

Antiparasitic defenses in hosts of South American cowbirds

Juan C. REBOREDA ✉, Vanina D. FIORINI, María C. DE MÁRSICO

Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales,
Universidad de Buenos Aires & IEGEBA-CONICET, Pabellón II Ciudad Universitaria, C1428EGA
Buenos Aires, Argentina

Abstract The cowbirds (*Molothrus*, Icteridae) are a monophyletic group that includes five extant brood-parasitic species. The Screaming (*M. rufoaxillaris*), Giant (*M. oryzivorus*) and Shiny (*M. bonariensis*) cowbirds range mostly in South America. Screaming and Shiny cowbirds are the ancestral and most recent species of the clade, respectively, therefore, differing in how long they have coevolved with their hosts. We present new experimental data on egg-rejection in a host of the Shiny Cowbird, the House Wren (*Troglodytes aedon*), review different lines of antiparasitic defenses in hosts of Screaming, Giant and Shiny cowbirds and assess whether hosts of different parasites differ in the type and extent of defenses. Hosts of all three parasites ejected non-mimetic eggs. Most hosts of Giant and Shiny cowbirds were grasp ejectors, whereas the main host of the Screaming Cowbird (the Baywing, *Agelaioides badius*) ejected parasitic eggs using its feet. Hosts smaller than Shiny Cowbirds neither ejected cowbird eggs nor deserted nests following parasitism. Some hosts also reacted more aggressively towards the parasite. The main host of Screaming Cowbird discriminated against non-mimetic chicks. Our results show that most hosts, regardless of the presumed evolutionary time of interaction with the parasite, have evolved some type of antiparasitic defense.

Keywords brood parasitism, cowbirds, egg rejection, *Molothrus*, nest defense

Introduction

Interspecific avian brood parasites lay their eggs in nests of other species, the hosts, which provide parental care to the parasitic eggs and chicks (Payne, 1977; Rothstein and Robinson, 1998; Davies, 2000). Brood parasitism reduces the reproductive success of hosts (Rothstein and Robinson, 1998), which select for the evolution of antiparasitic defenses (i.e., host traits that reduce the impact of parasitism, which have evolved in response to, or are currently maintained by, selection pressures arising from parasitism; Rothstein, 1990; Krüger, 2007). In turn, host defenses may select for parasite's counter-defenses and potentially create a co-evolutionary arms

race (Dawkins and Krebs, 1979; Rothstein, 1990; Davies, 2011).

Interspecific avian brood parasitism has evolved independently at least seven times in birds (Sorenson and Payne, 2002): three times among the cuckoos, once in each of the honeyguides and waterfowl, and twice among songbirds: the African brood parasitic finches and the cowbirds. The cowbirds comprise a monophyletic group (Lanyon, 1992), which is comprised of five species that vary greatly in the degree of host specificity (Ortega, 1998). The basal species of this clade, the Screaming Cowbird (*Molothrus rufoaxillaris*) separated from the lineage leading to other parasitic cowbirds 2.8–3.8 Mya (Rothstein et al., 2002) and is one of the most specialized brood parasites, using almost exclusively the Baywing (*Agelaioides badius*) (Friedmann, 1929; Fraga, 1998; De Mársico et al., 2010a). By contrast, the two most recently derived species of the clade (i.e., 0.8–1.2 Mya; Rothstein et al., 2002), the Shiny Cowbird (*M. bonariensis*) and the Brown-headed Cowbird (*M.*

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✉ Author for correspondence (Juan C. Reboreda)
E-mail: reboreda@ege.fcen.uba.ar

ater), are extreme generalist parasites at the population level, with nearly 250 host species documented for each species (Lowther, 2011) and ca. 150 host species recorded rearing cowbirds. The Giant Cowbird was the first species that split from the ancestral Screaming Cowbird (Lanyon, 1992), which involved a range expansion from southern South America to northern South America and Central America (Rothstein et al., 2002). It is known presently to parasitize 11 species, mainly caci-ques and oropendolas (Lowther, 2011).

Cowbird parasitism usually reduces the reproductive success of hosts in different ways. Brown-headed Cowbirds may remove host eggs in association with parasitism (Sealy, 1992; Payne and Payne, 1998) and Shiny and Screaming cowbirds puncture eggs when visiting host nests (Fraga, 1998; Massoni and Reboreda, 2002; Astié and Reboreda, 2006). The presence of cowbird eggs and chicks often reduces the hatchability of host's eggs (McMaster and Sealy, 1999; Trine, 2000; Hoover, 2003; Tuero et al., 2007). Cowbird chicks may outcompete host's chicks for food, lowering their growth rates and promoting brood reduction (Payne and Payne, 1998; Hoover, 2003; Tuero et al., 2007). Raising parasitic chicks can reduce the postfledging survival of host's young (Payne and Payne, 1998; Rasmussen and Sealy, 2006) or may reduce the host's future reproductive value (Rothstein and Robinson, 1998). In addition, cowbird parasitism may increase the probability of nest failure during the egg stage (Clotfelter and Yasukawa, 1999; Smith et al., 2003; De Mársico and Reboreda,

2010; but see McLaren and Sealy, 2000), or the nestling stage (Massoni and Reboreda, 1998; Dearborn, 1999).

Hosts may exhibit various lines of defense against brood parasitism that yield different benefits to their reproductive output (Table 1). As a first line of defense, hosts may increase nest attentiveness or aggressively mob cowbirds to prevent them from gaining access to the nest (Robertson and Norman, 1976; Neudorf and Sealy, 1994; Sealy et al., 1998; Burhans et al., 2001). Nest defense would allow hosts to avoid most costs of parasitism, but in practice it appears to have limited effectiveness to prevent egg-laying by cowbird females (Neudorf and Sealy, 1994; Sealy et al., 1998; Ellison and Sealy, 2007; Gloag et al., 2012) and can bear additional costs if increased host activity at the nest facilitates its detection by brood parasites or nest predators (Robertson and Norman, 1977; Smith et al., 1984; Uyehara and Narins, 1995, Gill et al., 1997; but see Clotfelter, 1998). A second and more effective line of defense is ejection of parasitic eggs (Rohwer and Spaw, 1988; Peer et al., 2000; Lorenzana and Sealy, 2001), which eliminates the costs of a decrease in host's hatching success and chick survival. Egg ejection can be nearly cost-free if hosts are able to reliably discriminate the parasitic eggs and remove them from the nest without damaging their own eggs (Lorenzana and Sealy, 2001; Rasmussen et al., 2009). This is more likely for large-billed hosts, which can remove the cowbird egg by grasping it whole between their mandibles. For small-billed hosts, which must eject cowbird eggs by piercing the shell, ejection

Table 1 Summary of main antiparasitic defenses shown by hosts, costs avoided by the host as a result of the defense, costs already paid by the host at the time the defense acted and potential costs associated with the defense

Host defense	Costs avoided by the defense	Costs incurred before the defense has acted	Costs associated with the defense
Nest defense and aggression towards the parasite	Egg losses, lower hatchability, lower chick and young survival, lower future reproductive success of parents	None	Time, increased detectability of the nest by other brood parasites or predators
Egg ejection	Lower hatchability, lower chick and young survival, lower future reproductive success of parents	Egg losses	Recognition errors, breakage of own eggs, retaliation by the parasite ("mafia" behavior)
Nest abandonment	Lower hatchability, lower chick and young survival, lower future reproductive success of parents	Egg losses	Time and energy for re-nesting, lower reproductive success with time of breeding
Chick discrimination	Lower chick and young survival, lower future reproductive success of parents	Egg losses, lower hatchability	Recognition errors
Young discrimination	Lower young survival, lower future reproductive success of parents	Egg losses, lower hatchability, lower chick survival	Recognition errors

can be costly because hosts may accidentally damage one or more of their own eggs while attempting to remove a larger and thick-shelled cowbird egg (Rothstein, 1977; Rohwer and Spaw, 1988; Røskaft et al., 1993). Alternatively, hosts may reject parasitism by abandoning the nest or burying the parasitized clutch (Sealy, 1995; Goguen and Mathews, 1996; Guigueno and Sealy, 2010). If subsequent re-nesting attempts are less likely to be parasitized, these tactics may rid hosts from parasitism, though at the expense of losing a complete clutch and delaying reproduction (Goguen and Mathews, 1996; Budnik et al., 2001; Guigueno and Sealy, 2010). However, whether the abandonment of parasitized clutches represents an evolved antiparasitic defense (Hosoi and Rothstein, 2000; Guigueno and Sealy, 2010, 2011) or a generalized response to nest disturbance (Hill and Sealy, 1994; Goguen and Mathews, 1996; Kosciuch et al., 2006) is still a matter of debate. Finally, as a last line of defense hosts may reject the parasitic young. Although by the nestling stage hosts have already paid most costs of parasitism (but see Rasmussen and Sealy, 2006), they might still save time and energy for current or future reproduction by avoiding prolonged parental care of unrelated nestlings and fledglings. Puzzlingly, discrimination and/or rejection of brood parasitic young is far less common than host defenses against adult parasites and eggs, in spite of the striking differences in appearance between parasite and host nestlings in several host-parasite systems (Grim, 2006). Among cuckoo hosts, antiparasitic defenses beyond the egg stage include the desertion of parasitized broods (Langmore et al., 2003), eviction of parasitic nestlings from the nest (Sato et al., 2010a; Tokue and Ueda, 2010), and time-limited provision of parental care (Grim, 2007).

Given the substantial costs of brood parasitism to host's fitness, it continues to be intriguing why some hosts have not evolved effective defenses against parasitic eggs or young. The evolutionary lag hypothesis states that defenses, though adaptive, may be absent because there has not been sufficient time for those behaviors to spread within the host population (Rothstein, 1975). In support of this hypothesis, some studies have revealed differences in the response to parasitism between host populations with varying degrees of sympatry with, or exposure to the parasite (Soler and Møller, 1990; Robert and Sorci, 1999; Hosoi and Rothstein, 2000). Alternatively, the equilibrium hypothesis proposes that antiparasitic defenses are not always adaptive as these may entail costs that outweigh the costs of parasitism.

Putative costs of host's defenses include recognition errors (i.e., mistakenly rejecting an own egg or chick at unparasitized nests [Davies and Brooke, 1988; Marchetti, 1992; Lotem et al., 1995; Sato et al., 2010a]), rejection errors (i.e., mistakenly rejecting an own egg or chick at parasitized nests [Davies and Brooke, 1988; Davies et al., 1996; Lorenzana and Sealy, 2001]), accidental damage to host eggs during ejection attempts (Rohwer et al., 1989; Røskaft et al., 1993; Underwood and Sealy, 2006; Antonov et al., 2009), increased risk of nest failure following the desertion of parasitized nests (Krüger, 2011), and possible retaliation by adult parasites after the rejection of parasite eggs (Hoover and Robinson, 2007). Evidence for the equilibrium hypothesis is indirect and based on studies documenting the existence of costs associated to hosts' antiparasitic defenses (Rohwer et al., 1989; Lotem et al., 1992; Antonov et al., 2009; Krüger, 2011).

The different lines of defenses by hosts of the Brown-headed Cowbird have been relatively well studied and reviewed in several works (i.e., Rothstein, 1975; Sealy et al., 1998; Hosoi and Rothstein, 2000; Peer and Sealy, 2004). On the contrary, antiparasitic defenses by hosts of South American cowbirds have been less studied and, so far, the results have not been comprehensively reviewed. In this work we present new experimental data on egg rejection in a host of the Shiny Cowbird, the House Wren (*Troglodytes aedon*), review the different lines of defense against parasitism evolved by hosts of South American cowbirds, and examine whether hosts of the most derived cowbird species differ from those of the more ancestral ones in the type and extent of defenses evolved. In addition, we discuss potential constraints and costs associated with antiparasitic behaviors that could explain why some hosts lack defenses against cowbird parasitism.

Methods

Study area

Experiments that simulated parasitism on House Wrens were conducted at "Reserva de Fauna y Flora El Destino" (35°08'S, 57°23'W) near the town of Magdalena, province of Buenos Aires, Argentina. The study site is within the Biosphere Reserve "Parque Costero del Sur" (MAB-UNESCO) and consists of semi-open grassland with patches of xeric thorny woodlands arranged in several strips, 20–100 m in width and up to several kilo-

meters in length, parallel to the edge of the “de la Plata” river. These patches are mainly dominated by native tree species such as *Celtis tala*, *Scutia buxifolia* and *Schinus longifolius*.

Study species

House Wrens nest in natural and artificial cavities. To facilitate data collection, we placed approximately 100 nest-boxes of 25 × 17 × 13 cm (height, width and depth) in trees at heights of 1.5–1.8 m and at least 20 m apart. At our study site, House Wrens breed from early October until mid-January and it is a common host of Shiny Cowbirds, with a frequency of parasitism of 60% and an intensity of 1.7 eggs per parasitized nest (Tuero et al., 2007). Wrens lay a modal clutch size of 5 eggs and 57% of parasitism occurs during host laying (Fiorini et al., 2009a).

At our study site, Shiny Cowbirds lay eggs from late September to mid-January, mainly in nests of Chalk-browed Mockingbirds (*Mimus saturninus*) (frequency of parasitism 60–70% [Fiorini et al., 2009a, Gloag et al., 2012]) and House Wrens. In eastern Argentina and neighboring parts of Uruguay and Brazil, Shiny Cowbird eggs are immaculate white or spotted, with a highly variable ground color and size of the spots (Mahler et al., 2008).

Experimental parasitism

We experimentally parasitized 42 House Wren nests with unincubated Shiny Cowbird eggs collected from active Chalk-browed Mockingbird nests. As mockingbirds eject white immaculate Shiny Cowbird eggs (see results), we created eggs of the white morph by coating spotted cowbird eggs with white acrylic paint, matching the appearance of real eggs (de la Colina et al., 2012). Similarly, to standardize the type of spots in the treatment with those on spotted eggs we painted the eggs with the same background color and spotting pattern. We conducted the experiments during host’s laying period without removing a host’s egg in conjunction with experimental parasitism because Shiny Cowbirds do not remove host eggs in association with laying. They peck (and sometimes puncture) one or more host eggs, instead, which afterwards are removed by the host (Astié and Reboreda, 2006). We checked nests daily for egg ejection and at each visit we examined host and parasite eggs for cracks or punctures and determined whether

the nest was active or abandoned. We considered a parasitic egg ejected if it was gone, and accepted if it remained in the nest for two days after its introduction. We considered that the egg was rejected by nest desertion if the nest was abandoned (i.e., no longer attended by adults) the day after the event of experimental parasitism. We conducted another 16 experiments with natural Shiny Cowbird eggs (8 with white painted spotted eggs and 8 with naturally spotted eggs) in which we left the parasite egg in the nest of House Wrens for five days and in none of these cases the egg was rejected (data not shown).

Analyses of data from other studies

We reviewed the literature on antiparasitic defenses in hosts of Screaming, Giant and Shiny cowbirds. To analyze nest defenses we considered studies in which hosts were presented simultaneously or sequentially with taxidermic models of the female parasite and a control species (i.e., Gill and Sealy, 1996; Røskaft et al., 2002). We considered three categories of nest defensive behaviors performed by either member of the pair: (1) attacks and close passes directed to the model (attack), (2) approaches towards the model (approach), and (3) moving to the nest and sitting in it (staying in the nest). We considered that any of these nest defensive behaviors was an antiparasitic defense when the level of response towards the parasite model was significantly higher than that directed towards the control model. Most of these studies used one model per species only and, therefore, they cannot discriminate whether the differential responses towards models were because they were different species or different models. Because of the limited experimental data available for hosts of the Giant Cowbird, we also included observations of nest defense from those species.

To analyze egg rejection we considered studies with experiments that simulated parasitism with at least 10 replicates. For hosts of the Shiny Cowbird, we did not include studies conducted in the Caribbean (i.e., Post et al., 1990), because sympatry between Shiny Cowbirds and hosts’ populations in this region is recent (i.e., less than 100 years; Post and Wiley, 1977a) and therefore, the time of interaction between host and parasites may not have been long enough for the evolution of antiparasitic defenses. In addition, we preferentially included studies that tested rejection of white immaculate and spotted Shiny Cowbird eggs (the only exception

was Kattan's [1998] study) because we wanted to test whether the level of mismatching in shell coloration between host and parasite eggs was a cue for egg-rejection. These studies considered that the parasite egg was accepted if it remained in the nest for at least five days after the experimental introduction, or otherwise rejected (Rothstein, 1975). In addition, the egg was considered rejected by nest desertion if the eggs were cold and adults no longer attended the nest the day after the event of experimental parasitism.

Results

Nest defense

Screaming Cowbird

De Mársico and Reboreda (2008a) tested nest defenses in Baywings by presenting dummy models of female Screaming and Shiny cowbirds, and a female White-browed Blackbird (*Sturnella superciliaris*), as a control species. Baywings attacked the Screaming Cowbird model more than the control model, and approached that model more often and spent a greater proportion of time close to it than to the control model. The rate of attacks, number of approaches and time spent close to the Shiny Cowbird model were intermediate, but did not differ significantly from those of the other two models.

Giant Cowbird

Observations at four hosts (two caciques and two oropendolas) showed that Giant Cowbirds were attacked by

hosts when approaching their nests. Robinson (1988) observed that Yellow-rumped Caciques (*Cacicus cela*) and Russet-backed Oropendolas (*Psarocolius angustifrons*) were invariably aggressive to Giant Cowbirds. Similarly, Webster (1994) reported that Giant Cowbirds that approached colonies of Montezuma Oropendolas (*P. montezuma*) were attacked and driven away from the colony, and Fraga (2011) reported attacks and chases by male and female Red-rumped Caciques (*C. haemorrhous*) on Giant Cowbirds perched near the colony.

Shiny Cowbird

Table 2 shows the results of studies that evaluated nest defenses against taxidermic models of Shiny Cowbirds: attacks and approaches towards the model and staying in the nest. Only three of the eight hosts tested in those studies, the House Wren, Chalk-browed Mockingbird and Brown-and-yellow Marshbird (*Pseudoleistes virescens*) attacked Shiny Cowbird models at a higher rate than control models. Mockingbirds also approached the Shiny Cowbird model at a higher rate than the control model.

Egg rejection

Screaming Cowbird

Baywings ejected all parasite eggs (whether Screaming Cowbird or Shiny Cowbird) laid before their own first egg and when already heavily parasitized (i.e., 3–4 parasite eggs), they ejected the entire clutch and laid a replacement clutch in the same nest (Fraga, 1998, De Mársico et al., in press). Although ejected and replace-

Table 2 Results of studies at which nests were presented with taxidermic models of parasitic and control species. Columns indicate body mass of the host, frequency of parasitism and presence (Y) or absence (N) of each type of nest defensive behavior. References: 1) De Mársico and Reboreda, 2008a; 2) Segura and Reboreda, 2012; 3) Astié and Reboreda, 2005; 4) Mermoz and Fernández, 1999; 5) Sackmann and Reboreda, 2003; 6) Fiorini et al., 2009b; 7) Mermoz et al., submitted.

Species	Body mass (g)	% Par	Stay in the nest	Approaches	Attacks	Ref.
House Wren (<i>Troglodytes aedon</i>)	12	60	N	N	Y	1
Baywing (<i>Agelaioides badius</i>)	40	13.5	N	N	N	1
Crested Cardinal (<i>Paroaria coronata</i>)	45	7	N	N	N	2
Creamy-bellied Thrush (<i>Turdus amaurochalinus</i>)	56	60	N	N	N	3
Scarlet-headed Blackbird (<i>Amblyramphus holosericeus</i>)	57	14		N	N	4
Chalk-browed Mockingbird (<i>Mimus saturninus</i>)	75	64	N	Y	Y	1, 5, 6
Rufous-bellied Thrush (<i>Turdus rufiventris</i>)	80	66	N	N	N	5
Brown-and-Yellow Marshbird (<i>Pseudoleistes virescens</i>)	80	74			Y	7

ment clutches did not differ in parasitism frequencies, the latter received significantly fewer cowbird eggs and the clutch contained more Baywing eggs (De Marsico et al., in press). Video recordings showed that Baywings consistently ejected intact eggs by kicking them out of the nest cup using their feet (De Marsico et al., in press). Regarding the two alternative hosts of Screaming Cowbirds, Brown-and-yellow Marshbird and Chopi Blackbird (*Gnorimopsar chopi*), although there are no experimental studies analyzing egg rejection by these hosts, observational data indicate that they do not eject Screaming Cowbird eggs (Mermoz and Fernandez, 2003; De Marsico et al., 2010b).

Giant Cowbird

In a controversial study, Smith (1968) reported that two hosts of the Giant Cowbird, Chestnut-headed Oropendola (*P. wagleri*) and Yellow-rumped Cacique, either ejected non-mimetic eggs (i.e., discriminators) or accepted them (i.e., non-discriminators), depending on whether they nested in colonies near nests of aggressive wasps, which protected colonies from botfly (Diptera: *Philornis*) parasitism. Smith recorded that Giant Cowbird nestlings removed subcutaneous botfly larvae from themselves and from their nest mates, therefore, benefiting the host because this in turn favored acceptance of parasitic eggs. Cunningham and Lewis (2006), in a study of egg rejection in Montezuma Oropendola, compared egg rejection rates in four experimental treatments in which a Giant Cowbird egg was added to clutches of one or two host eggs, with and without removal of one host egg. The overall frequency of rejection was 72%, regardless of whether there was another egg in the nest to which females could compare the model cowbird egg.

Shiny Cowbird

Table 3 shows the results of studies evaluating egg rejection of white immaculate and spotted Shiny Cowbird eggs in 14 hosts. Two hosts (Crested Cardinal *Paroaria coronata* and Rufous Hornero *Furnarius rufus*) ejected Shiny Cowbird eggs of the white and spotted morphs, four hosts ejected only white eggs and 7 hosts accepted all eggs of both morphs. The remaining host, the Baywing accepted white and spotted eggs, except when nests were already heavily parasitized, in which case the entire clutches were ejected. In the Crested Cardinal

the cue used to eject parasite eggs was divergence in color or a combination of color and shape (Segura and Reboreda, 2012), whereas in the Rufous Hornero egg size was the cue (they ejected eggs with a width of less than 88% that of their own eggs [Mason and Rothstein, 1986]). The selective pressure imposed by Rufous Horneros has favored, as a counterdefense, the increase in the size of parasitic eggs in areas where they are commonly parasitized by Shiny Cowbirds (Mason and Rothstein, 1986; Di Giacomo AG, Massoni V, Reboreda JC, unpublished data). The four host species that ejected white Shiny Cowbird eggs used divergence in color as a cue as all of them have spotted eggs. Of the six ejector species, five were grasp-ejectors, whereas one, the Crested Cardinal, was a puncture-ejector. Most non-ejector species weighed less than Shiny Cowbirds (i.e., < 32 g) and, except for 2 of 42 cases in House Wrens and 3 of 11 in Rufous-collared Sparrows (*Zonotrichia capensis*), they did not desert the nest in association with experimental parasitism.

Chick discrimination

Screaming Cowbird

Screaming Cowbird nestlings and fledglings look identical to those of Baywings (Fig. 1A, B) and it has been proposed that such a resemblance is an adaptation in response to host discrimination against odd-looking young (Fraga, 1998). De Marsico et al. (2012) tested this hypothesis by comparing the survival rates of young Screaming Cowbird and non-mimetic Shiny Cowbirds cross-fostered to Baywing nests. They found that Shiny Cowbirds suffered higher post-fledging mortality rates than Screaming Cowbirds due to host rejection. These authors also quantified the similarity in plumage color and begging calls between host and cowbird fledglings and found that only Screaming were indistinguishable from host young in plumage color and begging calls, supporting the hypothesis that visual and vocal similarity between Screaming Cowbirds and Baywings was a counterdefense driven by host discrimination against non-mimetic juveniles.

Shiny Cowbird

Lichtenstein (2001) reported that Shiny Cowbird chicks were fed significantly less frequently than host chicks in nests of the Rufous-bellied Thrush (*Turdus rufiventris*),

Table 3 Results of artificial parasitism experiments with white immaculate and spotted Shiny Cowbird eggs in hosts of this parasite. Columns indicate host body mass, frequency of parasitism, type of nest (C = cavity, O = open), host's egg type (S = spotted, I = white immaculate), % of eggs rejected and number of nests evaluated. References: 1) this study; 2) Kattan, 1998; 3) Mason, 1986; 4) Massoni and Reboreda, 1998; 5) De Mársico et al., 2010a; 6) Segura and Reboreda, 2012; 7) Astié and Reboreda, 2005; 8) Fraga, 1980; 9) Mermoz and Fernández, 1999; 10) Fraga, 1985; 11) Sackmann and Reboreda, 2003; 12) Mermoz et al., submitted.

Species	Body mass (g)	% Par	Nest type	Egg type	Immaculate eggs		Spotted eggs		Ref.
					% Rej.	<i>n</i>	% Rej.	<i>n</i>	
House Wren (<i>Troglodytes aedon</i>)	12	60	C	S	5	20	4.5	22	1
		94					0	8	2
Vermillion Flycatcher (<i>Pyrocephalus rubinus</i>)	14	0	O	S	0	6	0	6	3
Wren-like Rushbird (<i>Phleocryptes melanops</i>)	15	0	C	I	0	5	0	7	3
Rufous Collared Sparrow (<i>Zonotrichia capensis</i>)	20	22	O	S	33	6	20	5	3
Saffron Finch (<i>Sicalis flaveola</i>)	20	0	C	S	0	4	0	8	3
Yellow-winged Blackbird (<i>Agelaius thilius</i>)	32	26	O	S	0	6	0	8	4
Baywing (<i>Agelaioides badius</i>)	40	13.5	C	S	0	6	0	51	5
Crested Cardinal (<i>Paroaria coronata</i>)	45	7	O	S	100	18	98	51	6
Creamy-bellied Thrush (<i>Turdus amaurochalinus</i>)	56	60	O	S	61	28	19	26	7
Rufous Hornero (<i>Furnarius rufus</i>)	57	0	C	I	100	3	100	7	8
		0			80	5	83	6	3
Scarlet-headed Blackbird (<i>Amblyramphus holosericeus</i>)	57	14	O	S	0	4	0	6	9
Chalk-browed Mockingbird (<i>Mimus saturninus</i>)	75	73	O	S	100	10	18	17	10
		50			100	12	0	10	11
Rufous-bellied Thrush (<i>Turdus rufiventris</i>)	80	66	O	S	75	12	0	8	11
Brown-and-Yellow Marshbird (<i>Pseudoleistes virescens</i>)	80	74	O	S	100	7	8.3	12	12

and suggested that parents avoided feeding them. However, in her study and in another study of the same host (Sackmann and Reboreda, 2003), most Shiny Cowbird chicks survived, which indicates that even if hosts discriminate between their own and parasitic chicks, such discrimination apparently is not effective enough to preclude successful parasitism. More recently (Delhey et al., 2011), a putative case of early discrimination of cowbird nestlings was described in the Firewood-gatherer (*Anumbius anumbi*), a host known to accept non-mimetic, spotted Shiny Cowbird eggs (Mason, 1986). These authors reported that, although cowbird eggs usually hatched 4–5 days before host eggs, all parasitic nestlings died within 48 h, whereas hosts continued with their breeding attempts. They proposed that cow-

bird deaths were likely due to neglect because little food was found in stomachs of dead nestlings and this could be due to differences in visual or acoustic appearance between host and parasitic hatchlings.

Other antiparasitic defenses

De Mársico and Reboreda (2008b) reported that in Baywings the length of the prelaying period (time since nest lining was completed until the host laid its first egg) ranged from one to 19 days. Latency of Screaming Cowbird parasitism (time since nest lining was completed until laying of the first parasite egg) was 1–3 days. As a result, more than 30% of parasitic eggs were laid before hosts had started laying and were ejected.



Fig. 1 Photographs of (A) nestlings (7 days of age) and (B) fledglings (3 weeks after fledging) of Baywing (*Agelaioides badius*, host) and Screaming Cowbird (*Molothrus rufoaxillaris*, parasite). (C) Nest of House Wren (*Troglodytes aedon*) parasitized with two Shiny Cowbird (*M. bonariensis*) eggs, one white immaculate and the other spotted. (D) Nest of Chalk-browed Mockingbird (*Mimus saturninus*) parasitized with 4 Shiny Cowbird spotted eggs. Photographs were taken by (A) María C. De Mársico, (B) Cynthia Ursino, (C) Diego T. Tuero and (D) Vanina D. Fiorini.

These authors proposed that Baywings' prelaying behavior precludes an accurate synchronization of parasitism with the host's laying and, therefore, may act as an antiparasitic defense, as it decreases the incidence of successful parasitism.

Discussion

Most hosts of South American cowbirds have evolved some type of defense regardless of the presumed time of interaction with its brood parasite. Although egg ejection was the most common defense, there is evidence of defensive behavior against cowbirds at nests of hosts of the three parasites, and chick discrimination in the main host of the Screaming Cowbird. There also is indirect evidence of chick discrimination in two hosts of the Shiny Cowbird, but further studies are neces-

sary to confirm whether this behavior is truly an anti-parasitic defense. Most species that eject cowbird eggs were grasp-ejectors with only one documented case of puncture-ejection in a host of the Shiny Cowbird (the Crested Cardinal) and one case of egg ejection using the feet in the main host of the Screaming Cowbird (the Baywing). In response to host's defenses, the more ancestral Screaming Cowbird and the more derived Shiny Cowbird have evolved some type of counterdefenses, such as laying a larger egg size by Shiny Cowbirds parasitizing Rufous Horneros, and mimicking plumage color and begging calls of fledglings when Screaming Cowbirds parasitize Baywings. Thus, for most hosts analyzed the time they have coevolved with its brood parasite has been enough to favor the evolution of at least one line of defense against parasitism and in a few cases, the evolution of a reciprocal counterdefense in

the parasite. However, some hosts apparently do not exhibit antiparasitic defenses. Below, we discuss some of these cases and provide possible explanations.

Lack of egg rejection in small hosts of the Shiny Cowbird

Peer and Sealy (2004) analyzed correlates of egg rejection in hosts of the Brown-headed Cowbird using the pairwise comparative method and found that rejecter species are larger and have larger nests and bills than accepter species. They also found that species with longer periods of contact with the parasite show greater rejection behavior than those with shorter periods and proposed that this result supports evolutionary lag hypothesis (Rothstein, 1975).

Similarly, all small hosts of the Shiny Cowbird that have been tested for egg rejection accept parasite eggs and, in most cases, do not abandon parasitized nests although the degree of mismatching in size and coloration between host and parasite eggs is remarkable (Fig. 1C). One possible explanation for the absence of egg rejection in these hosts would be that there has been not enough time for those behaviors to evolve and spread within the host population (evolutionary lag hypothesis). However, at least one of the hosts (the House Wren) increases nest defensive behaviors when there is a Shiny Cowbird model close to its nest (De Mársico and Reboveda, 2008a), which suggests that it recognizes the female cowbird as a threat to its nest, thus, indicating that the time of interaction with the parasite has been long enough for the evolution of this type of antiparasitic defense. In addition, Shiny Cowbird hosts larger in body mass than the parasite have likely similar histories of sympatry than smaller hosts (i.e., they also nest in relatively open habitats and their ranges overlap the historic range of the parasite), but in most cases are egg ejectors. One explanation consistent with this pattern is that small hosts cannot puncture eject Shiny Cowbird eggs and because they have small bills they cannot grasp eject the eggs either. All cowbird species have thicker eggshells than nonparasitic icterids (Spaw and Rower, 1987; Rahn et al., 1988; Mermoz and Ornelas, 2004). The thicker eggshells of cowbirds may increase the costs of puncture-ejecting parasite eggs, forcing small-billed hosts to accept them (Rohwer and Spaw, 1988; Picman, 1989; Rohwer et al., 1989; Røskaft et al., 1993). Accordingly, the only host that puncture-ejects Shiny Cowbird eggs is the Crested Cardinal (Segura and Reboveda,

2012), which has a larger body mass than nonejector species (Table 3), but a bill not large enough to grasp eject cowbird eggs (but see Underwood and Sealy [2006] for a case of a small host in which bill size does not constrain grasp-ejection). If this interpretation is correct, we expect medium sized hosts of Shiny Cowbirds (i.e., 35–45 g) will be puncture-ejectors.

Although thicker eggshells in Shiny Cowbirds may preclude small hosts from puncturing parasite eggs, it is not clear why they do not abandon the nest or bury the parasitized clutch, as it happens in some hosts of the Brown-headed Cowbirds (Goguen and Mathews, 1996; Guigueno and Sealy, 2011). This behavior would be particularly advantageous for small hosts, as Shiny Cowbird parasitism reduces severely the hatching success of eggs and the survival of chicks (Fraga, 1978; Cruz and Andrews, 1997; Kattan, 1998; Tuero et al., 2007). Possible explanations for not abandoning the nest would be high costs of delaying reproduction and low probability to escape parasitism or depredation in future reproductive attempts (Kattan, 1998). Accordingly, Krüger (2011) found that Cape Bulbuls (*Pycnonotus capensis*), a small host of the Jacobin Cuckoo (*Clamator jacobinus*), do not eject parasitic eggs or desert the nest after being parasitized. Jacobin Cuckoos have large eggs with thick shells, making it almost impossible for Cape Bulbuls to puncture-eject them. In addition, higher predation and parasitism risks later in the season make nest desertion more costly for hosts than to accept the cuckoo egg (Krüger, 2011). Some of the small hosts of the Shiny Cowbird could have experienced a similar evolutionary scenario, which may have precluded the evolution of nest desertion. Interestingly, Kattan (1998) reported that House Wrens abandoned most nests that received more than two Shiny Cowbird eggs, but continued incubation in nests with one or two parasite eggs. This suggests that the decision of abandoning the nest by House Wrens is flexible and would depend on the relative costs of deserting the nest vs. accepting parasitism. Further studies analyzing the costs associated with abandoning the nest vs. accepting parasite eggs are necessary to understand the lack of defenses in most small hosts of Shiny Cowbirds.

Is there any benefit in accepting parasite eggs?

Most hosts larger than the Shiny Cowbird grasp-eject parasite eggs of the white morph, but accept those of the spotted morph (Fig. 1D). These hosts lay spot-

ted eggs, which suggests that they use the level of mismatching in shell coloration between their own and the parasitic eggs as a cue for egg-rejection (i.e., Peer et al., 2002; Moskát et al., 2008). In agreement with this explanation, de la Colina et al. (2012) found that the presence of spotting in Shiny Cowbird eggs significantly decreased the probability of ejection by Chalk-browed Mockingbirds, whereas increments in brightness significantly increased rejection frequencies. These authors proposed that the cognitive rules underlying mockingbird rejection can be explained by a decision-making model that predicts changes in the levels of rejection in direct relation to the number of relevant attributes shared between host and parasite eggs. However, in a study conducted in the same host, Gloag et al. (2012) reported a potential benefit of accepting parasite eggs, as these eggs dilute the probability of host egg losses in subsequent parasite attacks and may favor egg acceptance provided that parasitism does not affect host's offspring survival. Mockingbird nests with manipulated clutch compositions were more likely to escape puncture by female cowbirds as the number of cowbird eggs in the host's clutch increased. They also showed through a Monte Carlo simulation that acceptors enjoy higher egg survivorship than rejecters in host populations where multiple parasitism occurs. This "dilution effect" had been previously proposed by Sato et al. (2010b) to explain why Large-billed Gerygones (*Gerygone magnirostris*) sometimes reject parasite nestlings but not eggs. Results of Gloag et al.'s (2012) study raises the question of why do mockingbirds eject white immaculate Shiny Cowbird eggs if they can bear a net benefit to host's reproductive success. Recent experiments conducted in this host (De Mársico MC, unpublished results) indicate that the presence of white immaculate parasite eggs, but not spotted parasite eggs, increases the probability of depredation of mockingbird nests and suggest that the ejection of white immaculate Shiny Cowbird eggs in this host may have been driven by other selective pressures. Studies analyzing whether this "dilution effect" is present in multiple parasitized hosts of parasitic species that puncture or remove eggs may also help us to understand why some hosts do not eject parasite eggs.

Concluding remarks

South American cowbirds provide a very fruitful model for studying the evolution of antiparasitic defenses.

This group includes parasites with different degrees of specialization in host use, from the extreme specialist Screaming Cowbird, to the extreme generalist Shiny Cowbird. This allows us to study processes of pairwise as well as diffuse coevolution (Rothstein, 1990). Besides, Giant and Shiny cowbirds use hosts that differ markedly in body size, with some hosts much smaller and others much larger than the parasite (Ortega, 1998; Lowther, 2011). Costs of parasitism to host's fitness vary considerably according to the differences in body mass between parasites and hosts. For hosts larger than the parasite the main cost is the ruin or removal of their eggs (Sackmann and Reboreda, 2003; Astié and Reboreda, 2006), whereas hosts smaller than the parasites pay additional costs as parasitism lowers the hatchability of their eggs and survival of their chicks (Payne and Payne, 1998; Hoover, 2003; Tuero et al., 2007). Thus, different lines of antiparasitic defense are expected depending on the differences in size between hosts and parasites. Finally, the Shiny Cowbird has expanded considerably its range over the past century (Cruz et al., 1985; 1999) and during this expansion has included new hosts species that lack a history of sympatry with the parasite (Post and Wiley, 1977a, 1977b; Briskie et al., 1992). These new hosts provide a natural experiment to study the evolution of antiparasitic defenses (i.e. Cruz and Wiley, 1989; Post et al., 1990; Briskie et al., 1992; Robert and Sorci, 1999; Cruz et al., 2008). Most hosts of Giant and Shiny cowbirds remain unstudied and may provide very useful insights to unravel the evolutionary mechanisms underlying the development of host's defenses against parasitism.

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南美牛鹂宿主的反寄生防御行为

Juan Carlos REBOREDA, Vanina D. FIORINI, María C. DE MÁRSICO

(阿根廷布宜诺斯艾利斯大学生态、遗传和进化生物学系)

摘要: 牛鹂 (*Molothrus* 属, 拟鹂科) 是一个单起源的类群, 包括现存的 5 种寄生性繁殖鸟类。啸声牛鹂 (*M. rufoaxillaris*)、巨牛鹂 (*M. oryzivorus*) 和紫辉牛鹂 (*M. bonariensis*) 主要分布在南美。其中, 啸声牛鹂与紫辉牛鹂分别代表较古老和最近进化的两个支系, 因此有着各自不同的与宿主协同进化的历史。本文研究了紫辉牛鹂的宿主莺鹟 (*Troglodytes aedon*) 的拒卵行为, 同时综述了以上 3 种牛鹂的不同宿主的反寄生防御行为。3 种牛鹂的宿主均能识别和拒绝非模拟的寄生卵, 其中巨牛鹂和紫辉牛鹂的大部分宿主用嘴叨卵, 而啸声牛鹂的主要宿主栗翅牛鹂 (*Agelaioides badius*) 则用脚扔掉寄生卵。比紫辉牛鹂小的宿主, 在遭遇寄生时则不扔卵, 也不弃巢。有些宿主比另一些宿主种类对寄生的牛鹂更具有攻击行为。啸声牛鹂的宿主还能够识别非模拟的寄生雏鸟。我们的结果说明, 尽管与牛鹂协同进化的历史不同, 大部分牛鹂的宿主已经进化出不同类型的反寄生防御对策。

关键词: 巢寄生, 牛鹂, 拒卵行为, *Molothrus*, 护巢行为