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Coevolutionary arms race between a specialist brood parasite, the Screaming Cowbird, and its host, the Grayish Baywing

María C. De Mársico¹ · Cynthia A. Ursino¹ · Romina C. Scardamaglia¹ · Juan C. Reboreda¹

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Abstract

Interspecific brood parasites exploit the parental care of host species. This exploitation entails fitness costs for the hosts, which favor the evolution of antiparasitic defenses. Host defenses select for counter-defenses in the parasite, which in turn select for improved host defenses; this results in a coevolutionary arms race that may operate at each stage of the nesting cycle of the host. Most studied examples of the coevolutionary arms race in brood parasites are restricted to the egg stage, with relatively few studies showing coevolution between hosts and parasites at the nestling or fledgling stages; studies on the whole set of host defenses and potential parasite counter-defenses at each stage of the breeding cycle are still lacking. Systems in which parasites are host specialists are particularly well suited to an examination of the pairwise coevolutionary interactions before, during and after host egg-laying, and how these interactions have shaped host resistance or tolerance of parasitism. The Screaming Cowbird (*Molothrus rufoaxillaris*) is one of the most specialized brood parasites, and mainly parasitizes nests of a single host species, the Grayish Baywing (*Agelaioides badius*). Parasitism rates of Grayish Baywing nests are extremely high, with most nests parasitized several times. Several traits of this host-parasite system suggest ancient coevolutionary relationships encompassing the entire nesting cycle. In this paper we summarize the main results of a long-term study on the costs of Screaming Cowbird parasitism on the Grayish Baywing's reproductive success and how these costs have favored reciprocal adaptations and counter-adaptations at each stage of the nesting cycle.

Keywords Brood parasitism · Coevolution · Defense · Counter-defense · Host specialist · Parental care

Zusammenfassung

Koevolutionäre Rüstungsspirale zwischen einem Brutparasit, dem Rotachsel-Kuhstärkling, und seinem Host, dem Graukuhstärkling

Interspezifische Brutparasiten nutzen die Brutpflege ihrer Hosts aus. Diese Ausnutzung erzeugt Kosten bei den Hosts, die die Evolution von Verteidigungsmechanismen hervorbringt. Diese Verteidigungsmechanismen erzeugen wiederum Kontermechanismen im Parasit, die erneut verfeinerte Verteidigungsmechanismen im Host entwickeln. Dies erzeugt eine Rüstungsspirale die während der ganzen Brutphase des Hosts stattfinden kann. Die meisten Beispiele einer Rüstungsspirale in Brutparasiten findet man während der Eierphase, mit wenigen Studien die diese Koevolution in der Küken- und Jungphase zeigen. Studien, die Verteidigungs- und Kontermechanismen während der ganzen Brutphase bewerten, fehlen noch. Systeme

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in denen der Brutparasit einen einzigen Host benutzt sind besonders günstig um dieses koevolutionäre Zusammenspiel vor, während und nach der Eierlegephase zu studieren und die Resistenz oder Toleranz des Hosts dem Brutparasiten gegenüber zu evaluieren. Der Rotachsel-Kuhstarling (*Molothrus rufoaxillaris*) ist einer der spezialisiertesten Brutparasiten, der hauptsächlich die Nester einer einzigen Art parasitiert, die des Graukuhstärkings (*Agelaioides badius*). Der Anteil der parasitierten Nester im Graukuhstärking ist extrem hoch, und den Grossteil der Nester findet man mehrmals parasitiert. Mehrere Eigenschaften dieses Host-Brutparasitsystems weisen auf eine historische Koevolution, die die gesamte Brutphase umfasst. In diesem Beitrag fassen wir die bedeutendsten Ergebnisse einer langfristigen Studie zusammen, und zeigen die Kosten die ein Brutparasit, der Rotachsel-Kuhstärking, in einem Host, dem Graukuhstärking, hervorbringt und wie diese Kosten die gegenseitigen Adaptationen und Konteradaptationen während der gesamten Brutphase hervorrufen.

Introduction

Interspecific brood parasites exploit the parental care of host species. In birds, this breeding strategy has evolved independently at least seven times, and at present occurs in 109 species belonging to 27 genera and five families (Sorenson and Payne 2002; Mann 2017). Brood parasitism can decrease host reproductive success in different ways. When visiting host nests, parasitic females puncture or remove host eggs (Davies and de Brooke 1988; Soler et al. 1997; Peer 2006; Spottiswoode and Colebrook-Robjent 2007). Host eggs can also be damaged when thick-shelled parasite eggs strike them during laying (López et al. 2018). Also, the presence of parasite chicks can reduce the hatching success of host eggs (Burhans et al. 2000; Hoover 2003; Tuero et al. 2007) and increase the mortality of host nestlings either as a result of competition for food in non-evictor species (Soler and Soler 1991; Dearborn et al. 1998; Payne and Payne 1998; Hoover and Reetz 2006; Rasmussen and Sealy 2006) or because parasite chicks evict host chicks from the nest (Davies 2000; Martín-Gálvez et al. 2005) or kill host young (Morton and Farabaugh 1979; Spottiswoode and Koorevaar 2011; Wang and Kimball 2012). A parasitic chick can also increase the risk of nest depredation if its exaggerated begging behaviors attract potential predators (Dearborn 1999; De Mársico and Reboresda 2010; Ibáñez-Álamo et al. 2012; Jelínek et al. 2016). Lastly, parasitism can reduce post-fledging survival of host young or the future reproductive output of host parents (Payne and Payne 1998; Hoover and Reetz 2006; Rasmussen and Sealy 2006; Ridley and Thompson 2012).

The cost of brood parasitism on host's reproductive success generally results in the evolution of defenses, i.e., traits that reduce the impact of parasitism and have evolved in response to parasitism or are currently maintained by selection pressures due to parasitism (Rothstein 1990; Soler and Møller 1990; Briskie et al. 1992; Kilner and Langmore 2011), although there are also examples of antiparasitic defenses that have been maintained in the absence of selection pressures from parasitism (i.e., Rothstein 2001; Peer and Sealy 2004; Peer et al. 2011). Hosts have evolved different lines of defense operating at the different stages of the nesting cycle (Davies 2011). The first line of defense is

to increase nest attentiveness and aggressively mob parasitic females to discourage them from approaching the nest (Moksnes et al. 1991; Davies 2000; Røskoft et al. 2002; Gill et al. 2008). Although defenses used prior to the parasitic event, or frontline defenses (Feeney et al. 2012), allow hosts to avoid most costs of parasitism, in most cases they have limited effectiveness in preventing parasitism (Neudorf and Sealy 1994; Ellison and Sealy 2007; Gloag et al. 2013). The second line of defense is the rejection of parasite eggs either by ejection (Davies and de Brooke 1988; Sealy and Neudorf 1995; Moskát and Fuisz 1999; Soler et al. 1999), burial (Moskát and Honza 2002; Guigueno and Sealy 2010) or nest desertion (Goguen and Mathews 1996; Hosoi and Rothstein 2000). Beyond the egg stage, a third line of defense is to reject parasite young, which can be achieved through deserting parasitized broods (Langmore et al. 2003), ejecting parasitic nestlings from the nest (Sato et al. 2010; Tokue and Ueda 2010) or limiting the provision of parental care to chicks (Grim 2007; Delhey et al. 2011) or fledglings (De Mársico et al. 2012). Host defenses may select for counter-defenses in the parasites, which in turn may select for improved host defenses, and so on, thus resulting in an escalating coevolutionary arms race (Dawkins and Krebs 1979; Davies 2011; Soler 2014) at any stage of the nesting cycle (Soler 2017).

Most studied examples of the coevolutionary arms race in brood parasites are restricted to the egg stage and show that egg rejection by hosts has selected for the evolution of parasitic eggs that mimic host eggs in size or shape (Mason and Rothstein 1986; Spottiswoode et al. 2011) or in background color and spotting pattern (de Brooke and Davies 1988; Stoddard and Stevens 2010; Spottiswoode and Stevens 2012). In comparison, relatively few studies have shown coevolution between hosts and parasites at the nestling or fledgling stages. Examples of coevolution at these stages are found in the parasitic *Vidua* finches, whose chicks mimic the mouth color and patterns of their estrildid hosts (Nicolai 1964; Payne and Payne 1994; Payne 2005), and in two Australasian cuckoos, Horsfield's Bronze-cuckoo (*Chalcites basalis*) and the Little Bronze-cuckoo (*Chalcites minutillus*). Horsfield's Bronze-cuckoo chicks mimic the begging calls of its primary host, the Superb Fairy-wren (*Malurus cyaneus*), which may have

been favored by host discrimination against non-mimetic nestlings (Langmore et al. 2003). Meanwhile, Little Bronzecuckoo nestlings are striking visual mimics of its *Gerygone* spp. hosts (Langmore et al. 2011), and recent evidence suggests that Large-billed Gerygones are able to recognize and reject nestlings with experimentally altered phenotypes (Noh et al. 2018).

Because of their antagonistic interactions, brood parasites and their hosts are a model system for the study of coevolution (Rothstein 1990; Soler 2014). Over the past 30 years, a great deal of knowledge has accumulated on reciprocal adaptations driven by brood parasitism, providing new insights into coevolutionary theory and challenging early assumptions about the mechanisms underlying host rejection strategies (Rothstein 1990; Soler 2017). However, comprehensive studies on the whole set of host defenses and potential parasite's counter-defenses at each stage of the nesting cycle are still lacking for most species (Soler 2017). Systems in which a parasite is a host specialist are especially well suited to an examination of coevolutionary relationships throughout the host's nesting cycle, and how these interactions have shaped host resistance or tolerance to parasitism.

The Screaming Cowbird (*Molothrus rufoaxillaris*; hereafter “Cowbird”) is one of the most specialized brood parasites. It mainly has a single host species, the Grayish Baywing (*Agelaioides badius*; hereafter “Baywing”), over most of its geographic range (Fraga 1998; Lowther 2018). Parasitism rates of Baywing nests by Cowbird are extremely high (>90%) and most nests are parasitized several times (Mason 1980; Fraga 1998; De Mársico et al. 2010). In addition, approximately 15% of Baywing nests are also parasitized by Shiny Cowbirds (*Molothrus bonariensis*) (De Mársico et al. 2010). Several traits of the Baywing-Cowbird system suggest ancient coevolutionary relationships encompassing the entire nesting cycle. The most remarkable adaptation is probably the host-like plumage of Cowbird juveniles that lasts until they have attained nutritional independence (Hudson 1974; Fraga 1998; Ursino et al. 2012; De Mársico et al. 2012). In this paper we summarize the main results of a long-term study on the costs of Cowbird parasitism on the Baywing's reproductive success, and how these costs have favored reciprocal adaptations and counter-adaptations at each stage of the nesting cycle.

Frequency and intensity of Cowbird parasitism in Baywing nests

In our study population, parasitism rates by Cowbirds typically are >90% of Baywing nests [see De Mársico et al. (2010) for details on nest sampling]. Most nests are parasitized several times, and up to 14 Cowbird eggs have been found in a single nest (De Mársico et al. 2010). However, only half of the recorded parasitic events were synchronized

with host egg-laying. In the other half, ~31% occurred during the pre-laying stage and ~19% during the incubation and nestling stages (De Mársico and Reboreda 2008a). Baywings almost invariably reject the parasitic eggs that appear before they begin to lay, mostly by ejecting them from the nest cup (210 eggs, 91%) or, more rarely, by burying them into new lining material (17 eggs, 7%) [$n=231$ cowbird eggs laid before host laying in 116 nests (De Mársico et al. 2013)]. In turn, parasitic eggs laid after the onset of incubation often fail to hatch or hatch too late to survive competition with host nestmates. As a result, Baywings rarely fledge more than one or two parasitic nestlings per nest (De Mársico et al. 2010).

Costs imposed by Cowbird parasitism on Baywing reproductive success

Cowbird parasitism mainly reduces Baywing reproductive success in two ways. The first is the decrease in reproductive output of parasitized nests as a result of Cowbird females pecking and puncturing one or more host eggs during nest visits. Host egg survival is negatively associated with the number of Cowbird eggs laid during the egg stage. We estimated that, on average, host clutch size was reduced by 10% with each parasitic event (De Mársico et al. 2010; De Mársico and Reboreda 2014). The second way is through detrimental effects on nest survival. More than 40% of Baywing nests failed before or shortly after clutch completion due to ejection of the entire clutch or nest desertion (see De Mársico and Reboreda 2010). Models of daily nest survival rates showed that the probability that a Baywing nest survived until hatching decreased with the number of cowbird eggs laid and host egg losses (De Mársico and Reboreda 2010). Baywings were more likely to eject the entire clutch as the intensity of parasitism increased (see below), whereas repeated egg losses increased the risk of nest abandonment. Clutch ejection was strongly related to intensity of parasitism during host egg-laying, and usually occurred within 2 days of nest completion (see below). Of 153 nests monitored between 2002 and 2007, twenty-eight (18%) were deserted before the end of incubation, and we estimated that the occurrence of egg punctures increased the chances of nest desertion during host laying and incubation by roughly 14% and 58%, respectively (De Mársico and Reboreda 2010). Beyond the egg stage, we did not find any clear effect of Cowbird parasitism on the hatching success of host eggs, or on the growth and survival of host nestlings (De Mársico and Reboreda 2014). Brood reduction due to starvation or nest crowding was recorded in less than 5% of Baywing nests (De Mársico et al. 2010).

Considering the high incidence of Cowbird parasitism, the fitness costs to Baywings seem to be relatively insignificant. On average, Baywings fledged three hosts young per nest (range 1–5) and host productivity at nests that survived the entire breeding cycle was 0.78 fledglings per host egg laid (De Marsico et al. 2010). The costs are comparable to those experienced by larger hosts of parasitic cowbirds, for which egg destruction represents the major cause of reproductive losses (e.g., Clotfelter and Yasukawa 1999; Sackmann and Reboreda 2003; Astie and Reboreda 2006). There may be various explanations for this. First, Baywings have evolved several antiparasitic defenses that allow them to reduce the number of parasitic offspring they ultimately rear. Second, their eggs have thicker shells than expected by allometry (Mermoz and Ornelas 2004), which combined with host protective behaviors during cowbird visits, could reduce host egg losses during cowbird attacks. Finally, the fact that Baywings are cooperative breeders may help explain the rarity of brood reduction in their parasitized nests, even when Cowbirds typically hatch 1 or 2 days before their own offspring and attain a mass at fledging that is roughly between 15 and 40% higher than that of host nestlings [~ 42.5 – 51.6 g and ~ 36.7 g, respectively (De Marsico et al. 2010)]. This is because parents and helpers can collectively adjust their provisioning levels according to brood demands, thus relaxing competition for food within the brood (Ursino et al. 2011). Whether re-nesting following clutch ejection or nest desertion has long-term effects on Baywing fitness is yet to be determined. Nevertheless, it is reasonable to assume that such potential costs would be outweighed by the benefits of avoiding parental investment in broods of low reproductive value.

Defenses and counter-defenses before and during the egg stage

Baywing defenses

Differential aggression towards parasitic females

Mobbing of adult parasites is a widespread form of front-line defense, though this defensive behavior can vary broadly both within and among species (Neudorf and Sealy 1992; Welbergen and Davies 2009; Feeney et al. 2012). We assessed this defense in Baywings by measuring the response of breeding pairs ($n=21$) to taxidermic models of female Screaming Cowbird, female Shiny Cowbird and a harmless blackbird control [i.e., a female White-browed Blackbird (*Sturnella superciliaris*); see De Marsico and Reboreda (2008b)]. We found that Baywings responded more aggressively to Screaming Cowbird than to control models, whereas Shiny Cowbird models elicited an

intermediate response (Fig. 1). These results suggest that Baywings recognize parasitic females as specific threats and direct their aggression preferentially to the species that more frequently attack their nests (De Marsico and Reboreda 2008b).

The effectiveness of mobbing as a means of preventing parasitism is debatable (reviewed in Feeney et al. 2012; see also Gloag et al. 2013). In Baywing, this frontline defense seems to be of little help in preventing Cowbirds from laying eggs, based on the high rates of parasitism observed. However, host defensive behavior against adult parasites could serve to repel prospecting visits (see below), thus making it more difficult for parasitic females to synchronize parasitism with host laying.

Unpredictable start of egg-laying

Baywings are unusual in that they can begin egg-laying at any time between 1 day and more than 2 weeks after nest lining has been completed (De Marsico and Reboreda 2008a). The length of the pre-laying period is not strictly random in a statistical sense, but it is sufficiently unpredictable to

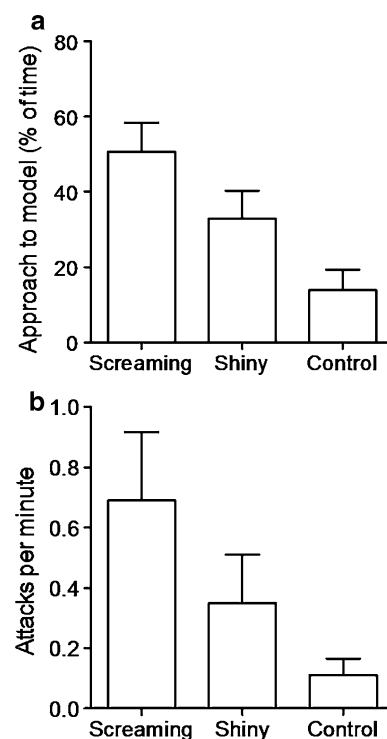


Fig. 1 Agonistic responses of breeding pairs of Grayish Baywings ($n=21$; hereafter “Baywing”) to taxidermic models of female Screaming Cowbird (hereafter “Cowbird”; Screaming), female Shiny Cowbird (Shiny) and a harmless control species (female White-browed Blackbird; Control). **a** Approach to the models (proportion of time that at least one member of the pair was perched at less than 0.5 m from the models). **b** Attack rate (frequency of attacks and close passes directed at the models) Redrawn from De Marsico and Reboreda (2008b)

make synchronization of parasitism difficult (De Marsico and Reboreda 2008a). The latency to the first event of Cowbird parasitism after nest lining has been completed does not match the length of the pre-laying period. In nearly half of the nests in our sample (see De Marsico and Reboreda 2008a), the first Cowbird egg appeared within 1–3 days after the nest was ready, but only 20% of Baywings began to lay in the same period. This suggests that parasitic females cannot anticipate the beginning of host laying from cues associated with nest appearance or host behavior. Given that Baywings reject nearly all parasitic eggs laid prematurely, delaying egg-laying in such an unpredictable way allows them to reduce the number of Cowbird eggs that they ultimately incubate, thus this behavior serves as an antiparasitic defense. Further support for this idea comes from the observation that Cowbirds synchronize parasitism significantly better in nests of two alternative hosts, the Brown-and-yellow Marshbird (*Pseudoleistes virescens*) (Mermoz and Fernandez 2003) and the Chopi Blackbird (*Gnorimopsar chopi*) (Di Giacomo and Reboreda 2014). Shiny Cowbird females also often parasitize Baywing nests in advance of host laying, but they seldom do this in nests of alternative hosts (De Marsico and Reboreda 2008a; Mermoz and Fernandez 2003; Di Giacomo and Reboreda 2014).

Egg protection against cowbird attacks

As mentioned above, egg puncturing by cowbird females during nest visits is one of the major reproductive costs of parasitism that Baywings face (Fraga 1983; De Marsico and Reboreda 2014). However, the incidence of egg punctures at Baywing nests appears rather low, especially when considering that most nests are visited several times by the same or different Cowbird females (Fraga 1998; De Marsico and Reboreda 2014; Scardamaglia et al. 2017). In our study population, only 22% of Baywing clutches that lasted until the end of incubation had one or more host eggs punctured (De Marsico and Reboreda 2014). Experiments in captivity (Llambas et al. 2006; Cossa et al. 2017) and video recordings made in Baywing nests (De Marsico et al. 2013) showed that Cowbird females regularly engaged in pecking and puncturing behavior when presented with model or natural eggs. The costs resulting from egg puncture may have favored protective behaviors that reduce egg losses during cowbird visits. Video recordings of nests showed that Baywing females were inside the nest, or immediately rushed to the nest, sitting tight in the nest cup, for 68% of the Cowbird visits recorded (Masok et al., unpublished data). This sitting-tight behavior does not deter parasitism because cowbird females managed to lay their eggs in 12 out of 13 of these visits, but it could serve to block the access of cowbird females to host eggs (De Marsico et al. 2013; Masok et al., unpublished data). This idea needs further investigation. In

addition, the thick-shelled eggs of Baywings (Mermoz and Ornelas 2004) may also contribute to reduce egg losses, since they require increased effort on the part of Cowbird females to puncture them.

Ejection of parasite eggs

There are two instances in which Baywings reject parasitic eggs. One is during the pre-laying stage; the other is upon finishing egg-laying, when they typically eject the entire clutch if it has been heavily parasitized. Experimental parasitism of Baywing nests with fresh, non-mimetic Shiny Cowbird eggs showed that hosts do not reject individual non-mimetic eggs once they began to lay, regardless of their differences in size, coloration and spotting patterns [$n = 46$ nests (De Marsico and Reboreda 2008a, b)]. This is in agreement with previous studies indicating the lack of host rejection behavior towards natural or model cowbird eggs after clutch initiation (Mason 1986; Fraga 1998).

We observed entire clutch ejection in nearly one-third of the nests in which hosts completed laying, and its occurrence was positively correlated with the number of Cowbird eggs deposited during host laying (Fig. 2). When parasitism exceeded a certain threshold of eggs, Baywings stopped incubation and ejected all eggs present in the clutch (De Marsico et al. 2013). In nearly all cases of clutch ejection, hosts laid a replacement clutch in the same nest. Replacement clutches received fewer Cowbird eggs than ejected ones, and they had more host eggs remaining because of reduced egg puncturing (De Marsico et al. 2013). Based on our estimations, pre-laying and clutch rejections combined allowed Baywings to reduce by 75% the effective intensity of parasitism (i.e., the number of Cowbird eggs they incubate), from a median of four to one Cowbird egg per nest.

Interestingly, eggs were mostly rejected intact, although Baywing bill morphology precludes grasping Cowbird eggs

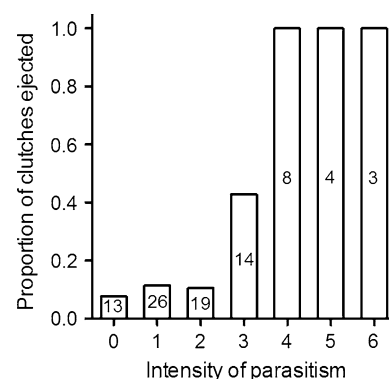


Fig. 2 Proportion of Baywing nests of which the entire clutch was ejected as a function of the intensity of Cowbird parasitism during the host laying period. Numbers inside bars indicate Baywing nests. Redrawn from De Marsico et al. (2013)

whole. Therefore, the question arose: how do they do this? We placed microcameras inside Baywing nests to record host rejection behavior. Video recordings revealed that Baywings reject eggs one by one by rolling them out of the nest using their feet (De Mársico et al. 2013). This unique “kick-ejection” accounted for ~90% of all rejections before host laying, and for all cases of entire clutch rejection. Another method of egg rejection exhibited during the pre-laying period was to bury parasitic eggs under new lining material

(De Mársico et al. 2013), as reported previously for other cowbird hosts (Sealy 1992).

Baywing behavior towards parasite eggs provides an example of rejection without discrimination (*sensu* Grim et al. 2003), in which host defense is “all-or-nothing” and relies on indirect cues such as timing of parasitism and total clutch volume or surface. Cowbird eggs are similar to Baywings’ in shape, size, coloration and spotting (Fraga 1983; Fig. 3a, b), so they can be difficult to distinguish in the

Fig. 3 **a** Unparasitized Baywing clutch and **b** Baywing clutch (eggs 1–4) multi-parasitized by Cowbirds (eggs 5–8). **c** Baywing and Cowbird nestlings 2–3 days of age identified by bill and skin color. Sub-terminal dark tip of the bill is present only in Baywings. Skin color is more orange in Baywings (chicks 1 and 2) and pink in Cowbirds (chick 3). **d** Baywing (1) and Cowbird (2) nestlings at 6–7 days of age, indistinguishable by the human eye. **e** Baywing juvenile, **f** Cowbird juveniles at two different stages of their first molt, **g** Baywing adult, **h** Cowbird adult Credits: **a, c** Cynthia Ursino; **b, d** María Cecilia De Mársico; **e, g** Alec Earnshaw; **f** José Larenti (Macaulay Library ML144840981); and **h** Iván Eroles (Macaulay Library ML136067711) (color figure online)



dark interior of Baywing nests. It is possible that the costs incurred by recognition errors have constrained the evolution of egg discrimination and ejection, thereby favoring alternative, recognition-free strategies.

Screaming Cowbird counter-defenses

High rate of nest visits

One form of counter-defence against an unpredictable start of laying and clutch ejection is for Cowbirds to visit Baywing nests repeatedly before and during host laying. We recorded the visits of radio-tagged Cowbird females to Baywing nests using proximity data loggers placed at host nests during pre-laying, laying and early incubation (see Scardamaglia et al. 2017). Females visited Baywing nests numerous times per day from several days before the host started laying until the onset of incubation (Fig. 4). These prospecting non-parasitic visits occurred throughout the day and even after the nest was parasitized (Scardamaglia et al. 2017).

Timing of parasitism

Cowbirds parasitize host nests in a very short time window from 55 to 40 min before sunrise (Scardamaglia et al. 2017). Pre-sunrise, very low light conditions may help parasites to approach Baywing nests undetected, at least until they are very close to or inside the nest. Parasitism visits are usually very short in length; Cowbird females take an average of 10 ± 3 s to lay an egg [range 5–16 s, $n=20$ parasitic events (Masok et al., unpublished data)]. These short visits may also help to reduce the probability of the Cowbird being detected when the host is not in the nest.

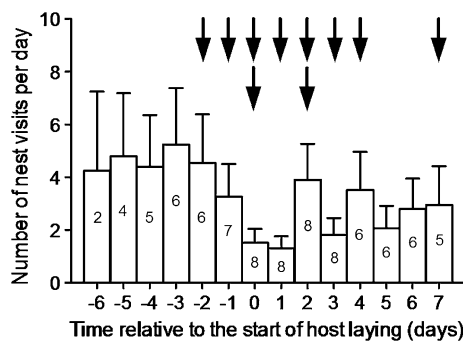


Fig. 4 Number of prospecting visits of radio-tagged Cowbird females ($n=8$) to Baywing nests. Visits were recorded using proximity data loggers placed at Baywing nests. *x-axis* Time relative to the start of host laying (day 0); numbers inside bars indicate the number of different females visiting Baywing nests on each day. Arrows represent parasitic events

Social monogamy

Long-lasting pair bonds have been reported in Cowbirds (Mason 1987; Scardamaglia and Reboresda 2014; Scardamaglia et al. 2018). Studies with radio-tagged females and males that were caught together showed that they remained associated 88% of the time during the morning (range 74–100%) and 63% of the time during the afternoon (range 42–83%) (Scardamaglia and Reboresda 2014). These pairs maintained their association during the night [89% of the nights in the same roost, range 75–100% (Scardamaglia et al. 2018)]. In addition, using proximity data loggers placed at Baywing nests, we monitored prospecting visits throughout the day. Males and females that were caught together also visited nests together in 95% of cases (Scardamaglia et al., unpublished data).

The presence of social monogamy in a brood parasite is striking, since in the absence of parental care a promiscuous mating system and lack of pair bonds are expected (Hauber and Dearborn 2003). These latter authors suggested that social monogamy in brood parasites could have evolved in association with male–female cooperative behaviors (cooperative nest-searching hypothesis). According to this hypothesis, males may provide females with services such as help in nest-searching and relocation or facilitation of access to nests by distracting hosts. A competing, but non-mutually exclusive hypothesis, proposes that males do best by defending exclusive access to a single female, and that social monogamy is the result of male mate-guarding behavior (Hauber and Dearborn 2003). In conclusion, as Feeney and Riehl (2019) pointed out, cooperation may be a by-product of pre-existing pair bonding between a male and female, rather than the factor shaping the pair bond.

Defenses and counter-defenses during the nestling stage

Baywing defenses

Discrimination of mimetic from non-mimetic begging calls

There is some evidence that Baywings are able to discriminate between begging calls of their own chicks and those of Screaming Cowbird chicks or non-mimetic Shiny Cowbird chicks. Playback experiments conducted at Baywing nests on day 6 post-hatching showed that begging calls of host and Cowbird chicks were equally effective in stimulating parental provisioning, but non-mimetic begging calls of Shiny Cowbird chicks failed to increase nest-provisioning rates compared to the control (no broadcast) treatment (Ursino et al. 2018; Fig. 5). However, Shiny Cowbird nestlings cross-fostered in Baywing nests grew normally and fledged

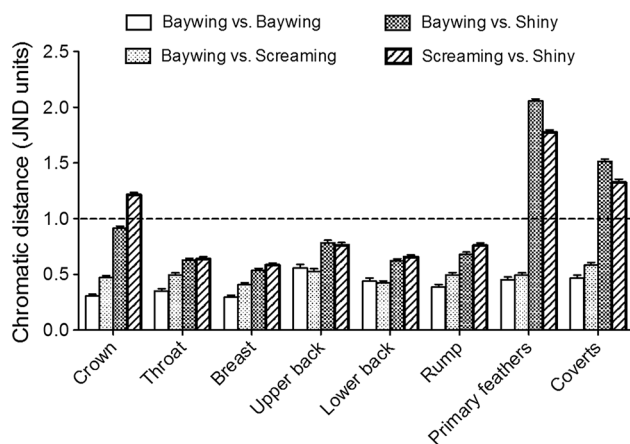


Fig. 5 Degree of similarity in plumage coloration among fledglings (13–20 days of age) of Screaming Cowbirds ($n=14$), Shiny Cowbirds ($n=25$) and Baywings ($n=15$). Plumage coloration was measured by reflectance spectrometry on eight parts of the body. Bars indicate the chromatic distances (mean \pm se) expressed as just noticeable differences (jnds) among Baywing fledglings, between fledglings of Baywings and Screaming Cowbirds, Baywings and Shiny Cowbirds, and Screaming Cowbirds and Shiny Cowbirds. Dashed line indicates the discrimination threshold of 1 jnd Redrawn from De Mársico et al. (2012)

at similar rates to host or Cowbird nestlings (De Mársico et al. 2010). Thus, despite their ability to recognize parasite offspring, and their observed preference for the begging calls of their own offspring, Baywing parents accept and feed Shiny Cowbird nestlings to the same extent as their own young. This could be a case of recognition without rejection, similar to that reported during the egg stage in Great Reed Warblers (*Acrocephalus arundinaceus*) parasitized by Common Cuckoo (*Cuculus canorus*) (Moskát and Hauber 2007), and in Blackbird (*Turdus merula*) parasitized by Great Spotted Cuckoo (*Clamator glandarius*) (Soler et al. 2017). How Baywings integrate vocal and visual cues in nestling recognition is not yet known. Nevertheless, considering the dim light conditions of Baywing nests, it is possible that the costs of mistakenly rejecting their own nestlings are high enough to constrain the evolution of effective antiparasitic defenses at this stage.

Screaming Cowbird counter-defenses

Vocal and visual mimicry

Rojas Ripari et al. (2019a, b) studied the development of begging calls in Cowbirds that were reared in Baywing nests or experimentally cross-fostered in nests of a non-host species [Chalk-browed Mockingbird (*Mimus saturninus*)]. Their study showed that begging call structure of Cowbird nestlings was mainly innate because cross-fostered nestlings

developed begging calls that were overall similar to those of Baywing nestlings and Baywing-reared Cowbirds. A playback experiment further demonstrated that adult Baywings responded similarly to begging calls of cross-fostered and Baywing-reared Cowbirds, suggesting that both call types were functionally equivalent from the host's perspective, despite minor differences in acoustic structure (Fig. 6). In addition, begging displays of Cowbird nestlings are more intense than those of Baywings with the same degree of need (Lichtenstein 2001; De Mársico et al. 2012), which may allow them to compete more effectively for parental feeding with host young.

Nestling Cowbirds also look similar to those of Baywing (Fig. 3c). Before 5 days of age, host and parasitic nestlings can be identified by subtle differences in bill and skin color (Fraga 1979). After 5 days of age, visual identification becomes virtually impossible (Fraga 1979, Fig. 3d). The visual resemblance between parasite and host nestlings plays no apparent role before fledging, since Baywings do not discriminate against nestlings that are visually dissimilar from their own. Cross-fostering experiments showed that Baywings never rejected non-mimetic Shiny Cowbird nestlings, regardless of whether they were reared in mixed broods with host chicks [$n=12$ of 12 nestlings accepted (De Mársico et al. 2012)] or reared alone

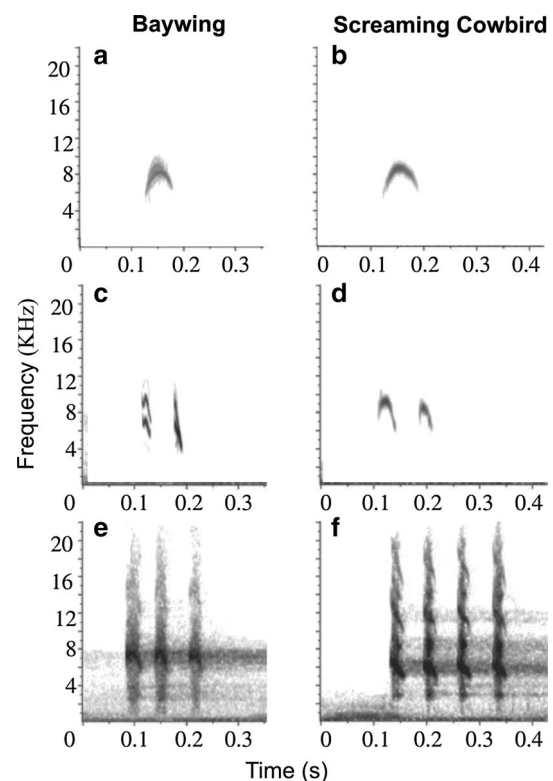


Fig. 6 Representative spectrograms of the begging calls of Baywings (a, c, e) and Cowbirds (b, d, f) at 4–5 (a, b), 8–9 (c, d), and 14–16 (e, f) days of age

[$n=9$ of 9 nestlings accepted (Rojas Ripari et al. 2019a). This suggests that visual (and vocal) mimicry of Cowbird chicks may have evolved as a result of Baywing discrimination during the fledgling stage (see below).

Defenses and counter-defenses during the fledgling stage

Baywing defenses

Discrimination of non-mimetic young

As soon as fledglings left the nest, Baywings stopped providing parental care to non-mimetic Shiny Cowbirds but continued to provision Screaming Cowbird and their own young for at least 2 more weeks (De Mársico et al. 2012). We collected data on fledgling survival from six breeding groups with color-banded Shiny Cowbird fledglings and found that all but one of these fledglings died or disappeared within a week after nest departure. The exception was a fledgling that was fed by individuals other than their foster parents. In all other cases, Shiny Cowbird fledglings were seen begging repeatedly alone on the tops of trees or on the ground, without attracting Baywing adults that were nearby, before they disappeared (De Mársico et al. 2012). Consistent with this finding, experimental broadcasts of fledgling begging calls near active Baywing nests with old nestlings demonstrated that begging calls of Shiny Cowbirds were ignored, whereas calls of Screaming Cowbird were equally or even more effective than those of Baywings in eliciting approach by host parents and helpers (Lama et al., unpublished data).

Recent experiments suggest that discrimination against non-mimetic Shiny Cowbird fledglings is not fixed. Instead, it depends on whether the fledglings are reared alongside host young or not (see also Soler et al. 2014). Shiny Cowbird fledglings that were reared alone in Baywing nests received parental care from adult Baywings after leaving the nest, and survived equally well as host young that fledged from singleton broods (Rojas Ripari et al. 2019a).

It is puzzling why Baywings have evolved fledgling discrimination. One possibility is that hosts save energy for future reproduction by avoiding parental investment in unrelated young. Hosts may also reduce further reproductive losses by reducing the competition between their own and parasitic fledglings, which has been pointed out as a late cost of parasitism (Rasmussen and Sealy 2006). Clearly, more data are needed to assess the selective advantages of this last line of defense against brood parasitism and the cognitive mechanisms underlying fledgling recognition by Baywings.

Screaming Cowbird counter-defenses

Vocal and visual mimicry

The vocal similarity and visual resemblance of Cowbird and Baywing fledglings are perhaps the most remarkable characteristics of this host-parasite system (Hudson 1874; Fraga 1998). Using standardized recordings and discriminant function analyses, De Mársico et al. (2012) showed that begging calls of Cowbird fledglings match the acoustic structure of those of host fledglings (Fig. 6). Also, a detailed study of the juvenile plumage coloration of Baywings, Screaming Cowbirds and Shiny Cowbirds using reflectance spectrophotometry and models of visual discrimination in birds to quantify the degree of similarity showed that fledglings of Screaming Cowbirds, but not those of Shiny Cowbird, are indistinguishable from those of Baywings from the host's perspective (De Mársico et al. 2012, Fig. 7).

Host discrimination of non-mimetic fledglings is probably the selective force that has led to the evolution of vocal and visual mimicry in Cowbirds as a counter-defense that secures them parental care after leaving the nest. Cowbirds begin their first molt, which “reveals” their identity, around 25 days after fledging (Fig. 3e–h; Ursino et al. 2012). Interestingly, they start molting underwing coverts, then feathers of the breast and the rest of the body, and lastly the tail feathers and external coverts. This molting sequence differs from that of most birds and is likely an adaptation to trick Baywing hosts for as long as possible. Underwing coverts are not easy to see, thus this would allow Cowbird young to conceal their plumage as it turns black until they attain nutritional independence. It is still not known at which point of the molting sequence Baywings begin to discriminate between Screaming Cowbird juveniles and their own, and

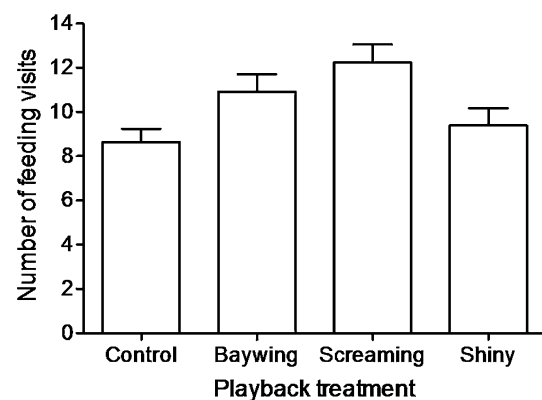


Fig. 7 Number of feeding visits by Baywing parents to nests with 6-day-old chicks ($n=25$). During each visit, the brood begging calls were supplemented with the broadcast of one additional Baywing, Cowbird (Screaming) or Shiny Cowbird (Shiny) nestling. Control treatment corresponded to no broadcast Redrawn from Ursino et al. (2018)

Table 1 Summary of Baywing defenses and Cowbird counter-defenses at the different stages of the nesting cycle

Nest stage	Baywing defenses	Cowbird counter-defenses
Before and during the egg stage	Unpredictable start of egg-laying Aggression towards parasite females Egg protection against Cowbird attacks (sitting tight) Ejection of entire highly parasitized clutches	High rate of nest visits Timing of parasitism Social monogamy (male–female cooperation?)
During the nestling stage	Discrimination of non-mimetic begging calls	Vocal and visual mimicry of nestlings?
During the fledgling stage	Discrimination of non-mimetic begging calls and plumage coloration of fledglings	Visual and vocal mimicry of fledglings

parasitic juveniles definitively leave their foster parents to join flocks of conspecifics.

Conclusion

The host-specialist Cowbird and its main host, the Baywing, provide an excellent system for the study of coevolutionary interactions throughout the nesting cycle. In Table 1, we summarize Baywing defenses and Cowbird counter-defenses at the different stages of the nesting cycle. Before the egg stage, the host's quite unpredictable egg-laying behavior and aggression towards parasitic Cowbird females that approach the nest make it difficult for the latter to synchronize parasitism with egg-laying. After egg-laying, the ejection of highly parasitized clutches allows Baywings to further reduce the number of parasitic offspring they care for. These host defenses have presumably shaped nest-prospecting behavior by Cowbird females, as they have to frequently visit Baywing nests to gather information about nest status and to detect new opportunities for parasitism. The arms race between Cowbirds and Baywings has escalated as far as the fledgling stage, but by then it is clear that host defenses have been overcome. The accurate mimicry of host nestlings and fledglings in terms of vocalizations and visual appearance of Cowbirds completely counteracts the host discrimination against foreign young. Why Baywings have evolved the ability to discriminate parasitic young remains puzzling and additional studies are needed to determine post-fledging costs of brood parasitism and the mechanisms underlying host discrimination.

This review highlights some future avenues of research that may help us to better understand the long-term outcomes of host-parasite coevolution. For instance, studies focusing on host frontline defenses will be useful in assessing how susceptibility to parasitism (and thus selective pressure on hosts) varies within a host population, and may reveal additional adaptations that minimize the negative impact of parasitism (e.g., sitting-tight behavior). Baywings and Cowbirds also provide an interesting system to examine if social monogamy in brood parasites has evolved as a result of male–female cooperative behaviors and the

interplay between cooperative breeding and brood parasitism, and in particular if the presence of helpers at the nest results in increased tolerance to parasitism.

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