 (early November-mid-January). The study site is a 300-ha area within the Biosphere Reserve "Parque Costero del Sur" (MAB-UNESCO) that comprises a mosaic of marshy grasslands and woodland patches dominated by *Celtis ehrenbergiana* and *Scutia buxifolia*. Mockingbirds are year-round residents in the area where they breed from early October to mid-January. They build their nests in trees and bushes with dense foliage at a height of 1.50–2.50 m above the ground. The nests are large, open cups made of twigs and lined with dried grasses and horsehair. In the study population, egg laying usually begins within 3 days from nest completion and the modal clutch size is four eggs (range: 3–5; Fiorini and Reboreda 2006). The mean annual parasitism rate in mockingbird nests ranges from 60 to 89 %, with over two-third of the nests being multiply parasitized (Fiorini and Reboreda 2006; Gloag et al. 2012). The estimated frequency of pure white cowbird eggs in mockingbird nests varies from 7 to 14 %, but this might be an underestimation because of the rapid rejection of this egg morph (Salvador 1984; Fraga 1985; Gloag et al. 2014). Predation rates of mockingbird nests in the study population ranges from 7–12 % during egg laying to 36–45 % during the incubation stage (VD Fiorini, pers. comm.). Potential predators include birds (e.g. *Milvago chimango*, *Caracara plancus*, *Guira guira*), snakes (e.g. *Philodryas* sp., *Liophys* sp.) and mammals (e.g. *Didelphis albiventris*, *Lutreolina crassicaudata*).

We searched for mockingbird nests throughout the breeding season using parental activity within breeding territories to locate active nesting sites. We georeferenced all nests found using a portable GPS unit (eTrex Legend, Garmin Inc., USA) and monitored them twice a week until the nest failed or the young fledged. The mockingbird nests that were inactive for at least a week and maintained their structure almost intact were used to conduct the nest predation experiment to test the effect of different egg morphs on nest predation risk.

Experimental procedure

To test the effect of pure white and spotted parasite eggs on the likelihood of nest predation, we conducted an experiment using artificial clutches and natural, inactive mockingbird nests placed in their original locations. We used inactive nests to remove the effect of host's parental activity and a repeated measures design to control for nest site characteristics that might influence nest predation, such as nest placement, height and concealment (Westmoreland 2008). Every experimental nest received three sequential treatments, each consisting in an artificial two-egg clutch as follows: one host egg plus one pure white parasite egg ('pure white' treatment), one host plus one spotted cowbird egg ('spotted' treatment) and two host eggs ('unparasitized' treatment; Fig. 1b–d). Artificial eggs were made of plaster using silicone moulds of natural mockingbird and cowbird eggs (mean length × width, 26.2 × 19.1 and 22.7 × 18.2, respectively) and coated with non-toxic acrylic paint (Eureka® and AD®, Argentina) to resemble the coloration of natural eggs in human-visible wavelengths (Fig. 1e; see Online Resources 1 for details). Using artificial instead of natural stimuli in behavioural studies is not ideal (Lahti 2015; but see Hauber et al. 2015), but the low availability of natural pure white cowbird eggs and the large amount of host eggs needed for the experiment preclude the use of natural eggs in this study. Nevertheless, previous studies showed that the responses of mockingbirds and cowbirds towards plaster eggs like the ones used in this study are comparable to those observed towards natural eggs (Fiorini and Reboreda 2006; de la Colina et al. 2012). Therefore, we believe that our artificial clutches were likely to work as realistic substitutes of natural host and cowbird eggs with regard to visual cues for potential predators of mockingbird nests in our study population.

We conducted the experiment in a total of 81 inactive mockingbird nests. Each treatment lasted for five consecutive days, starting with the placement of the artificial clutch in the nest cup previously cleaned from debris. Most parasitism events in the mockingbird nests take place within 5 days from the start of host's egg laying (Fiorini and Reboreda 2006), and mockingbirds usually reject pure white eggs shortly after parasitism (de la Colina et al. 2012). Based on this, we reasoned that if egg rejection in mockingbirds evolved as an antipredatory rather than an antiparasite defence, then 5 days would be sufficient to detect a differential effect of cowbird egg morphs on the likelihood of nest predation. It is possible that considering the entire incubation period lead to different results. This might occur if the probability of 'spotted' clutches being detected increases with exposure time, resulting in similar predation rates of both egg morphs by the end of incubation. However, even if predation risk was independent of clutch composition by the end of the incubation period, a higher predation risk of pure white eggs earlier in the laying stage may still favour a rapid rejection of this morph. Under such scenario, rejector hosts could save more time and energy for current and future reproduction than acceptors if early removal of pure white eggs allows them avoiding the costs of renesting.

We did not visit experimental nests during clutch treatments to avoid as much as possible the effect of our own presence on nest predation risk. On day 5, we checked the nest and recorded the nest fate as depredated if one or both eggs were missing or not depredated if both eggs remained at the nest (Westmoreland 2008). It was not possible to record data blind because the study involved focal nests in the field. The remaining eggs (if any) were removed from the nest cup, and consecutive treatments were separated by a 2-day period in which we did not visit the nest. Each artificial clutch was used only once. The treatment order was rotated and counterbalanced across nests to avoid order biases.

Data analysis

We analysed the effect of clutch treatment on the likelihood of nest predation using generalized linear mixed models (GLMM) with binary response variable (depredated/not depredated) and logit link function. The models were fitted by the Laplace approximation using the glmer function in lme4 library (Bates et al. 2014) and the mixed function in afex library (Singmann et al. 2015) in R 3.2.3 (R Core Team 2015). The binary response variable was the nest fate, and the nest identity was included as a random factor. The explanatory variables were clutch treatment (categorical: 'pure white', 'spotted', 'unparasitized'), treatment order (ordinal: 1, 2, 3) and date of treatment initiation (continuous: day 0 = November 2). The effect of each variable in the model was assessed using likelihood ratio tests of the model fitted without the variable of interest against the full model. Parameter estimates for significant terms and the associated *P* values were derived from the minimal model including only significant parameters and the random effect. Post-hoc pairwise contrasts between all clutch treatment levels were obtained through dummy coding, by changing the reference level (intercept) in the model. Confidence intervals for parameter estimates were obtained using 'confint' function in lme4 library (Bates et al. 2014; R Core Team 2015). Estimates of mean predation rates were obtained by averaging the predicted values (in the response scale) for each clutch treatment across all levels of the random effect. Nest predators may revisit already depredated nests within the same reproductive period (Weidinger and Kočvara 2010), which may have influenced the outcomes of the experiment. To explore this possibility we conducted two additional analyses. First, we tested the effect of original nest fate on the probability of experimental nests being depredated at least once. We were able to determine the original nest fate for 72 mockingbird nests in our sample, of which 11 were successful, 50 depredated and 11 were deserted or failed due to other causes (e.g. high ectoparasites loads). Based on this subsample, we conducted a generalized linear model (GLM) with the experimental nest fate (predated at least once or not depredated) as the binary response variable and original nest fate and date of clutch treatment initiation as the explanatory variables. Second, for all experimental nests that were predated in at least one clutch treatment (i.e. nests that were detected by predators at least once; $n = 29$ nests), we tested if the likelihood of predation in the second and third treatments was affected by the previous outcome. We fitted a generalized linear mixed model with a binary response variable (predated yes/no) and logit link function, and nest identity was included as a random factor. Explanatory variables were the outcome in the previous clutch treatment (predated or not) and treatment order (2 or 3). All statistical tests had a significance level of 5 %.

Results

From the 81 experimental mockingbird nests, 29 (36 %) were depredated in one or more treatments, involving a total of 43 artificial clutches (Fig 2a). At five depredated nests, we could retrieve one of the attacked eggs that were on the ground nearby. These few eggs showed breakages, scratches and teeth marks suggestive of mammalian predators, but predator identity and time of predation (diurnal vs. nocturnal) could not be reliably determined (Fig. 2b).

The likelihood of nest predation varies among experimental nests suggesting broad heterogeneity among mockingbird nests in their susceptibility to predation (GLMM: variance estimate for the random effect ± SD, 5.3 ± 2.3). Taking this variation into account, the results of the model analysis support an effect of clutch treatment on the probability of predation of experimental mockingbird nests (likelihood ratio (LR) test: $\chi^2_2 = 12.8$, $p = 0.002$), whereas treatment order and date of treatment initiation had non-significant effects ($\chi^2_1 = 1.0$, $p = 0.32$, $\chi^2_1 = 0.05$, $p = 0.83$). According to the model results, the artificial 'pure white' clutches were more likely to be depredated than the 'unparasitized' (odds ratios, 7.1) and 'spotted' ones (odds ratios: 2.9), but the latter did not significantly differ from each other in their effect on the probability of predation of experimental mockingbird nests (Table 1, Fig. 3). The estimated mean predation rates for each clutch treatment were 0.08, 0.24 and 0.14 for 'unparasitized', 'pure white' and 'spotted' clutch treatments, respectively.

We did not find an effect of nest predation history on the likelihood of subsequent attacks. The original nest fate did not affect the probability of experimental nests being predated during clutch treatments (LR test: original fate, $\chi^2_2 = 0.87$, $p = 0.65$; date, $\chi^2_1 = 0.097$, $p = 0.76$; $n = 72$ nests with known fate). Likewise, for the experimental nests that were depredated at least once ($n = 29$), the likelihood of nest predation in the second and third clutch treatments was unrelated to the outcome of the previous treatment (LR tests: previous outcome, $\chi^2_1 = 0.001$, $p = 0.97$; treatment order, $\chi^2_1 = 0.63$, $p = 0.43$).

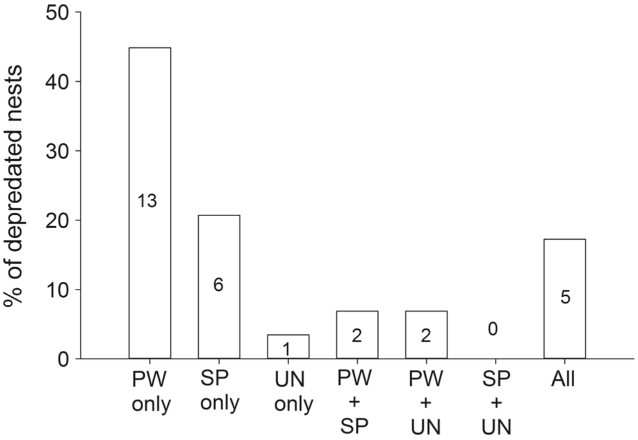

Fig. 2 Experimental eggs recovered near depredated nests showing signs of predator attacks

Discussion

This study indirectly supports the idea that the selective rejection of pure white cowbird eggs in mockingbirds can be favoured by the predation costs associated with this conspicuous egg morph. We found that the artificial pure white eggs increased predation rates of the experimental nests approximately three- to sevenfold compared to the spotted eggs. Because our experimental design removed the effect of host parental activity and controlled for nest site effects, the observed differences among treatments are likely to be due to pure white eggs increasing the detectability of mockingbird nests to potential predators in the absence of other visual, auditory or olfactory cues. These results revealed that, all else being equal, the pure white cowbird eggs would impose higher fitness costs to mockingbirds than the spotted ones, which may result in stronger selection to reject the pure white egg morph. The observed predation costs suggest that the selective rejection of pure white eggs could be an adaptive response to the combined selective pressures of nest predation and brood parasitism (Gloag et al. 2012).

It can be argued that the observed effect of clutch coloration on nest predation could be of minor importance in active mockingbird nests (Götmark 1992; Weidinger 2001). Previous studies that involved active nests failed to find a differential effect of non-mimetic parasite eggs on nest predation rates (Mason and Rothstein 1987; Davies and Brooke 1988; Krüger 2011). This could be due to nest predators cueing on nest site characteristics rather than eggs to locate active nests (Götmark 1992) or parental activity being more influential on the risk of nest predation than egg conspicuousness (Martin et al. 2000). Parental activity could mask clutch

Table 1 Post-hoc pairwise comparisons of the effect of clutch treatments on the probability of predation of experimental mockingbird nests

Model parameters	Estimate	SE	Wald χ^2_1	*P* value	95 % CI
'Pure white' treatment ('unparasitized′)	1.96	0.64	3.06	*0.0022*	0.81, 3.42
'Spotted' treatment ('unparasitized')	0.87	0.62	1.42	0.16	−0.29, 2.18
'Pure white' treatment ('spotted')	1.08	0.53	2.07	*0.039*	0.10, 2.21

Figures indicate the estimated coefficients with their standard errors and the corresponding Wald statistics, *P* values and 95 % confidence intervals for parameter estimates obtained by fitting generalized linear mixed models with clutch treatment as explanatory variable and nest identity as a random effect (see the "Materials and methods" section for details). Reference levels for the estimated effects are shown in parentheses and significant *P* values are shown in italics

coloration effects on nest predation if host parents cover the eggs during nest attendance (Westmoreland and Best 1986; but see Ibañez-Alamo and Soler 2012) or if the presence and behaviour of incubating adults serve as cues for nest location by potential predators (Martin et al. 2000; Brennan 2010). Of course, it would be impossible to conduct the present study in active mockingbird nests because host parents would remove pure white eggs soon after being placed in the nest cup. Future studies that investigate the relationship between parental activity and nest predation in parasitized and unparasitized mockingbird nests would help to disentangle the effect of host parents on predation risk. However, it is important to note that cowbird parasitism in mockingbird nests occurs mostly before the onset of incubation (~75 % of all parasitism events), when the level of nest attendance is lower and the eggs are less likely to be concealed by the incubating adults (Fiorini and Reboreda 2006). Interestingly, the predation rates of our 'spotted' and 'unparasitized' clutches (~16 and 10 %) were close to the predation rates of natural mockingbird nests during host's egg laying in our study population (nests naturally parasitized with spotted eggs, 7–12 %; unparasitized, 13 %; V. D. Fiorini pers. com.; MCDM pers. obs.). This would support the assumption that our experimental nests provide realistic estimates of the predation costs of the spotted and pure white egg morphs in real mockingbird nests in the study population during the time window in which parasitism takes place, although the actual effect of pure white eggs on real mockingbird nests is yet to be determined. Such predation costs could be at play in other large-sized hosts of the shiny cowbird known to reject this egg morph such as the brown-and-yellow marshbird, rufous-bellied thrush and creamy-bellied thrush (Mason 1986; Mermoz and Reboreda 1994; Lichtenstein 1998; Sackmann and Reboreda, 2003; Astié and Reboreda 2005). Like mockingbirds, these hosts are open nesters, lay speckled eggs and are parasitized mainly during the egg-laying stage, so it is likely that pure white cowbird eggs have similar effects in eliciting nest predation (Underwood and Sealy 2002; Kilner 2006). However, further studies are necessary to assess this possibility and determine whether the risk of nest predation can influence egg rejection decisions in those host species.

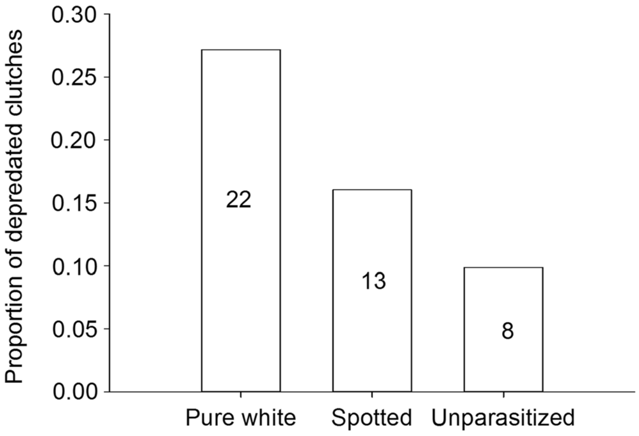

Fig. 3 Observed nest predation rates in each clutch treatment. *Bars* represent the proportion of depredated clutches over the total number of experimental mockingbird nests ($n = 81$)

Interestingly, two recent studies further suggest that nest predation could operate as part of the fitness trade-offs shaping host responses towards foreign eggs, though in the opposite way to that shown here. In the rufous-collared sparrow (*Zonotrichia capensis*), a small-sized host of the shiny cowbird, experimental and simulation results suggest that the often high rates of nest predation can reduce the fitness advantages of rejecting parasite eggs, especially if hosts incur in recognition errors or rejection costs during egg rejection decisions (Carro and Fernández 2013). Under these circumstances, rufous-collared sparrows would not be under strong selective pressure to reject parasitic eggs, which would explain why they lack antiparasite defences despite their presumably long history of sympatry with cowbirds and the fact of being heavily parasitized (Carro and Fernández 2013). Likewise, a study in a South African population of the cape bulbul (*Pycnonotus capensis*) parasitized by the Jacobin cuckoo (*Clamator jacobinus*) suggests that, although hosts could avoid most costs of parasitism by deserting parasitized nests, the increase in predation and parasitism rates over the breeding season would make that strategy more costly than egg acceptance, provided that parasitic eggs sometimes fail to hatch (Krüger 2011). These previous reports and the findings presented here highlight the importance of considering the effect of nest predation in the studies of host defences against brood-parasitic eggs and young, as it may have profound implications for the fitness outcomes of alternative rejection strategies and, ultimately, on the evolutionary interactions between parasites and hosts.

Although our results are consistent with an antipredatory function of egg rejection behaviour in mockingbirds, there are other non-mutually exclusive explanations for host differential behaviour against pure white and spotted cowbird eggs. In the first place, we cannot rule out the possibility that mockingbirds and other large-sized cowbird hosts evolved egg rejection in response to the costs of brood parasitism, as it is usually assumed. Even if cowbird eggs and nestlings have negligible effects on hatching success and nestling survival in mockingbirds (Sackmann and Reboreda 2003), hosts may still benefit from rejecting parasite eggs if this allows them to reduce their parental investment in the current brood and save time and energy for future reproduction. Under this scenario, the differential rejection of pure white and spotted cowbird eggs could be an evolutionary stable strategy that minimizes recognition errors and rejection costs (de la Colina et al. 2012; Gloag et al. 2012) or it may reflect an early stage in the coevolutionary arms race between shiny cowbirds and their large-sized hosts. A second possibility is that mockingbirds reject pure white eggs in the context of nest sanitation rather than as an antiparasite or antipredatory strategy (Guigueno and Sealy 2009). Pure white cowbird eggs are so different from mockingbirds that hosts could simply treat them as strange objects in the nest in the same way as they remove faecal sacs, broken egg-shells and other non-egg objects to keep the nest clean (MCDM pers. obs.). The role of nest sanitation in the rejection of foreign eggs in mockingbirds and other large-sized hosts of the shiny cowbird deserves further investigation. Nevertheless, regardless of the evolutionary causes of host behaviour towards pure white eggs, if the predation costs observed in this study were at play in real mockingbird nests, they would reinforce this defence.

To explain the mechanisms and evolutionary forces shaping host responses to foreign eggs has been a major topic of empirical and theoretical research in avian brood parasitism. Our results suggest that the differential rejection of pure white parasite eggs by mockingbirds and other large-sized hosts of the shiny cowbird could be adaptive as an antipredatory strategy, driven by the effect of conspicuous pure white eggs in facilitating host nest predation. However, it is important to note that our study does not demonstrate a causal relationship between nest predation risk and egg rejection behaviour in mockingbirds, and the lack of data on predator identity (i.e. visual vs. olfactory-oriented predators) may obscure the interpretation of the results. More comprehensive studies that include identifying the predators involved in nest attacks and testing the effect of parasitism on nest predation while controlling for other confounding effects would be useful to further assess whether predation costs could shape host rejection decisions in the current and other host-parasite systems. Based on our findings, we propose that a broader approach that considers both the fitness costs of parasitism and the influence of nest predation on the fitness pay-offs of alternative egg rejection strategies will help to better understand the evolution and expression of antiparasite defences in host populations, especially when hosts seem to behave suboptimally against parasitism.

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Compliance with ethical standards

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

Ethical approval This article does not contain any studies with human participants or animals performed by any of the authors.

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