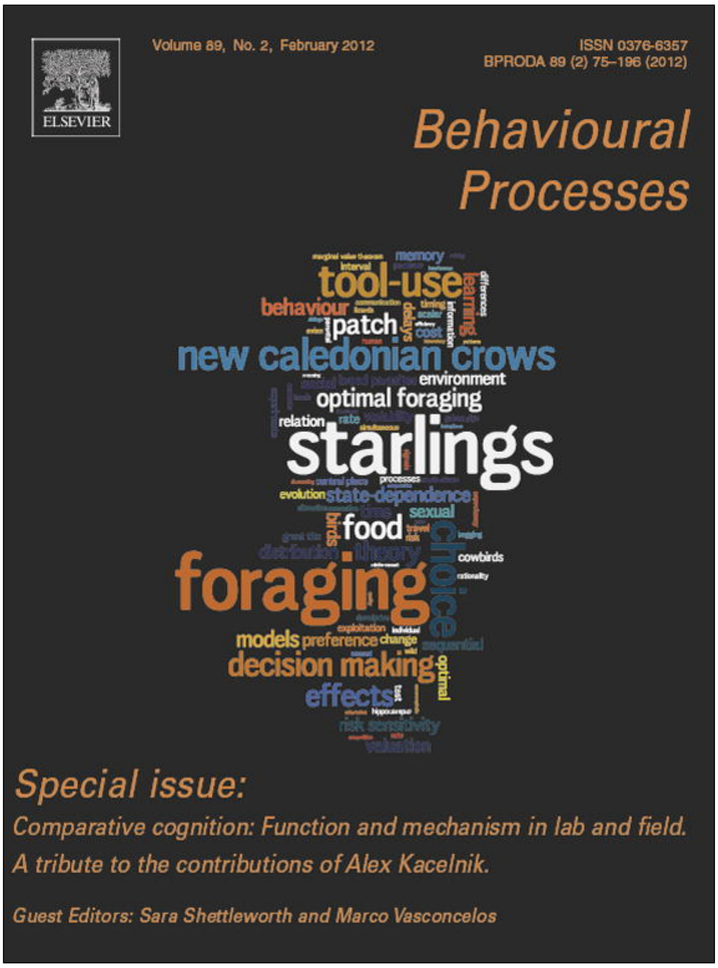

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Do shiny cowbird females adjust egg pecking behavior according to the level of competition their chicks face in host nests?

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ABSTRACT

Interspecific brood parasites, like the shiny cowbird (*Molothrus bonariensis*), lay eggs in nests of other species. Shiny cowbird females peck and puncture eggs when they parasitize host nests. This behavior increases the survival of cowbird chicks when they have to compete for food with larger nestmates. However, cowbird chicks may benefit from smaller nestmates as they increase food provisioning by parents and the cowbird chicks secure most extra provisioning. We investigated whether egg-pecking behavior by female shiny cowbirds might be adjusted to the competition that their chicks face in host nests. We found that more host eggs are destroyed per cowbird egg laid in a larger-bodied host (chalk-browed mockingbird, *Mimus saturninus*, 70–75 g) than a smaller-bodied host (house wrens, *Troglodytes aedon*, 12–13 g). We also tested egg-pecking preferences in choice experiments with female cowbirds in captivity and found cowbirds presented with eggs in artificial nests pecked first and more frequently, and punctured more frequently the larger egg when this was a host egg, but not when this was a cowbird egg. Our results are partially consistent with the hypothesis that shiny cowbird females adaptively adjust their egg pecking behavior according to the competition that their chicks face in host nests.

1. Introduction

Interspecific brood parasites lay eggs in nests of other species, the hosts, which provide parental care for their progeny. This breeding strategy has evolved independently at least seven times in birds (Sorenson and Payne, 2002) and currently it is present in approximately 1% of all bird species. One group in which brood parasitism has evolved is the New World cowbirds (genus *Molothrus*, family Icteridae). The cowbirds include five species that show marked differences in the degree of specialization in host use, from host specialists like the screaming cowbird (*Molothrus rufoaxillaris*), to host generalists like the brown-headed (*Molothrus ater*) and the shiny (*Molothrus bonariensis*) cowbird (Ortega, 1998). The latter species is an extreme generalist whose eggs have been found in nests of more than 250 species (Lowther, 2011). Nearly 100 of these species have successfully reared cowbird young (Lowther, 2011) and they possess a wide range of body masses, some of them much smaller than the parasite (i.e. 10 vs. 45 g) and others much bigger (i.e. 80 vs. 45 g) (De Mársico et al., 2010; Ortega, 1998).

Although shiny cowbird females do not provide any parental care to their progeny, they can enhance the hatchability of their eggs by synchronizing parasitism with host laying and the survival of their chicks by reducing the competition for food that their young face in the brood. Synchronization between parasitism and host laying provides cowbird eggs enough time for incubation to ensure successful hatching. Several studies indicate that most shiny cowbird parasitism occurs during host laying (Fiorini and Reboreda, 2006; Mermoz and Reboreda, 1999), and because cowbird eggs have a shorter incubation period than eggs of similar size (Briskie and Sealy, 1990), parasite chicks tend to hatch before host chicks, which gives them a head start in competition for food with their nestmates (Fiorini et al., 2009a; Mermoz and Reboreda, 2003). Shiny cowbird females also peck and puncture eggs when visiting host nests (Friedmann, 1929; Hudson, 1874). Hosts remove punctured eggs as part of their nest sanitation behavior (Kemal and Rothstein, 1988), which result in a reduced brood. Puncture of host eggs significantly increases the survival of a parasite's chicks when they have to compete for food with nestmates larger in body mass than the parasite (Astié and Reboreda, 2009a,b; Fiorini et al., 2009a). However, egg punctures also increase the probability of nest abandonment by the host (Astié and Reboreda, 2006; Fraga, 1978, 1985; Massoni and Reboreda, 1998) and therefore the benefits of increasing the survival of a parasite's chicks must outweigh the costs of increased probability of nest abandonment. In addition, Kilner et al. (2004) have shown that brown-headed cowbird chicks may benefit from sharing the nest with host chicks when they are smaller than the parasite. In this situation, begging by host chicks solicits a higher provisioning rate than does begging by the

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parasite alone, and because the cowbird chick is larger than host chicks it can secure the majority of this extra provisioning and so grow more rapidly (Kilner et al., 2004). Kilner (2005) proposed that brood parasites might face a 'virulence' trade-off between killing their host nestmates, so eliminating competition for food, and not killing host nestmates so gaining their assistance in stimulating parental provisioning.

In a recent study Gloag et al. (2012a) modeled this trade-off and proposed that the optimal strategy depends on the interaction between a parasite's stimulative and competitive abilities during begging, relative to host young. These authors also showed experimentally that shiny cowbird chicks reared by a host smaller than the parasite (the house wren, *Troglodytes aedon*, 12–13 g) had higher food intake and mass growth when they shared the nest with host young than when alone, while shiny cowbirds chicks reared by a host larger than the parasite (the chalk-browed mockingbird, *Mimus saturninus*, 70–75 g) had lower food intake, mass growth and survival when sharing the nest with host young than when alone. Therefore, to optimize the survival of their chicks, shiny cowbird females should puncture more host eggs (i.e. eliminate more competitors for their chicks) when they parasitize a large host than when they parasitize a small one.

It has been suggested that brown-headed cowbirds may remove host eggs more frequently in large than in small hosts (Davies, 2000), and Fiorini et al. (2009a) showed that shiny cowbird females puncture more host eggs when they parasitize chalk-browed mockingbirds than when they parasitize house wrens. In the latter case, this differential puncture success may arise due to properties of the nest or eggs that lead to lower rates of egg breakage for the same puncturing effort. Alternatively, female cowbirds may adjust their egg pecking behavior according to host characteristics. Such an adjustment could be the result of either an adaptation of shiny cowbird host specific races to host characteristics, or behavioral flexibility of individual females. Consistent with nonrandom host use (i.e., host specific races), Mahler et al. (2007) have shown that shiny cowbird females that parasitize mockingbirds and wrens differ in the frequency distribution of their control region's mDNA haplotypes. However, Llambías et al. (2006) have shown in laboratory experiments that shiny cowbirds that face a choice between one shiny cowbird egg and one host egg larger than the parasite one, preferentially peck the host egg, which would occur if egg pecking behavior by individual females was simply influenced by egg size.

In addition to competing against host chicks, shiny cowbird chicks may compete against unrelated parasite chicks. This arises when two or more cowbird females parasitize the same nest, a situation that occurs regularly in several common hosts of shiny cowbirds (De Mársico et al., 2010; Ortega, 1998). In these cases, to enhance the survival of their chick shiny cowbird females should peck and puncture host eggs when they are larger than parasite eggs, but other shiny cowbird eggs when host eggs are smaller than parasite eggs.

In this study we investigated whether egg-pecking behavior by female shiny cowbirds might be adjusted to the competition that their chicks face in host nests. As in Fiorini et al. (2009a) we investigate parasitism in two hosts that differ markedly in body mass: chalk-browed mockingbirds, a host larger than the cowbird and house wrens, a host smaller than the parasite. We used a larger observational dataset than that of Fiorini et al. (2009a; i.e. data from eight consecutive breeding seasons instead of two) on egg punctures inflicted by shiny cowbirds when they parasitize nests of wrens and mockingbirds.

More than 60% of the nests of these hosts are parasitized by shiny cowbirds and because 40–60% of parasitized nests are multiply parasitized (i.e. they receive more than one cowbird egg) we could also evaluate rates of egg loss due to puncturing when both host and parasite eggs were in the nest. If large eggs are punctured preferentially to small eggs we should observe more host eggs than cowbird eggs punctured in mockingbird nests but more cowbird eggs than host eggs punctured in wren nests. In addition, we conducted an experiment with female shiny cowbirds captured during the breeding season and tested in the laboratory for egg pecking preferences in a choice between one host (either mockingbird or wren) and one parasite egg. If shiny cowbirds are capable of adjusting their egg-pecking behavior on the basis of egg size alone, when they face a choice between host and shiny cowbird eggs, they should peck and puncture host eggs when they are larger than parasite eggs (i.e. mockingbird eggs), but other shiny cowbird eggs when host eggs are smaller than parasite eggs (i.e. wren eggs).

2. Methods

2.1. Study site

Field data were collected at Reserva El Destino (35°08′S, 57°23′W), in the province of Buenos Aires, Argentina, during the breeding seasons (October–January) 2002–2003 to 2009–2010. The study site is a flat area of 320 ha within the Biosphere Reserve Parque Costero del Sur (MAB-UNESCO). This area comprises a mosaic of marshy grasslands and woodland patches dominated by Talas (*Celtis tala*) and Coronillos (*Scutia buxifolia*).

2.2. Study species

Main reproductive variables of shiny cowbirds, house wrens and chalk-browed mockingbirds are presented in Table 1. Shiny cowbirds breed from early October to late January. They peck and puncture one or more eggs when they visit host nests (Friedmann, 1929; Hudson, 1874) and this behavior precedes parasitism (Gloag et al., 2012b). Chalk-browed mockingbirds breed from early October to mid-January and build open-cup nests in shrubs or trees with dense foliage (Fiorini et al., 2009b). At our study site, most mockingbird nests are built in Talas and Coronillos at a height of 1.5–2.5 m, and approximately 70% of them are parasitized by shiny cowbirds with an intensity of parasitism of 2.2 eggs per parasitized nest (Fiorini and Reboreda, 2006; Fiorini et al., 2009a). House wrens breed from early October to mid-January and nest in natural and artificial cavities (Johnson, 1998; Kattan, 1998). To facilitate data collection in wrens we placed 150 nest boxes in our study area. Nest boxes were located in Tala trees at a height of 1.5–1.8 m and they were separated from each other by at least 20 m. External measurements of the boxes were 25 cm × 17 cm × 13 cm (height, width, depth). The box had an entrance hole 4.5 cm in diameter that allowed female cowbirds to go in and a roof opening that allowed us to monitor the progress of the nest. At our study site, approximately 60% of wren nests are parasitized by shiny cowbirds with an intensity of parasitism of 1.7 eggs per parasitized nest (Tuero et al., 2007).

Table 1
Main reproductive variables of brood parasitic shiny cowbird (*Molothrus bonariensis*) and the two hosts analyzed in this study, house wren (*Troglodytes aedon*) and chalk-browed mockingbirds (*Mimus saturninus*). Data are from Fiorini (2007), Tuero et al. (2007) and Llambias and Fernandez (2009).

	Cowbird	Wren	Mockingbird
Egg length and width (mm)	23.5 × 18.3	17.5 × 13.1	28.3 × 20.4
Egg volume (cm^3)	3.9	1.5	5.9
Modal clutch size (range)	–	5 (4–6)	4 (3–5)
Incubation period (days)	12–13	14–16	13–14
Weight at hatching (g)	4	1.5	6
Weight at fledging (g)	40	13	50–55
Adult weight (g)	45–50	12–13	70–75

2.3. Field data collection and analysis

We found mockingbird nests by observing the behavior of territorial pairs (Martin and Geupel, 1993) or by inspecting potential nesting sites within the territories. We visited mockingbird and wren nests daily until the chicks fledged or the nest failed. We conducted our visits from 09:00 to 12:00, by which time hosts and parasites had already laid their eggs. At each visit we recorded the number of host and parasite eggs (each egg was numbered with waterproof ink) and the occurrence of punctures. We collected data of egg punctures in mockingbird nests during the breeding seasons 2002–2003 to 2009–2010 ($n = 232$ nests) and in nests of wrens during the breeding seasons 2003–2004 to 2009–2010 ($n = 106$ nests).

We assumed that the number of eggs in the nest at the time of parasitism was the one we observed the previous day because cowbird's parasitism occurs at dawn, before host laying (Gloag et al., 2012b). We considered that a host egg had been punctured when we observed the punctured egg (approximately 60% of the cases) or when we observed that one host egg that was present in the nest the day before, disappeared in association with a parasitic event. We consider that this assumption is reasonable as video records of parasitic events indicate that mockingbirds and wrens remove punctured eggs shortly after parasitism (Gloag et al., 2012b; V. Fiorini, R. Gloag, unpublished results). We excluded from our analysis nests that received more than one cowbird egg in a single day because in these cases we cannot ascertain the number of eggs present in the nest at the time each cowbird visited the nest. We focused our analysis on mockingbird and wren nests with 1–4 host eggs at the time the first parasitic event occurred (i.e. only host eggs present in the nest; $n = 107$ mockingbird nests and $n = 84$ wren nests). We also tested if egg punctures in nests where the parasite female had the choice to peck host and parasite eggs were at random by analyzing 85 mockingbird and 18 wren nests that had one or more host eggs and one parasite egg at the time they were parasitized.

2.4. Choice experiments with captive shiny cowbird females

During November and December 2010 we captured 16 female shiny cowbirds using walk-in traps placed near active mockingbird and wren nests. Because mockingbird and wren nests were in the same patches of forest and relatively close to each other, we cannot ascertain whether the females we trapped were visiting mockingbird or wren nests. After capture, we moved the females to a laboratory located at the study site where we kept them for 1–3 days in individual cages (90 cm × 30 cm × 30 cm) at room temperature and with a natural light:dark cycle until they were tested for egg pecking behavior. During this period birds were visually but not acoustically isolated and they had ad libitum access to food (a mix of chicken feed, millet and birdseed) and water. Each cage contained an empty, artificial open cup nest, 10 cm in diameter, with lining material such as that used by bird breeders placed at the cage's end opposite to the food and water containers.

The experiment consisted in adding one host and one cowbird natural eggs to the artificial nest and recording females pecking behavior. Each female experienced two treatments: (1) one wren plus one cowbird egg, and (2) one mockingbird plus one cowbird egg. Host and parasite eggs were obtained from wren and mockingbird nests that had been deserted during laying. Each treatment lasted 30 min and there was an interval between treatments of 60 min. The order of treatments was counterbalanced across females. We video-recorded the sessions and we scored the tapes back in the laboratory to determine: (1) the identity of the first egg pecked, (2) the number of pecks each egg received, and (3) the identity of the eggs punctured. Out of the 16 females captured, 14 responded in one of the treatments (12 in the wren-cowbird treatment and 13 in the mockingbird-cowbird treatment) and 11 in both treatments.

2.5. Statistical analysis

We tested differences between hosts in number of eggs punctured using a generalized linear model (GLM) with a log link function and a Poisson error term. We entered the predictable variables (host and number of host eggs at the time of parasitism) as fixed factors into the model. We employed a stepwise backward selection procedure to obtain the minimal adequate model removing non-significant interaction from the model. We conducted this analysis using Rcmdr package from R software, Version 2.13.0 (R Development Core and Team, 2011). In natural nests where the parasite female had the opportunity to peck both types of eggs we tested differences in the proportion of host and parasite eggs punctured with Fisher exact tests. In the choice experiments we tested preferences for identity of the first egg pecked with a binomial test, differences in the number of pecks directed toward host and parasite eggs with a Wilcoxon test, and differences in the proportion of host and parasite eggs punctured with a Fisher exact test. All statistical tests were two-tailed and values reported are means ± SE.

3. Results

3.1. Egg punctures in natural nests of wrens and mockingbirds

The number of host eggs punctured per parasitic event (i.e. cowbird egg laid) in wren and mockingbird nests with 1–4 eggs at the time parasitism occurred was higher in mockingbird than in wren nests ($Z = -2.23$, $P = 0.02$) and it differed with number of host eggs ($Z = 4.91$, $P = 0.001$). Visual inspection of Fig. 1 indicates that number of host eggs punctured increases with number of host eggs at the time of parasitism. When female cowbirds had the opportunity to peck host and parasite eggs (i.e. they parasitized nests that already had a cowbird egg) they punctured a higher proportion of host than parasite eggs in mockingbird nests (50/212 mockingbird eggs vs. 8/85 cowbird eggs, $P = 0.006$, $n = 85$ nests), but the proportion of host and parasite eggs punctured did not differ in wren nests (8/74 wren eggs vs. 0/18 cowbird eggs, $P = 0.35$, $n = 18$ nests).

3.2. Experiments with captive shiny cowbird females

Shiny cowbird females showed no preference for the first egg pecked when they faced a choice between one wren and one cowbird egg (Binomial test, $P = 1$, $n = 12$), but they more frequently pecked the host egg first when the choice was

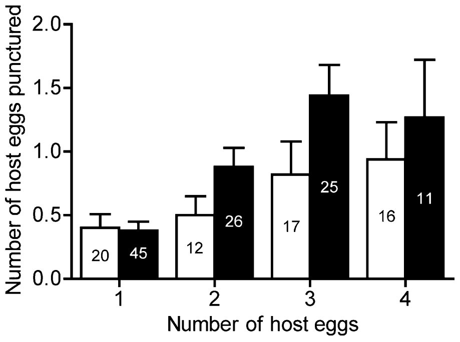

Fig. 1. Number (mean ± SE) of house wren eggs (white bars) and chalk-browed mockingbird eggs (black bars) punctured during the first shiny cowbird's parasitic event in nests that had 1–4 wren or mockingbird eggs at the time parasitism occurred.

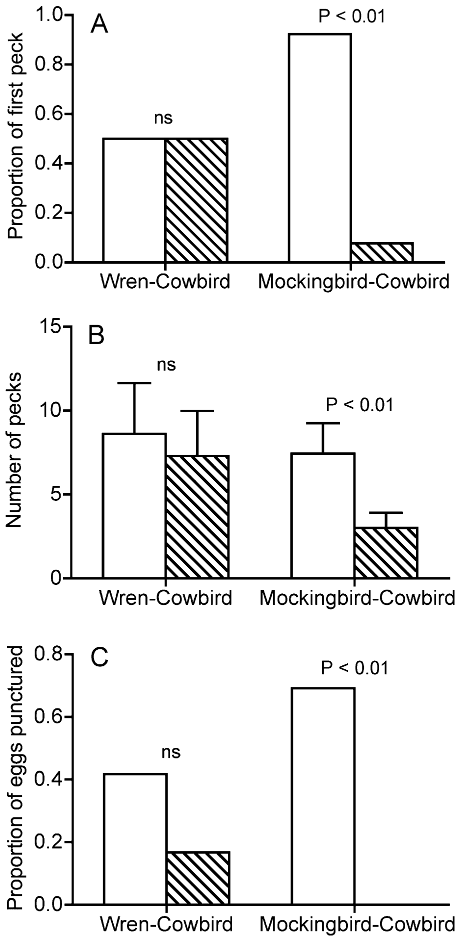

Fig. 2. (A) First egg pecked, (B) number of pecks (mean ± SE), and (C) number of eggs punctured by female shiny cowbirds when they faced a choice between one wren and one cowbird egg ($n = 12$) or between one mockingbird and one cowbird egg ($n = 13$). White and black bars indicate host and parasite eggs, respectively. Values within bars indicate number of nests.

between one mockingbird and one cowbird egg (Binomial test, $P = 0.003$, $n = 13$, Fig. 2A). Similarly, the number of pecks did not differ between eggs when the choice was between one wren and one cowbird egg (Wilcoxon test, $Z = -0.08$, $P = 0.94$, $n = 12$), but it was higher for host than parasite eggs when the choice was between one mockingbird and one cowbird egg (Wilcoxon test, $Z = -2.63$, $P = 0.009$, $n = 13$, Fig. 2B). Latency to the first peck and total number of pecks did not differ between treatments (Latency: wren-cowbird = 308 ± 128 sec; mockingbird-cowbird = 393 ± 173 sec; Wilcoxon test, $Z = -0.18$, $P = 0.85$, $n = 11$; total number of pecks: wren-cowbird = 18.5 ± 3.9; mockingbird-cowbird = 10.8 ± 3.1; Wilcoxon test, $Z = -1.58$, $P = 0.11$, $n = 11$). Finally, when the choice was between one wren and one cowbird egg the frequency of punctured eggs did not differ between host and parasite (host: 5/12, parasite: 2/12, Fisher exact test, $P = 0.37$), but when the choice was between one mockingbird and one cowbird egg females punctured a larger proportion of host than parasite eggs (host: 9/13, parasite: 0/13, Fisher exact test, $P = 0.0005$, Fig. 2C).

4. Discussion

In many brood parasite species (i.e. honeyguides and most cuckoos) young parasites eliminate competition with host chicks through eviction of host eggs or chicks or through direct killing of nestmates (Davies, 2000; Payne, 2005). In contrast, in other brood parasites like cowbirds, parasite chicks do not actively eliminate host chicks, but parasite females reduce competition for their chicks by puncturing host eggs. In these species, the virulent behavior is performed by the parasite female at the egg stage only instead of also by the parasite young at the chick stage. Puncture of host eggs has been reported not only in shiny cowbirds, but also in screaming cowbirds (De Mársico and Reboreda, 2010; Fraga, 1998), bronzed cowbirds (*Molothrus aeneus*, Carter, 1986; Peer and Sealy, 1999) and brown-headed cowbirds (Rogers et al., 1997; Smith and Arcese, 1994), although in the latter species the reduction of the host's clutch is generally achieved through egg removal (Peer, 2006).

Kilner (2005) proposed that parasite chicks face a trade-off for maximum growth: killing host young to eliminate them as competitors, or tolerating host young to gain their assistance in stimulating provisioning. This virulence trade-off is also faced by a female shiny cowbird when parasitizing a nest, as she may destroy some host eggs to eliminate them as competitors for her future chick or not destroy eggs such that the future chick gains assistance in soliciting food. If female shiny cowbirds have been selected to adaptively adjust egg pecking behavior to optimize the survival of their chicks, they should puncture more host eggs when they parasitize a large host than when they parasitize a small one, as chicks of hosts larger than shiny cowbirds reduce the survival of the parasite chick (Astié and Reboreda, 2009a,b; Fiorini et al., 2009a), while chicks of hosts smaller than shiny cowbirds increase the amount of food delivered to the nest and the growth rate of the parasite chick (Fiorini et al., 2009a; Gloag et al., 2012a). Similarly, when shiny cowbird females visit a nest that was parasitized by another female, they may preferentially target host or parasite eggs. In this case they should peck and puncture host eggs when they are larger than parasite ones, but parasite eggs when they are larger than host ones, as in the latter case the other parasite chick will be the stronger competitor in the nest.

Our observations of egg loss from natural nests are partially consistent with these predictions, as shiny cowbirds punctured more host eggs in mockingbird nests than in wren nests and, in mockingbird nests that contained one cowbird egg from previous parasitism, the mockingbird egg was broken more frequently than the cowbird egg. In wren nests however that had previously been parasitized, there was no evidence that cowbird eggs were more frequently broken on a second parasitic event. One limitation of these results is that we did not observe pecking, but the result of this behavior (egg punctures). As such, our field data would be also consistent with other explanations; for example, egg types are equally pecked but some qualities of the eggs or nests lead to eggs not being equally broken. Cowbird eggs are more rounded in shape and have a thicker eggshell than eggs of their non-parasite relatives (Mermoz and Ornelas, 2004; Rahn et al., 1988; Spaw and Rohwer, 1987), which make them more resistant to egg punctures (Picman, 1989). Therefore, with the data from natural nests we cannot rule out the possibility that female shiny cowbirds pecked host and parasite eggs at random, but because eggs differ in shape and thickness, parasite eggs were more resistant to breakage. Another possibility that could explain why mockingbird eggs were punctured more frequently than cowbird eggs is that female cowbirds lay more than one egg in the same nest (de la Colina et al., unpublished; McLaren et al., 2003) and thus, to reduce the risk of breaking their own eggs, pecking behavior is less frequent or less intense on subsequent nest visits or, less likely, these females recognize their own eggs and avoid pecking them. In addition, our observations from natural nests do not allow us to distinguish whether differences between hosts were the result of differences between host-specialist shiny cowbird females, or flexibility at the individual level.

The results of the choice experiments with captive shiny cowbird females also partially support the hypothesis that individual females adjust their egg pecking behavior according to host egg characteristics. Consistently with our observations of egg punctures in parasitized natural nests, when female shiny cowbirds faced a choice between one mockingbird and one cowbird egg, they pecked host eggs first and more frequently and, as a result of that, punctured host eggs more frequently, but when the choice was between one wren and one cowbird egg, there were no differences in the previous variables. These results indicate that the observation of more mockingbird than cowbird eggs punctured in multiple parasitized nests may not be only the result of differences in egg shape or thickness between parasite and host eggs, but also the result of differences in the number of pecks elicited by egg characteristics. However, pecking behavior of cowbirds presented with one wren egg and one cowbird egg was not consistent with cowbird's adaptively targeting the larger egg, with no significant difference in pecking or puncture success between egg types. Relative differences in egg size are larger between wren and cowbird eggs than between mockingbird and cowbird eggs (Table 1) and color patterns of host eggs are similar (both are spotted). Therefore, it seems unlikely that differences in pecking and puncture success between treatments are attributable to discrimination failures in one case, but not in the other.

That pecking behaviors with respect to egg type or size varied between treatments within individuals lends some support to the idea that shiny cowbird females show flexibility in pecking behaviors at the individual level and can adjust their egg pecking behavior according to host characteristics. Differential virulence by individual females could result from the simple rule of pecking more frequently or intensely eggs that are larger than the parasite's own eggs. This rule would require that shiny cowbird females 'know' the size of their own eggs and then adjust their pecking behavior according to the relative size of eggs present in the nest. However, more complex rules involving volume and number of eggs, or sensorial feedback through bill mechanoreceptors cannot be ruled-out. Field studies that observe first-hand cowbird pecking behavior in natural nests are needed to confirm whether the differences we observe in captive birds occur in practice, when the full range of behavioral cues relating to eggs, nests and hosts are available.

Our results are consistent with our proposal that the virulence trade-off postulated by Kilner (2005) for brood parasitic chicks could also apply to egg-pecking behavior of shiny cowbird females. Unlike the virulent behaviors of nestlings, egg pecking has the restriction that it does not allow elimination of all other young in the nest, as most hosts abandon their nests after extensive egg destruction. However, egg pecking has the advantage that is easy to adjust to host characteristics, which can be particularly relevant for generalist brood parasites.

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