

Egg Discrimination and Sex-Specific Pecking Behaviour in Parasitic Cowbirds

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Abstract

We studied egg-pecking behaviour in males and females of three cowbird species: the shiny cowbird (*Molothrus bonariensis*), a host generalist brood parasite, the screaming cowbird (*M. rufoaxillaris*), a host specialist brood parasite, and the bay-winged cowbird (*Agelaioides badius*), a non-parasitic species. We conducted three experiments in which we offered each bird an artificial nest with two plaster eggs and recorded whether egg pecking occurred and the number of pecks on each egg. In expt 1, we tested if there were species and sex differences in egg-pecking behaviour by offering the birds two spotted eggs of similar pattern. Shiny and screaming cowbirds responded in 40.3% and 44% of the trials, respectively, with females and males presenting similar levels of response. In contrast, bay-winged cowbirds did not show any response. In expt 2, we tested if shiny cowbirds responded differentially when they faced a choice between one host and one shiny cowbird egg, while in expt 3, we tested if screaming cowbirds responded differentially when they faced a choice between one shiny and one screaming cowbird egg. Shiny cowbirds pecked preferentially host eggs while screaming cowbirds pecked more frequently shiny cowbird eggs. Our results show that egg-pecking behaviour is present in both sexes of parasitic cowbirds, but not in non-parasitic birds, and that parasitic cowbirds can discriminate between eggs of their own species and the eggs of their hosts or other brood parasites.

Introduction

Parasitic cowbirds have several specializations including a high fecundity (Payne 1976; Scott & Ankney 1980, 1983; Jackson & Roby 1992; Kattan 1993), thick and round eggshells (Blankespoor et al. 1982; Spaw & Rohwer 1987; Rahn et al. 1988; Picman 1989), short incubation periods (Briskie & Sealy 1990; Kattan 1995; but see Mermoz & Ornelas 2004), and pecking or removal of host eggs (Friedmann 1929; Sealy 1992; Peer 2006).

Egg-pecking behaviour has been observed in the wild in the shiny cowbird, *Molothrus bonariensis*

(Hudson 1874; Hoy & Ottow 1964; Post & Wiley 1977), the screaming cowbird, *M. rufoaxillaris* (Fraga 1998) and the bronzed cowbird, *M. aeneus* (Carter 1986; Peer & Sealy 1999). In contrast, in the brown-headed cowbird, *M. ater*, the reduction of the host's clutch is generally achieved through egg removal (Sealy 1992; Arcese et al. 1996; Peer 2006), although some studies also report egg punctures (Hofslund 1957; Smith & Arcese 1994; Rogers et al. 1997). In brief, four of the five species of parasitic cowbirds are known to pierce host eggs.

Several hypotheses have been proposed to explain egg removal and egg-pecking behaviour of parasitic

cowbirds. Some researchers have proposed that cowbirds might peck or remove eggs to increase the efficiency of incubation of their eggs, or to reduce the competition for food of their chicks (Friedmann 1929; Hoy & Ottow 1964; Blankespoor et al. 1982; Sealy 1992; Peer & Bollinger 1997). However, cowbirds also peck or remove eggs in nests that they do not parasitize (Arcese et al. 1992, 1996; Nakamura & Cruz 2000; Massoni & Reboreda 2002). Arcese et al. (1996) suggested that, by removing eggs in these nests, brown-headed cowbirds might induce the host to re-nest and, in this way, gain new opportunities for parasitism. Similarly, Peer & Sealy (1999) also suggested that bronzed cowbirds puncture eggs to force host re-nesting. In addition, Massoni & Reboreda (1999) proposed that, by puncturing eggs, cowbirds could assess the degree of embryonic development of the host egg to decide whether to parasitize a given nest.

Recent studies using genetic parentage analysis indicate that realized female fecundity of cowbirds is relatively low (Alderson et al. 1999; Hahn et al. 1999; Strausberger & Ashley 2003; Woolfenden et al. 2003) compared with previously published estimates (Payne 1976; Scott & Ankney 1980, 1983; Jackson & Roby 1992; Kattan 1993). Consequently, the reproductive value of each cowbird egg should be higher than that previously supposed. Therefore, there are likely to be strong selection pressures on cowbirds to increase the viability of their eggs and chicks by synchronizing parasitism with laying of the host, and by enhancing the efficiency of incubation of their eggs and the survival of their chicks.

Here, we look at species and sex-specific differences in egg-pecking behaviour in three South American cowbirds: two parasitic species (shiny and screaming cowbirds), and a non-parasitic species, the bay-winged cowbird (*Agelaioides badius*), which belongs to the same family (Icteridae) as parasitic cowbirds (Lanyon 1992; Lanyon & Omland 1999). We selected these three species because of differences in their breeding biology. The shiny cowbird is an extreme generalist that uses more than 200 different hosts (Friedmann & Kiff 1985; Ortega 1998), while the screaming cowbird is a specialist that uses mainly one host, the bay-winged cowbird (Fraga 1998). Shiny cowbirds apparently have a promiscuous mating system with females searching for host nests without the assistance of the male, while in screaming cowbirds, the mating system is monogamous and males and females inspect host nests together (Mason 1987; Fraga 1998). Shiny cowbirds usually parasitize hosts that are larger than them-

selves (Mason 1986; Mermoz & Reboreda 2003; Sackmann & Reboreda 2003). In these cases, their chicks are often outcompeted for food by the host's chicks (Fraga 1985; Lichtenstein 1998; Astié & Reboreda 2006). Screaming cowbirds parasitize bay-winged cowbirds, which are 10–20% smaller in size than themselves. However, bay-winged cowbirds are also parasitized by shiny cowbirds (Fraga 1998), which are similar in size to screaming cowbirds. In these cases, the main competitor of a screaming cowbird chick is a shiny cowbird chick.

The aim of this study was to determine whether egg-pecking behaviour is exclusive to parasitic female shiny and screaming cowbirds and whether these species can discriminate between conspecific and heterospecific eggs. We conducted three experiments in which we offered each bird an artificial nest with two plaster eggs and recorded whether egg pecking occurred and the number of pecks on each egg. In expt 1, we tested if there were species and sex differences in egg-pecking behaviour. In expt 2, we tested if shiny cowbirds responded differentially when they faced a choice between one egg of a large host and one conspecific egg. Finally, in expt 3, we tested if screaming cowbirds responded differentially when they faced a choice between one egg of a shiny cowbird and one conspecific egg.

Methods

Subjects

We caught shiny, screaming and bay-winged cowbirds with mist nets close to the city of Buenos Aires, Argentina, at the end of the non-breeding season (September) of 2000. After capture, we colour-banded and weighed the birds. We kept the birds in captivity for at least 60 d prior to the experiments. All birds used were adults, as they had gone through their post-juvenile moult. We housed the birds in an indoor–outdoor aviary. The indoor room was $2 \times 2 \times 3$ m [length \times width \times height ($l \times w \times h$)] while the outdoor aviary was $3 \times 2 \times 2.5$ m. Both aviaries received natural light from the outside. Experiments were conducted during the breeding season and we did not manipulate temperature and photoperiod. We placed screaming and bay-winged cowbirds together in the same outdoor aviary, as they normally form heterospecific flocks. We placed shiny cowbirds in a different outdoor aviary, next to the one we used for the other two species.

Both before and during the experiments, we fed captive birds ad libitum on a diet of millet and food

for insectivorous birds, which contained dried insects, fruits, dried eggs, minerals and vitamins. We also provided calcium and water ad libitum. After the experiments were completed, the birds were returned to the outdoor aviary for 3–4 wk to allow them to reacclimatize to outdoor conditions and to gain exercise, especially in flight, and then they were released into the wild, in an area regularly occupied by free-living cowbirds. No egg laying occurred in any of the three species during their captivity.

Experimental Procedure

For experimental trials, we moved the birds from the outdoor aviary to cages of $60 \times 40 \times 40$ cm ($l \times w \times h$) located in the indoor room. We housed the birds individually and they were visually, but not acoustically, isolated from other birds.

Each cage contained an empty, artificial open cup nest, 12 cm in diameter, with lining material such as that used by bird breeders. We placed the nest at the end opposite to the food source, calcium and water. On the day an experiment was initiated, and up to the day it ended, we divided the cage with an opaque partition so that the bird would not see the nest. This cover was only removed during the experimental trials. Experimental sessions started at 08:30 hours and ended at 13:00 hours. Given the limited availability of individual cages, we were not able to test all the birds at the same time. However, for each species, we randomly assigned the birds to experimental group, order of testing, and cage.

We video-recorded the sessions with a Hi-8 Sony video camera, placed in a way that allowed us to see the nest contents (Sony Hi8 XR CCD-TR 940; Sony Corporation, Tokyo, Japan). We scored the tapes back in the laboratory to analyse the pecking behaviour of the three species.

We carried out three different experiments. However, all experiments were similar in that we offered the caged birds an artificial nest with two plaster eggs in it and recorded whether egg pecking occurred and the number of pecks on each egg.

Experiment 1

We tested if there were species and sexual differences in egg pecking behaviour by offering birds two spotted eggs of similar pattern. We tested 12 shiny cowbirds (six males, weight 50.3 ± 1.8 g and six females, weight 41.7 ± 1.5 g), 11 screaming cowbirds (six males, weight 52.8 ± 1.1 g and five

females, weight 46.0 ± 0.6 g) and 11 bay-winged cowbirds of unknown sex. We discriminated between male and female shiny cowbirds by differences in plumage coloration and body weight (Ortega 1998). Screaming cowbirds are sexually dimorphic in size (i.e. males are 20–25% heavier than females, Mason 1987; Clayton et al. 1997) and the size of the patch of rufous axillar feathers is larger in males (J.C. Reboreda pers. obs.). We moved the birds to the cages 18 h before the beginning of the experiment to allow them to become accustomed to the new environment. The birds experienced two trials per day (with an inter-trial interval of 120 min) on three consecutive days. Each trial lasted 30 min and started with the removal of the opaque partition and the presentation of the nest with the two plaster eggs in it. For all three species, the plaster eggs were 22.8 mm in length and 18.2 mm in width and were painted to resemble speckled passerine eggs. The weight of plaster eggs was approx. 3.5 g.

Experiment 2

We tested whether shiny cowbirds responded differentially when faced with a choice between one host and one shiny cowbird egg. We tested 14 shiny cowbirds (seven males and seven females). Twelve of these birds had been tested in expt 1 while the other two birds were naive. We moved the birds from the outdoor aviary to the experimental cages 42 h before the beginning of the experiment. The birds experienced one trial per day on two consecutive days. Each trial lasted 30 min and started with the removal of the opaque partition and the presentation of the nest with two plaster eggs in it. To test for a pecking preference, we presented each subject with two differently painted plaster eggs. One of the eggs resembled a shiny cowbird spotted egg (length: 22.8 mm, width: 18.2 mm, whitish background and brown and grey spots concentrated at the larger end) and the other resembled a white egg of the rufous hornero, *Furnarius rufus* (length 27.7 mm, width 21.9 mm). This species is a common host of shiny cowbirds in several regions of Argentina and in Uruguay (Hoy & Ottow 1964; Mason & Rothstein 1986).

Experiment 3

We tested whether screaming cowbirds responded differentially when they were faced with a choice between one screaming and one shiny cowbird egg.

We tested 10 screaming cowbirds (six males and four females). All these birds had been tested in expt 1. The experimental conditions were the same as in expt 2 with the exception that the plaster eggs used (length 22.8 mm, width 18.2 mm) were replicas of a shiny cowbird's and a screaming cowbird's eggs. Shiny and screaming cowbird eggs are similar in colour, size and shape, but screaming eggs have distinctive thick dark lines in the eggshell (scrawls, Fraga 1983).

Video Analysis

We watched the videotapes in the laboratory to determine whether the birds pecked the eggs and measured the latency to the first peck (time elapsed from the beginning of the trial until the first egg was pecked), and peck intensity (number of pecks per egg during the trial).

Statistical Analysis

For the analysis we used nonparametric statistics because of lack of normality of the data and small sample sizes of the experimental groups. Statistical tests were performed using StatView 5.0 (SAS Institute Inc. 1998) with $p < 0.05$ (two-tailed). Values reported are mean \pm SE.

Results

In expt 1, seven of 12 shiny cowbirds (4/7 females and 3/5 males) and nine of 11 screaming cowbirds (5/5 females and 4/6 males) responded (i.e. pecked either of the plaster eggs) in at least one trial. In contrast, none of the bay-winged cowbirds responded in any trial. On average, shiny cowbirds pecked in 40% of the trials (2.42 ± 0.75 trials with pecks, range 0–6, $n = 12$), screaming cowbirds in 44% (2.64 ± 0.64 , range 0–6, $n = 11$), and bay-winged cowbirds in 0% (Kruskal–Wallis test; $H = 12.8$; $p = 0.002$). There were no sexual differences in the number of trials with response in shiny cowbirds (Mann–Whitney U-test; $Z = -0.68$; $p = 0.50$) and screaming cowbirds (Mann–Whitney U-test; $Z = -0.93$; $p = 0.35$). With respect to the latency until the first peck, it was lower for shiny than for screaming cowbirds (shiny cowbirds: 214.3 ± 58.7 s, $n = 7$; screaming cowbirds: 629.1 ± 143.0 s, $n = 10$; Mann–Whitney U-test; $Z = -2.17$, $p = 0.03$).

In expt 2, 10 of 14 shiny cowbirds (4/7 females and 6/7 males) responded in at least one trial. These birds pecked the host egg significantly more times

than the shiny cowbird egg (Wilcoxon signed-rank test: $Z = -2.7$, $n = 10$, $p = 0.007$; Fig. 1a), but there were no significant differences in the latency to the first peck between host and shiny cowbird eggs (host eggs: 213.5 ± 103.8 ; shiny cowbird eggs: 241.1 ± 103 ; Wilcoxon signed-rank test: $Z = -0.86$, $n = 10$, $p = 0.39$). Similar to expt 1, there were no sexual differences in the pecking response (Mann–Whitney U-test: $Z = -1.28$, $p = 0.2$ for host eggs; and Mann–Whitney U-test: $Z = -0.21$, $p = 0.83$ for shiny cowbird eggs).

In expt 3, six of 10 screaming cowbirds (2/4 females and 4/6 males) responded in at least one trial. These birds pecked shiny cowbird eggs significantly more often than screaming cowbird eggs (Wilcoxon signed-rank test: $Z = -2.02$, $n = 6$, $p = 0.04$; Fig. 1b). In this experiment, the latency to the first peck was smaller for shiny than for screaming cowbird eggs (shiny cowbirds: 510.3 ± 195.0 s;

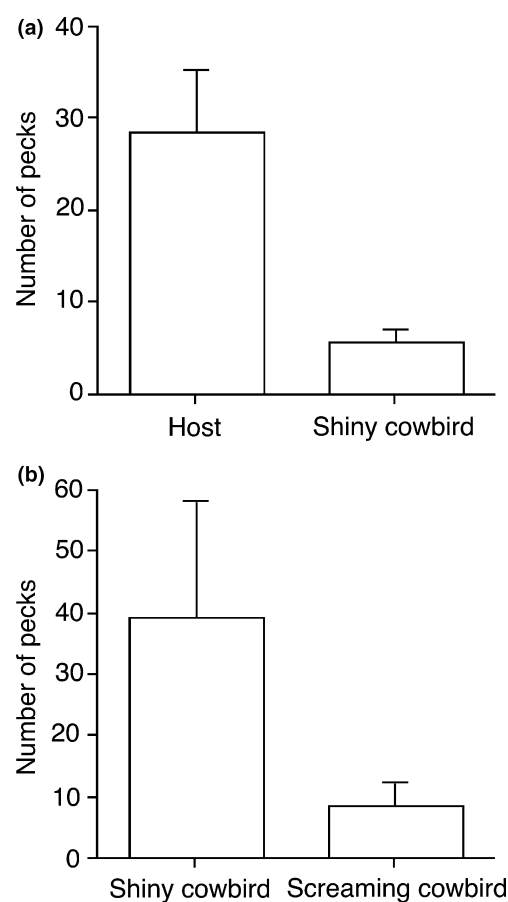


Fig. 1: (a) Average number of pecks per trial inflicted by shiny cowbirds ($n = 10$) on host and shiny cowbird eggs in expt 2. (b) Average number of pecks per trial inflicted by screaming cowbirds ($n = 6$) on shiny and screaming cowbird eggs in expt 3

screaming cowbirds: 760.2 ± 200.7 s; Wilcoxon signed-rank test: $Z = -2.20$, $n = 6$, $p = 0.03$).

Discussion

Our results show that in laboratory conditions, males and females shiny and screaming cowbirds peck eggs at similar frequencies and are able to discriminate between different eggs. When faced with the same experimental conditions, the bay-winged cowbird (a non-parasitic control) did not peck eggs. Given that the egg-pecking response was observed in the parasitic but not in the control species, we do not think that our observations are a consequence of captivity or food deficiency. Before and during the experiments, birds were supplemented with calcium and food containing egg yolk and proteins, so it is unlikely that the pecking behaviour observed was a consequence of the birds being calcium or food-deprived. With respect to egg discrimination, we cannot rule out the possibility that shiny cowbirds in expt 2 preferentially pecked larger eggs. However, we also observed egg-pecking preferences in expt 3, where screaming cowbirds faced a choice between eggs that were similar in size.

Although we registered egg pecking in parasitic but not in the non-parasitic species, not all the parasitic birds pecked eggs during our experiments. We noted that two shiny cowbirds that did not peck eggs in expt 1 responded during expt 2. Similarly, one screaming cowbird that did not peck in expt 1 responded during expt 2, but three screaming cowbirds that pecked in expt 1 did not respond in expt 3. These observations indicate that cowbirds will not always peck when faced with a nest containing eggs. This result is consistent with field observations that note that not all parasitized nests suffer from egg destruction from shiny cowbirds (Wiley & Wiley 1980; Cruz et al. 1990; Astié & Reboreda 2006), screaming cowbirds (Fraga 1998), bronzed cowbirds (Carter 1986), and brown-headed cowbirds (Smith 1981; Burgham & Picman 1989; Sealy 1992; Smith & Arcese 1994).

Several hypotheses have been proposed to explain egg pecking and egg removal behaviour by parasitic cowbirds in nature (Sealy 1992; Peer 2006). One hypothesis states that cowbirds peck or remove eggs to reduce the competition for food during the nestling period. The reduction in competition may involve not only pecking the host's eggs, but also pecking eggs of the same or other parasitic species, as the most severe competition in multiple-parasitized nests may come from other parasitic chicks

(Fraga 1998; Mermoz & Reboreda 2003). With respect to egg pecking or removal in nests that cowbirds do not parasitize, Arcese et al. (1992, 1996) posited that by destroying the total contents of the nest, cowbirds force hosts to re-nest and in this way gain new opportunities for parasitism. In addition, Massoni & Reboreda (1999) proposed that cowbirds may peck eggs to determine the degree of embryonic development of the host's eggs to further decide whether to parasitize a given nest.

These hypotheses make different predictions with respect to egg discrimination in nests that have already been parasitized, and regarding which sex should peck the eggs. One prediction of the reduction-of-competition hypothesis is that cowbirds should be able to discriminate between eggs when they are at the nest, and preferentially peck the one that represents the worse competitor for their nestlings. If the host's egg is bigger than a cowbird's egg, they should peck the former, whereas if it is smaller, or about the same size, they should peck the latter. However, this hypothesis does not require a sex-specific behaviour. Both males and females should be able to discriminate and peck eggs, especially if males follow females to the nests to copulate right after they have laid their egg (V. Ferretti & P. E. Llambías, pers. obs.) or if they visit nests on their own (Hoy & Ottow 1964). According to the forced-renesting hypothesis, cowbirds should peck all the eggs on a nest to cause re-nesting of the host pair. Thus, they are not expected to discriminate between a cowbird and the host's eggs. However, the prediction regarding which sex should peck eggs is not as straightforward and could depend on other variables such as mating system, territoriality and/or male courting and guarding behaviour. Finally, in line with the developmental-test hypothesis, both parasitic cowbird species should only peck the host's eggs, because the host's eggs should represent the only reliable source of information about the incubation stage. Moreover, female cowbirds are expected to be the only sex to peck the host's eggs, because male pecking behaviour could remove important information needed by the female to decide where to lay its eggs.

Although we did not attempt to test one hypothesis against the other, our results are more consistent with the predictions of the competition hypothesis. Unless males and females have different strategies, the embryonic development hypothesis cannot explain male pecking behaviour, because male pecking might eliminate useful information for assessing egg development in a particular host clutch. On the

other hand, if cowbirds pierce eggs to induce re-nesting, it is not clear why cowbirds should discriminate between them. The competition hypothesis is the only one able to explain both male pecking behaviour and egg discrimination. Males and females can destroy eggs in host nests and, in cases of multiple parasitism, the decision of which egg to pierce might be important (in nests of small hosts, the most severe competition comes from nestlings of other cowbirds, where in nests of bigger hosts, the most severe competition comes from the host's own nestlings).

Several field studies have reported male pecking behaviour in parasitic cowbirds. Male brown-headed cowbirds are known to pierce or remove the host's eggs (Burgham & Picman 1989; Sealy 1994). Moreover, male shiny cowbirds have been reported to pierce eggs (Hudson 1874; Friedmann 1963; Hoy & Ottow 1964) and we have observed several times male shiny cowbirds visiting nests of host species (rufous hornero and rufous-bellied thrush, *Turdus rufiventris*) in Argentina. R.M. Fraga (pers. obs.) has observed males of screaming cowbirds visiting nests of bay-winged cowbirds and has even observed a male screaming cowbird pecking the eggs of a picui dove (*Columbina picui*). Consequently, male egg pecking could be a potential cause of egg losses and should be considered when studying the costs of parasitism.

Previous studies in parasitic cowbirds have suggested that cowbirds might discriminate between different eggs. Brown-headed cowbirds kept in captivity remove small eggs more often than large host's eggs (King 1979), and bronzed cowbirds may be able to distinguish between cowbird and the host's eggs (Carter 1986). Similarly, in the brown-and-yellow marshbird (*Pseudoleistes virescens*), when host and parasitic eggs are both present in the nest, the probability of the host's egg being pierced is higher (Mermoz & Reboreda 1999).

Males and females cowbirds might have different strategies and they could be destroying eggs for different adaptive reasons, or this behaviour might just be adaptive for one sex. Alternatively, egg-pecking behaviour could be an incidental effect of encounters of non-laying cowbirds at the nests and may reflect interference competition among parasites (Nakamura & Cruz 2000). If male pecking behaviour is a common strategy, then it might explain why egg piercing by shiny cowbirds is not always followed by parasitism (Lichtenstein 1998; Mermoz & Reboreda 1999; Nakamura & Cruz 2000; Massoni & Reboreda 2002), and why shiny cowbirds pierce eggs outside

their own breeding season (Friedmann 1963; Hoy & Ottow 1964). Similarly, in the brown-headed cowbird, not all the nests where eggs are removed are parasitized (Blincoe 1935).

Future field and laboratory studies should focus on female and male pecking behaviour and egg discrimination to better understand the evolutionary significance of such tactics in parasitic cowbirds.

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