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HIGH RATES OF SHINY COWBIRD PARASITISM ON THE BROWN-AND-YELLOW MARSHBIRD SELECT FOR COMPLEMENTARY HOST DEFENSES

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Abstract. Hosts of brood parasites may have not developed antiparasitic defenses either because host and parasite are recently sympatric or because costs of potential defenses outweigh their benefits. We studied antiparasitic defenses of the Brown-and-yellow Marshbird (*Pseudoleistes virescens*) against the Shiny Cowbird (*Molothrus bonariensis*), evaluating recognition and aggression toward female and male Shiny Cowbirds, estimating rates of rejection of cowbird eggs of different colors, and testing the effect of the size of parasite eggs on host rejection. We also observed and video-recorded host nests to estimate hosts' nest attentiveness, frequency of cowbird visits, and interactions between marshbirds and cowbirds. When marshbirds were faced with dummy models, they attacked first and more intensively those of cowbirds (both sexes) than those of a control species. Frequency of egg ejection increased as differences between cowbird and spotted marshbird eggs increased (immaculate > intermediate > spotted), and spotted eggs were ejected more frequently when laid before than during or after the hosts' laying. Marshbirds ejected artificially added immaculate eggs independently of their size. Cowbirds visited marshbird nests only at the egg stage. Hosts' nest attention was low during egg laying and increased during incubation and after hatching, but aggressiveness against cowbirds was always high. Nest defense was inefficient, as losses due to egg pecking by cowbirds were high. Ejection of cowbird eggs avoided the cost of lower survival of marshbird nestlings in highly parasitized nests. As this defense is cost-free, this small benefit would be sufficient to select for the evolutionary maintenance of egg ejection.

Key words: *brood parasitism, cowbird nest searches, egg rejection, enemy recognition, host defenses, nest attention*.

Altas Tasas de Parasitismo de *Molothrus bonariensis* sobre *Pseudoleistes virescens* Seleccionan Defensas Complementarias del Hospedador

Resumen. Los hospedadores de los parásitos de cría no han desarrollado defensas antiparasitarias ya sea porque son simpátricos recientes o porque los costos de las defensas potenciales superan a sus beneficios. Estudiamos las defensas antiparasitarias de *Pseudoleistes virescens* en contra de *Molothrus bonariensis*. Evaluamos el reconocimiento y la agresión de este hospedador en contra de hembras y machos de *M. bonariensis*, estimamos las tasas de rechazo de los huevos de *M. bonariensis* de distinta coloración, y probamos el efecto del tamaño del huevo parásito sobre el rechazo por parte del hospedador. También observamos y filmamos nidos para estimar la atención al nido del hospedador, la frecuencia de las visitas por parte de *M. bonariensis*, y las interacciones entre *P. virescens* y *M. bonariensis.* Al enfrentarlos a modelos ficticios, los individuos de *P. virescens* atacaron primero y más intensamente a los de hembras y machos de *M. bonariensis* que a los de una especie control. La frecuencia de rechazo de huevos se incrementó al aumentar las diferencias entre los huevos parásitos y los huevos manchados del hospedador (inmaculados > intermedios > manchados), y los huevos parásitos manchados puestos antes de que el hospedador iniciara su puesta fueron rechazados más frecuentemente que aquellos puestos luego de iniciada la puesta. *P. virescens* rechazó los huevos parásitos inmaculados introducidos experimentalmente independientemente de su tamaño. *M. bonariensis* sólo visitó nidos de *P. virescens* en el estadío de huevo. La atención al nido de los hospedadores fue baja durante la puesta y aumentó durante la incubación y la cría de pichones, pero su agresividad en contra de *M. bonariensis* fue siempre alta. La defensa del nido fue ineficiente dado que las pérdidas de huevos debidas a picaduras de *M. bonariensis* fueron altas. El rechazo de los huevos de *M. bonariensis* evitó el costo de la menor supervivencia de los pichones del hospedador en nidos altamente parasitados. Dado que este mecanismo de defensa no implica costos, este pequeño beneficio sería suficiente para seleccionar por el mantenimiento evolutivo del rechazo de huevos parásitos.

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INTRODUCTION

Parasitic cowbirds (*Molothrus* spp.) lay eggs in nests of other species (hosts), leaving all remaining duties of parental care to them. Cowbird parasitism reduces host fitness in three main ways: (1) female cowbirds remove or destroy the host's eggs (Sealy 1995, Fraga 1998, Massoni and Reboreda 2002, Peer 2006), (2) cowbird eggs reduce the hatching success of the host's eggs (Hoover 2003, Astié and Reboreda 2006, Tuero et al. 2007), and (3) cowbird chicks outcompete the host's chicks for food (Marvil and Cruz 1989, Hoover 2003, Tuero et al. 2007).

In some hosts, this decrease in fitness has selected for antiparasitic defenses such as nest guarding and defense (Uyehara and Narins 1995, Sealy et al. 1998) or egg recognition and rejection (e.g., Rothstein 1975, 1976, Mason 1986a, Briskie et al. 1992, Peer and Sealy 2004). Hosts may reject by deserting the nest (Goguen and Mathews 1996, Hosoi and Rothstein 2000) or by burying (Sealy 1995, Moskát et al. 2002) or ejecting (Sealy and Neudorf 1995, Moskát et al. 2002) the parasite's egg. However, antiparasitic defenses may be costly. Nest guarding and defense is time consuming and could be used as a cue by parasites or predators to locate the host's nest (Robertson and Norman 1977, Soler et al. 1999). When hosts are smaller than the parasite, as cowbird hosts frequently are (Friedmann 1929, Carter 1986, Strausberger and Ashley 1997, De Mársico et al. 2010), nest guarding and defense can be ineffective or dangerous (Sealy et al. 1995, Sharp and Kus 2004). In addition, errors in the recognition of the parasite's eggs could result in hosts rejecting their own eggs (Davies and Brooke 1988, Marchetti 1992), so hosts may rely on several cues to distinguish their own and the parasite's eggs (Spottiswoode and Stevens 2011). Last, attempting to eject the parasite's eggs may result in a host breaking its own eggs (Davies and Brooke 1988, Rohwer et al. 1989). Therefore, the evolution of egg rejection depends on the trade-off between the costs associated with recognition and rejection of the parasitic egg and the costs that the hosts pay when they are parasitized (Sealy et al. 1998, Strausberger and Rothstein 2009). For example, if hosts learn the appearance of their own eggs, they could be misimprinted with cowbird eggs if they are parasitized before they have completed the learning process (Lotem et al. 1992, Moskát and Hauber 2007). Because cowbirds usually remove or destroy at least one of the host's eggs, their hosts usually bear other costs in addition to those exacted by the parasite's egg and chick (Carter 1986, Sealy 1992, Fraga 1998, Massoni and Reboreda 1998, 2002, Tewksbury et al. 2002). Therefore, when the costs associated with parasitism are high, hosts should evolve more than one defense mechanism (complementary, sensu Soler et al. 1999), such as nest defense and egg rejection (Davies 2011).

The Shiny Cowbird (*Molothrus bonariensis*) was historically confined to open grasslands in South America and it is assumed that the center of its distribution was the pampas, a vast plain of south-central South America (Friedmann 1929, Rothstein et al. 2002). This species parasitizes more than 250 hosts (Lowther 2012) and, as a result of habitat transformation, its distribution has expanded greatly (Cruz et al. 1985, Kluza 1998, Marín 2000, but see Rothstein and Peer 2005 for an alternative view on cowbird expansions). In the pampas Shiny Cowbird eggs are polymorphic in color, varying from completely immaculate white to heavily spotted (Fraga 1978, Mason 1986a, Mermoz and Reboreda 1999, Mahler et al. 2008). Some hosts reject all cowbird eggs (Segura and Reboreda 2012), others reject only those with a particular coloration (Fraga 1985, Mason 1986a, Mermoz and Reboreda 1994, Astié and Reboreda 2005), and others accept cowbird eggs of all morphs (Mason 1986a, Massoni and Reboreda 1998).

The Brown-and-yellow Marshbird (*Pseudoleistes virescens*) inhabits marshy areas and humid grasslands in the pampas of Argentina and neighboring areas of Uruguay and Brazil (Ridgely and Tudor 1989). Its distribution is completely contained within the Shiny Cowbird's purported historic distribution, and all previous studies have reported that the cowbird parasitizes the marshbird heavily (Hudson 1874, Gibson 1918, Orians 1980, Mermoz and Reboreda 1999). Shiny Cowbird parasitism reduces the marshbird's reproductive success notably as a result of female cowbirds puncturing marshbird eggs and reduced survival of marshbird chicks in multiply parasitized nests (Mermoz 1996, Duré Ruiz et al. 2008). Because it is very likely that this host has had a long history of sympatry with the Shiny Cowbird, it should be expected that it has evolved defenses to reduce the burden of parasitism. We found that this host ejects white Shiny Cowbird eggs and accepts the spotted ones that are more similar to its own eggs (Mermoz and Reboreda 1994). However, this defense is only partially effective in reducing the cost of parasitism, as it does not eliminate the cost of punctured eggs. In addition, because the frequency of white Shiny Cowbird eggs in the pampas region varies from 20 to 50% (Fraga 1978, Lyon 1997, Massoni and Reboreda 1998, Tuero et al. 2007), ejection eliminates only a fraction of the parasitic eggs.

In this study we experimentally tested whether marshbirds recognize adult Shiny Cowbirds of either sex as enemies and analyzed the influence of the size and spotting of the parasite's egg and the timing of parasitism on the probability of egg ejection. In addition, we observed and video-recorded nests to estimate the host's attentiveness, frequency of cowbird visits, and frequency of interactions between host and parasite. As the main cost of Shiny Cowbird parasitism on the marshbird's reproductive success is the puncture of eggs, we expected that the marshbird has developed recognition of and aggressiveness toward adult cowbirds. In addition, we expected high levels of nest attentiveness during the stages when cowbirds visit the nest more frequently. Finally, as cowbird eggs are smaller than those of the marshbird, we expected this host to reject cowbird-sized eggs in greater proportion and/or more rapidly than marshbird-sized ones.

METHODS

STUDY AREA AND GENERAL METHODS

Our study was carried out near the town of General Lavalle (36º 26′ S, 56º 25′ W) in the province of Buenos Aires, Argentina, from 1992 to 1996 and 2001 to 2003 (see below). Seasonally, it extended from late September to mid-December, encompassing all of the marshbird's breeding season. The study area is within the flooding pampas, a flat region no more than 4 m above sea level. The area included marshes and humid grasslands with scattered patches of native woodlands (mainly of *Celtis ehrenbergiana*) in the higher areas. The area is crossed by many artificial drainage canals. The climate is temperate subhumid with mean monthly temperatures of 23 ºC in January and 13 ºC in July and an average annual rainfall of 1000 mm (Soriano 1991).

Marshbirds built open cup nests 15–20 cm in diameter 0.3 to 2.0 m above ground in exotic thistles (*Cynara cardunculus*, *Carduus* spp.) and native black rushes (*Juncus acutus*), pampas grasses (*Cortaderia selloana*), and cattails (*Typha* sp.). We searched for nests along the sides of a 15-km stretch of unpaved secondary road parallel to an artificial drainage canal. Once we found a nest, we tagged it with a flagging tape at least 10 m from the nest. We checked nest contents daily or every other day during the breeding seasons of 1992–1994 and 2001–2003 and every 4–7 days during that of 1995–1996. For the analysis of rejection behavior at naturally parasitized nests, we did not use data for the breeding seasons of 2001–2003 because we experimentally removed nearly all Shiny Cowbird eggs as a part of a parallel study during these years.

Nest defenses against adult Shiny Cowbirds. We simulated visits to marshbird nests by female or male Shiny Cowbirds with dummy models in a lifelike perching position. Marshbirds respond aggressively toward individuals of its own or other species when they are very close to the nest (Mermoz and Fernández 2003). Therefore, to test the recognition of adult Shiny Cowbirds as potential enemies we compared aggressive responses toward the model of the parasite with those directed against a model of a control species, a female Yellow-winged Blackbird (*Agelasticus thilius*). Yellow-winged Blackbirds do not depredate nests, and females of this species are similar in size to female Shiny Cowbirds and nest in large colonies in nearby cattail marshes (Massoni and Reboreda 1998). We simultaneously placed the cowbird and control models 0.5 m far from the marshbird nest and 1 m apart from each other. We performed the experiments during the morning (06:00–09:00) and at nests in which the marshbird was laying, with up to three marshbird eggs. Shiny Cowbirds parasitize host nests before sunrise ("laying visits"), and during these visits they may puncture host eggs, but they also visit host nests throughout the day and during those visits they may also peck and puncture host eggs (puncture visits) (Gloag et al. 2012, this study). Besides, most parasitism and puncture visits occur while the host is laying (Mermoz and Reboreda 1999, Fiorini and Reboreda 2006, Astié and Reboreda 2006, this study). Therefore, our experiment encompassed the period when Shiny Cowbird visits are most frequent and therefore when the costs of parasitism are higher. We observed experimental nests from a distance of 20–30 m with 8 × 30 binoculars. We recorded the marshbirds' time of arrival, the number of individuals that responded, and the type and number of aggressive responses directed against each model. Observations lasted 15 min after the first marshbird returned to the nest. The experiment encompassed two treatments: one presenting a female cowbird plus the control species model, the other presenting a male cowbird plus the control species model. To avoid a positive reinforcement of the host's response (Knight and Temple 1986), we tested each nest once. We categorized four different marshbird behaviors and ranked them from 1 to 4 according to increasing degree of aggressiveness: (1) hovering: marshbirds remained in the air near the model but did not contact it, (2) leg-strikes: they flew over the model and contacted it with their legs, (3) pecking: they pecked the model, and (4) repeated pecking: one marshbird stood on the back of the model and pecked it repeatedly. As during each trial the adults expressed only one or two of these behaviors, we created an additional category a posteriori: aggression with physical contact. In this category we added the frequencies of categories 2, 3, and 4. This grouping was conservative, as it gave the same weight to all categories with physical contact.

Recognition and rejection of Shiny Cowbird eggs. We assessed whether marshbirds used egg size in addition to egg color to distinguish immaculate white eggs of the Shiny Cowbird and their own spotted eggs. We used natural marshbird eggs painted with white acrylic paint as "same size immaculate eggs" and spotted Shiny Cowbird eggs painted with white acrylic or artificial eggs made with plaster of Paris as "small size immaculate eggs." Most marshbird nests are parasitized during laying (Mermoz and Reboreda 1999). So, we added an immaculate white cowbird or marshbird egg during early laying (1 or 2 host eggs) in early morning. To minimize disturbing the hosts, we waited until the adults left nest vicinity to introduce the egg. We monitored the focal nest (Altmann 1974) continuously for 45 min after experimental parasitism. Observations were done with binoculars from a distance of 40 m. If marshbirds did not return to the nest or if they returned but did not eject the egg, we checked the nest contents 2–4 hr after experimental parasitism and every 24 hr thereafter up to a total of 5 days. To control for the effect of artificial parasitism, we experimentally parasitized 18 nests with natural spotted Shiny Cowbird eggs. Each nest was parasitized only once. The experimental protocol was identical to that with white eggs except that we made focal observations after parasitism in 5 nests only and checked nest content daily for up to 5 days. All natural eggs used in the experiments were collected from abandoned marshbird nests.

In addition, we analyzed the host's responses at naturally parasitized nests. We categorized Shiny Cowbird eggs as immaculate white (without spots), intermediate (eggs with a very light, small spots), or spotted (conspicuously so; Mason 1986a, Mermoz and Reboreda 1999).

We considered parasitic egg accepted if it remained in an attended nest for at least 5 days, rejected if we observed the host rejecting it or if the egg disappeared from the nest within 5 days after parasitism (Rothstein 1975). Female Shiny Cowbirds peck and usually puncture the host's eggs when visiting host nests (Hudson 1874, Fraga 1985, Mermoz and Reboreda 1999, Gloag et al. 2012). Although Shiny Cowbird eggs have a, eggshell thicker than that of marshbird eggs (Mermoz and Ornelas 2004), in some cases they are also punctured if the nest is parasitized repeatedly (Mermoz and Reboreda 1999). Marshbirds remove punctured eggs quickly when they return to the nest (Mermoz 1996). Furthermore, in our study area marshbirds also suffer partial depredation (Mermoz and Reboreda 1998, Svagelj et al. 2009). Consequently, we excluded from the analysis those cases where the disappearance of natural or experimental cowbird eggs coincided with parasitism or with the disappearance of host eggs, as these may not have been true ejections. We presumed that instances of partial depredation involving the Shiny Cowbird egg exclusively were minimal.

Nest attentiveness. We measured the proportion of time marshbirds were near their nest by making focal observations at different stages of the nesting cycle. All observations took place between 06:30 and 11:00. The modal size of a marshbird clutch is 4 eggs (range 3–6), and females begin incubation after laying the penultimate egg (Mermoz and Reboreda 1998, 2003). We classified focal nests in three categories: early laying (laying in progress, nest with up to 2 eggs, $n = 8$), laying–incubation (laying in progress, nest with 3–5 eggs, $n = 4$), and full incubation (clutch complete, $n = 7$). To minimize disturbance, we made all observations from a vehicle 30 m from the nest. Observations lasted 40 min, and during this period we recorded the presence of marshbirds, their distances to the nest, and their behaviors. We assigned their behaviors to four categories indicating increasing nest attentiveness: "unattended nest," when there were no adults within 20 m of the nest; "close adult," when at least one adult remained within 20 m; "vigilant adult," when at least one adult remained within 10 m and stood on a conspicuous perch not feeding; and "in the nest," when one adult was sitting in the nest. The marshbirds have helpers at the nest (Orians 1980) that can be associated with the nest from egg laying onward (Mermoz and Fernández 2003), Therefore, we expressed results as proportion of time at least one adult was performing the activity.

Frequency of Shiny Cowbird visits to marshbird nests. We video-recorded a total of 3600 min during 2001 (40 video records at 28 nests), 4944 min during 2002 (50 video records at 25 nests), and 880 min during 2003 (9 video records at 7 nests). Ninety of 99 videos were recorded during the morning (from 06:30 to 11:30), the remainder during the afternoon (from 16:00 to 19:00). We used the same categories defined for measuring nest attentiveness (laying, laying–incubation, and full incubation) plus "chick rearing" for nests with nestlings. Nests were video recorded with a camouflaged Sony Hi8 video camera from a distance of 5–10 m. Video records of focal nests lasted approximately 1 hr during laying and 2 hr at the other stages. During the recording of 71 of 90 morning videos and of all 9 afternoon videos we also made focal observations of the nest. Videos showed the frequency of nest visits by cowbirds, while focal observations allowed us to evaluate the cowbird's nest-searching behavior and marshbird–cowbird interactions. We recorded the number of cowbird searches (close passes of a cowbird within 10 m of the focal nest) and instances of a marshbird chasing a cowbird.

STATISTICAL ANALYSES

We tested whether first aggressive response was more likely to be directed toward the model of the cowbird or to that of the control species with binomial tests. We compared nest defenses of marshbirds against Shiny Cowbird adults and control species models with Wilcoxon tests. To assess whether time elapsed until ejection differed by the size parasitic eggs, we used Mann–Whitney tests. Similarly, to assess whether cowbird eggs were ejected independently of their size, color, or type of parasitism (natural vs. artificial), we used chi-squared tests of Independence or Fisher exact tests. Finally, to test whether the marshbird's nest attentiveness, the cowbird's nest searches, and the marshbird's aggressiveness against cowbirds differed by nest stage, we used Kruskal–Wallis tests (Daniel 1978, Siegel and Castellan 1988).

For continuous variables with a normal distribution (e.g., egg size), we present data as means ± SE. Counts and proportions we present as medians (quartile 1, quartile 3). Unless stated, all tests were two tailed, and level at which we accepted significance was $P < 0.05$.

RESULTS

NEST DEFENSE AGAINST THE SHINY COWBIRD

At 13 of 14 nests where we presented the models of the female cowbird and control species, marshbirds attacked one of the models. At nine nests one or two marshbirds participated in the attack; at four nests three marshbirds did so. At 12 of 13 nests the first aggressive behavior was directed toward the model of the female cowbird, while at the other it was directed toward the model of the control species (one-tailed binomial test, $P = 0.002$). Pecking behavior was directed more frequently to the model of the female cowbird than to that of the control species, while repeated pecking was always directed to the female cowbird (Wilcoxon test, $T = 0$, $n = 5$, $P = 0.05$; $T = 0$, $n = 6$, $P = 0.025$, respectively, Fig. 1A). We did not analyze other aggressive behaviors because they were expressed at fewer than five nests.

Marshbirds attacked one of the models at all eight nests where we presented the models of the male cowbird and the control species. At four nests the attacks were performed by one or two marshbirds, at four nests by three or four marshbirds. At seven nests marshbirds directed their first aggressive

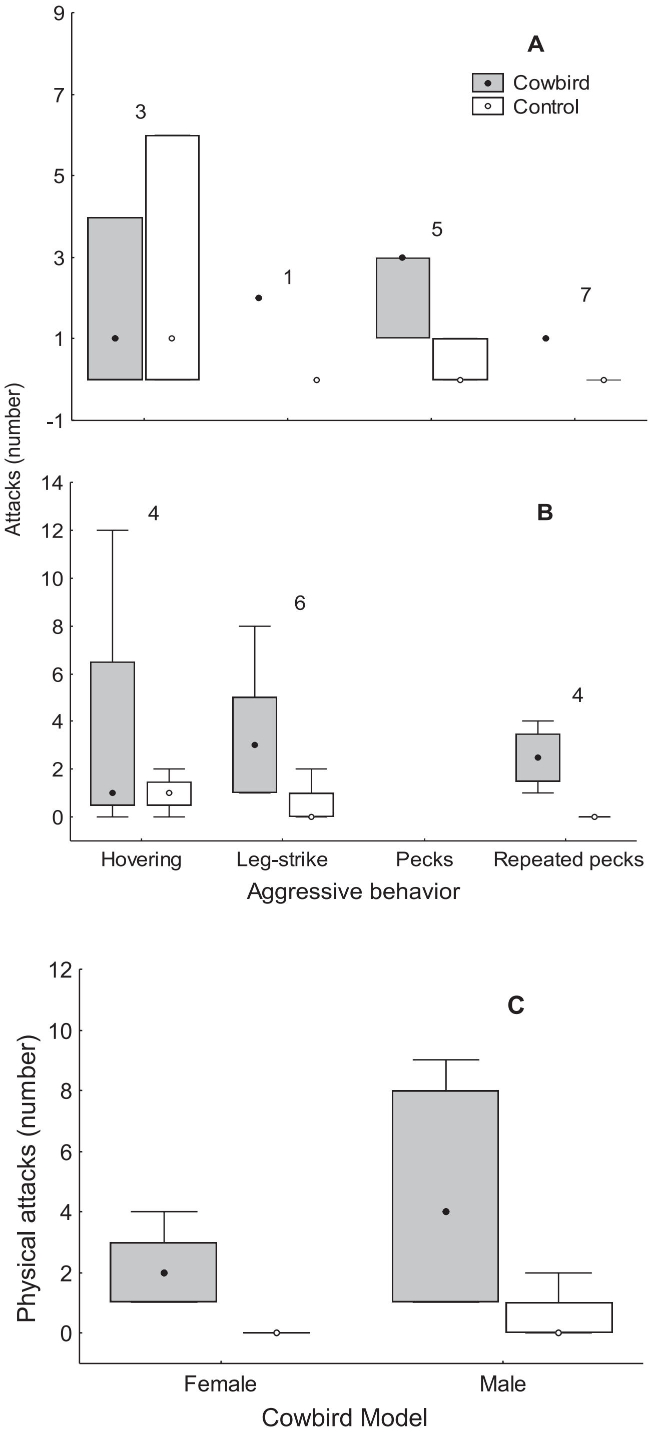

FIGURE 1. Agonistic responses of Brown-and-yellow Marshbirds to dummy models of male and female Shiny Cowbirds and female Yellow-winged Blackbirds (control species). Bars indicate number of attacks on the models during the experiment. (A) Treatment with models of female cowbird and control species (*n* = 13 nests). (B) Treatment with models of male cowbird and control species (*n* = 8 nests). (C) Total number of attacks with physical contact on models of female and male cowbirds. Points indicate the median, rectangles the interquartile 1–3. Numbers above box plots indicate the number of experimental nests at which Brown-and-yellow Marshbirds showed the agonistic response.

response toward the male cowbird; at the other, it was directed toward the control species (one-tailed binomial test, $P = 0.04$). Leg-strike behavior was directed more frequently to the model of the male cowbird than to that of the control species (Wilcoxon paired-test, $T = 1.5$, $n = 6$, $P = 0.05$, Fig. 1B). "Repeated pecks" were observed at four nests, always directed to the male cowbird (Fig. 1B). Overall, aggressive responses to cowbird models contrasted markedly with those to the control species. All aggressive responses with physical contact pooled, both models of female and male cowbirds were attacked more frequently than were those of the control species (Wilcoxon test, $T = 3.5$, $n = 13$, $P = 0.0025$, and $T = 1.5$, $n = 7$, $P = 0.025$, respectively, Fig. 1C).

RECOGNITION AND EJECTION OF SHINY COWBIRD EGGS

We parasitized seven nests with immaculate white Shiny Cowbird eggs (mean ± SE, length 2.19 ± 0.05, width 1.75 ± 0.04 cm) and six nests with marshbird eggs painted white (length: 2.67 ± 0.10, width: 1.90 ± 0.02 cm). In all cases the eggs were ejected within 24 hr after the experimental introduction. In 10 of 13 cases marshbirds returned to the nest during the 45 min of observation and in eight of these cases they ejected the experimental egg. In four cases the ejections occurred in less than 1 min, in the other four cases in 3–18 minutes. In all cases, one member of the pair grasped the experimental egg with its beak at the narrower end and left it intact at the ground 3–10 m from the nest. The other ejections took place within 4 hr (three cases) and 4–24 hr (two cases) after the experimental introduction. None of the host's eggs was damaged in association with the ejection of the parasite egg. There was no difference between the small white cowbird eggs and the larger painted white marshbird eggs in the time elapsed until egg ejection (Mann–Whitney test, $U = 25$, $P = 0.3$).

At all nests experimentally parasitized with spotted Shiny Cowbird eggs the marshbirds returned within the observation period. At only 1 of 12 nests monitored for 5 days was the experimental egg ejected (within 24 hr after the experimental introduction). In addition, in 2 of 2 nests monitored for 3 days and at 2 of 2 monitored for 2 days the experimental parasitic egg had not been ejected prior to those nests being depredated. Marshbirds ejected white eggs more often than spotted ones, and this difference was significant whether the comparison was with all white eggs or with white Shiny Cowbird eggs only (13/13 vs. 1/12, and 7/7 vs. 1/12, respectively; Fisher exact test, $P < 0.001$).

We observed 542 cases of natural Shiny Cowbird parasitism at 273 nests. Because of the high rate of depredation of marshbird nests, only 309 of these parasitic eggs could be assigned unambiguously as accepted or rejected according to our criteria. The probability of ejection of Shiny Cowbirds eggs differed by color morph. White eggs were ejected in 12 of 16 cases, intermediate eggs in 5 of 13 cases, and spotted eggs in 21 of 280 cases (chi-squared test of independence, $\chi^2 = 72$, $P < 0.0001$, Fig. 2A). The probability of ejection of spotted eggs varied according to the stage of the nest at the time of parasitism. Restricting our analysis to eggs for which we knew the exact day they were laid, spotted eggs were ejected in 10 of 17 cases when parasitism occurred one or two days before the host started to lay but in only 6 of 115 when parasitism occurred after the host started to lay (Fisher exact test, $P = 0.002$, Fig. 2B). Only cowbird eggs laid after the host started laying considered, marshbirds ejected 11 of 14 white eggs, 3 of 7 intermediate eggs, and 6 of 115 spotted eggs (chi-squared test of independence, $\chi^2 = 58$, $P < 0.001$). During laying, the probability of ejection of white eggs from naturally (11/14) or experimentally (13/13) parasitized nests did not differ (Fisher exact test, $P > 0.99$). Similarly, neither did the probability of accepting spotted eggs differ at naturally (109/115) or experimentally (11/12) parasitized nests (Fisher exact test, $P > 0.99$).

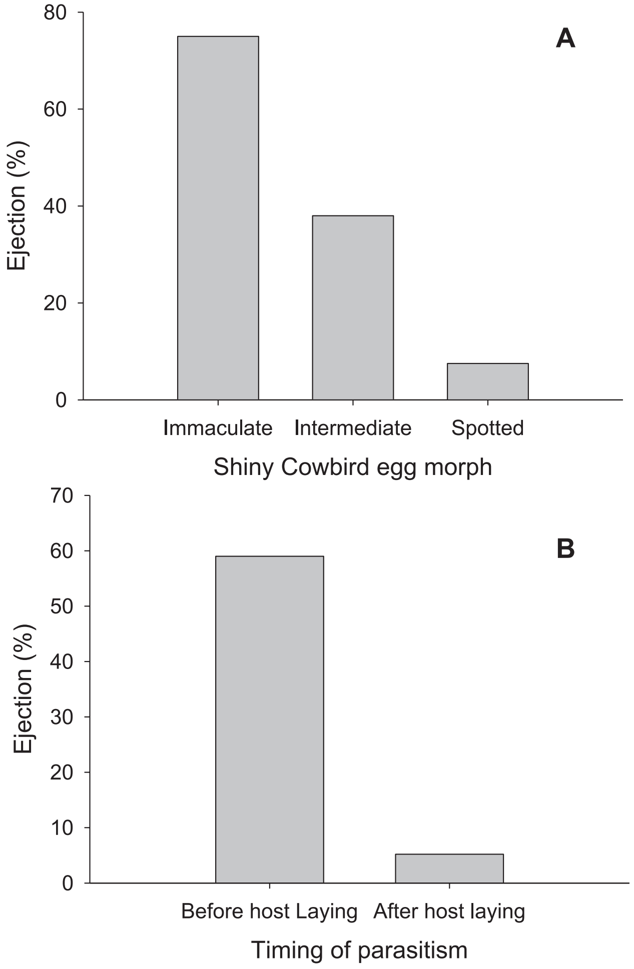

FIGURE 2. Effect of egg color and timing of parasitism on ejection behavior of Brown-and-yellow Marshbirds in response to natural parasitism by Shiny Cowbirds. (A) Percentage of ejection of Shiny Cowbird eggs by morphs ($n = 309$ eggs). (B) Percentage of ejection of spotted Shiny Cowbird eggs by the stage of the nest at which parasitism occurred ($n = 132$ eggs).

NEST ATTENTIVENESS

The proportion of time that marshbirds were in the nest was lower during early laying than during laying–incubation or full incubation (Kruskal–Wallis $H = 9.34$, $P = 0.009$ and posteriori contrasts $P < 0.05$, Fig. 3). These differences held also when we considered individuals that were in the nest or vigilant ($P = 0.006$, $H = 10.39$, posteriori contrasts $P < 0.05$). The host's nest attentiveness (i.e., marshbirds in the nest or vigilant) estimated from video records was also lower during early laying that during laying–incubation and full incubation (laying: median proportion 0.48 [quartile 1 = 0.21, quartile 3 = 0.62]; laying–incubation: 0.61 [0.44, 0.64]; incubation: 0.71 [0.46, 0.83]; chick-rearing: 0.58 [0.48, 0.78]; Kruskal–Wallis, $H = 9$, $P = 0.03$, and posteriori contrasts, $P < 0.05$).

FREQUENCY OF SHINY COWBIRD VISITS TO MARSHBIRD NESTS

We video-recorded 17 visits of female Shiny Cowbirds to eight nests during the egg stage. During these visits, we did not observe parasitism, but the cowbird inspected the nest and in most cases ($n = 14$ visits) pecked the eggs. Simultaneous focal observations showed that at one nest we recorded nine visits by four different female cowbirds; at another, two visits by two different females; at the other six nests, six visits by six females. Ten female cowbirds visited the nest in the morning and two in the evening (one nest at the laying and the other at the incubation stage). In the morning, frequency of visits by different females varied from 0.46 visits per hour during early laying (total film = 1173.5 min) and 0.063 during laying–incubation (954 min). No female cowbirds visited nests during the full incubation (1857 min) or chick-rearing (2675 min) stages.

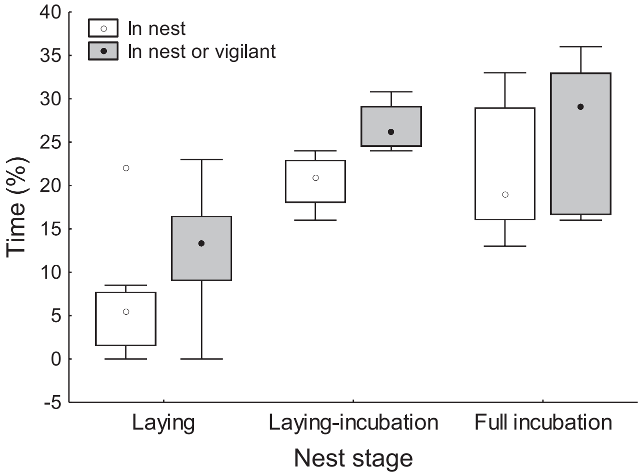

FIGURE 3. Nest attentiveness of the Brown-and-yellow Marshbird during the egg stage. Points indicate the median, rectangles the interquartile 1–3, and lines the range, excluding outliers, of the percentage of time one adult was in the nest or vigilant (within a radius of 10 m of the focal nest and not feeding) during the observation period (40 min). Laying, nests with 1 or 2 eggs; laying–incubation, nests with 3–5 eggs; full incubation, nests with complete clutches.

Focal observations of 71 nests showed that in 97 instances Shiny Cowbirds approached the focal nest within 10 m (we considered these cases of "nest searching"). Thirty-nine of these approaches were by solitary female cowbirds, 28 by pairs of females or mixed groups, 23 by males, and 7 by cowbirds that we could not sex. The frequency of cowbird searches per hour was higher at nests in laying–incubation than at nests in full incubation or with chicks (Kruskal–Wallis test, $H = 8$ and posteriori contrasts $P < 0.05$, Fig. 4). Marshbirds chased cowbirds that were up to 50 m from the nest. Chases consisted of flying toward cowbirds that were flying, standing on a perch, or feeding. During cowbirds' nest searches, the median of chases reached 100%, and there were no difference in the frequency of chases by stage of nesting (Kruskal–Wallis, $H = 1.1$, $P = 0.78$).

DISCUSSION

RECOGNITION OF THE SHINY COWBIRD

Marshbirds recognized both female and male Shiny Cowbirds as a threat, directing their first aggressive response and reacting more aggressively against them than against a control species. Female Shiny Cowbirds are the major threat to marshbirds, as they not only parasitize but also puncture host eggs when visiting a nest (Gloag et al. 2012). Therefore, by attacking female cowbirds, marshbirds may reduce the probability that they reach the nest and, consequently, the costs of these visits. In regard to males, they also approach marshbird nests together with females, and they may visit the host's nests (R. Gloag, unpubl.data) and peck and destroy its eggs (Llambías et al. 2006). Thus the marshbird's aggressive response to male Shiny Cowbirds could be either a true antiparasitic defense (i.e., it reduces the cost of parasitism) or a generalized agonistic response as a result of the frequent association of male and female Shiny Cowbirds during nest searches.

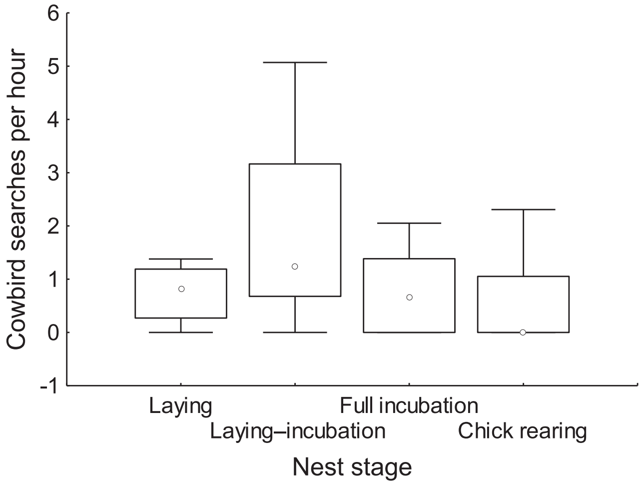

FIGURE 4. Nest-searching behavior by Shiny Cowbirds by the stage of nesting of the Brown-and-yellow Marshbird. Points indicate the median, rectangles the interquartile 1–3, and lines the range, excluding outliers, of the number of times that cowbirds were within 10 m of a marshbird nest. Laying, marshbird nests with 1 or 2 eggs; laying–incubation, nests with 3–5 eggs; full incubation, nests with complete clutches; chick-rearing, nests where at least one chick hatched.

The frequency of marshbirds chasing cowbirds did not differ by stage of the nesting cycle. It has been suggested that when hosts do not diminish their aggressiveness against a brood parasite through the nesting cycle, they are reacting as if the parasites were a nest predator (Neudorf and Sealy 1992, Sealy et al. 1998, Burhans 2001). This applies to hosts of the Common Cuckoo (*Cuculus canorus*) and Brown-headed Cowbird (*Molothrus ater*), as these parasites also behave as egg and chick predators (Elliot 1999, Granfors et al. 2001, Igl 2003, Moskát 2005). Although there is no evidence that Shiny Cowbirds kill their hosts' chicks, they may puncture and destroy eggs during incubation (although their visits at this stage are infrequent).

EJECTION OF SHINY COWBIRD EGGS

Marshbirds clearly eject Shiny Cowbird eggs. The probability of ejection was influenced by two variables: timing of parasitism and egg color. Shiny Cowbird eggs laid before the host laid were ejected more frequently than those laid during laying or incubation. This pattern has been described for hosts of the Common Cuckoo (Davies and Brooke 1988) and of other cowbirds (Sealy 1995, Peer and Bollinger 1997, Fraga 1998, but see Ortega and Cruz 1988, Hill and Sealy 1994). Once the host started laying, ejection depended on differences in color between the cowbird's and the host's eggs. Shiny Cowbird eggs of the spotted morph were ejected in <5% of cases, eggs of the intermediate morph were ejected in <40% of cases, and eggs of the white morph were ejected in 79% of cases. Experimentally added white eggs were ejected at high frequency regardless of whether they were similar in size to a Shiny Cowbird egg or a marshbird egg. Thus discrimination against white cowbird eggs was based more on egg color than on egg size. Similarly, most hosts that eject Shiny Cowbird eggs appear to use color as a cue (Mason 1986a, b, Fraga 1985, Sackmann and Reboreda 2003, Astié and Reboreda 2005, Segura and Reboreda 2012). An exception is the Rufous Hornero (*Furnarius rufus*), which ejects parasitic eggs by using egg size as a cue (Mason and Rothstein 1986). As expected by its large body mass (78.6 g; Mermoz and Reboreda 2003) and bill size (length 29.5 ± 1.5 mm; M. E. Mermoz, unpubl. data), the marshbird is a grasp-ejecter (Rohwer and Spaw 1988), and there was no cost associated with egg ejection (i.e., breakage of its own eggs). Consequently, the lower frequency of ejection of intermediate or spotted Shiny Cowbird eggs we detected was likely the result of an increase in the cost of ejection through recognition errors (Stokke et al. 2007).

EFFECTIVENESS OF THE BROWN-AND-YELLOW MARSHBIRD'S DEFENSES

A host's defenses are considered "antiparasitic" if they evolved or are maintained by selection pressures arising from brood parasitism (Rothstein 1990). This implies that, at present, any putative antiparasitic defense must reduce the negative effect that brood parasitism has on the reproductive success of the individuals practicing that defense (Sealy et al. 1998). The principal effect of Shiny Cowbird parasitism on the marshbird's reproductive success is the loss of eggs as a result of female cowbirds puncturing them (Mermoz 1996; C. Haupt and M. E. Mermoz, unpubl. data). During any visit to a nest, female Shiny Cowbirds may peck and puncture the host's eggs (Gloag et al. 2012). Therefore, the only defense mechanism that could counteract egg puncturing is to prevent the access of Shiny Cowbirds to the nest throughout both laying and incubation.

It has been suggested that nest defense is efficient only when the density of defending hosts is high (Robertson and Norman 1977, Clark and Robertson 1979). Descriptions of successful parasitism and nest visits by the Brown-headed and Bronzed (*M. aeneus*) Cowbirds include many in which aggression toward the female cowbird was fruitless (Neudorf and Sealy 1994, Granfors et al. 2001, Sharp and Kus 2004, Frisen et al. 2007). Hosts smaller than a female cowbird or similar to it in size successfully avoid parasitism in less than 15% of the cases (Ellison and Sealy 2007). Unlike those hosts, Brown-and-yellow Marshbirds are on average 75% heavier than female Shiny Cowbirds (Mermoz and Reboreda 2003). The Chalk-browed Mockingbird (*Mimus saturninus*), however, is similar in size to the Brown-and-yellow Marshbird and prevents Shiny Cowbird access to its nest in fewer than 5% of instances of attempted parasitism (Gloag et al. 2012). In contrast to those of the mockingbird, nearly 40% of marshbird nests have helpers (Orians 1980, Mermoz and Fernández 2003, Mermoz et al. 2008). Part of the ineffectiveness of the marshbird's nest defense is related to its low nest attentiveness during egg laying, which coincides with the peak of the Shiny Cowbird's nest visits (this work) and parasitism (Mermoz and Reboreda 1999). Female and male marshbirds could be constrained to remain in or near the nest during egg laying by different reasons. Female passerines increase their daily basal metabolic rate an average of 40% during egg laying because of the energy costs of egg formation (Ricklefs 1974). Consequently, for female marshbirds there is a trade-off between feeding and attending the nest. Males guard females during this period, the sexes arriving and departing from the nest together. Burgham and Picman (1989) described a similar pattern in the Yellow Warbler (*Setophaga petechia*), suggesting that cowbirds could take advantage of trade-offs that the hosts face during egg laying.

ORIGIN, COMPLEMENTARITY, AND MAINTENANCE OF NEST DEFENSE AND EGG EJECTION

It has been suggested that nest defense is the more ancestral defense against brood parasitism, as it is the most beneficial and could have evolved from predation pressure (Soler et al. 1999, Langmore and Kilner 2010). This defense is not very efficient in the marshbird, as egg losses due to egg pecking by Shiny Cowbirds are the principal cost of parasitism for this host (Mermoz 1996; C. Haupt and M. E. Mermoz. unpubl. data). A second line of defense is the rejection of parasitic eggs. Although Shiny Cowbird parasitism does not reduce the hatching success of marshbird eggs, early hatching of the cowbird decreases the survival of the host's last-hatched chicks (Mermoz 1996, Duré Ruiz et al. 2008). This small cost could favor the evolution of egg recognition and ejection as a complementary defense at a subsequent stage in the coevolution of parasite and host (Rothstein 1990, Soler et al. 1999). However, the similarity between marshbird eggs and spotted Shiny Cowbird eggs may preclude the evolution of fine-tuned discrimination in this host because of the high risk of recognition errors. Alternatively, egg ejection might have evolved prior to the Shiny Cowbird's egg-pecking behavior. Under that scenario, this defense would be favored, as it would have eliminated all costs of parasitism. Once evolved, egg rejection can be retained even if it does no longer has any benefit. Rejecter species have maintained that defense in absence of parasitism (Rothstein 2001, Lahti 2006, Hale and Briskie 2007). Moreover, egg rejection could pass down from rejecter ancestors to descendant species that are allopatric with brood parasites (Peer et al. 2007, 2011). We found that ejection of immaculate eggs implies no costs to marshbirds. Therefore the small benefit of preventing immaculate eggs from hatching is enough to favor the maintenance of egg ejection. However, other selective pressures may favor hosts rejecting immaculate eggs of the Shiny Cowbird. Experiments with the Chalk-browed Mockingbird found that the presence of immaculate white parasitic eggs, but not of spotted ones, increases the probability of depredation of their open-cup nests (M. C. De Mársico, unpubl. data). Therefore, ejection of immaculate white Shiny Cowbird eggs by Brown-and-yellow Marshbirds may have been driven by both brood parasitism and predation pressures.

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