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Egg-laying behaviour by shiny cowbirds parasitizing brown-and-yellow marshbirds

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We studied the laying behaviour of shiny cowbirds, *Molothrus bonariensis*, parasitizing brown-and-yellow marshbirds, *Pseudoleistes virescens*. Shiny cowbirds lay two egg morphs, spotted and white immaculate. Brown-and-yellow marshbirds eject the white egg morph but accept the spotted morph. The incidence of parasitism in this host was 66.5%, and half of the parasitized nests had more than one shiny cowbird egg. There was a positive relationship between the number of parasitic events and the availability of nests in the laying stage, but parasitic events reached a plateau when the availability of nests was high. The distribution of parasitic eggs per nest was more clumped than expected by chance. Shiny cowbird females synchronized parasitism with host laying in 80% of the cases. They seldom parasitized nests before the host started laying or after the nest had been deserted or predated. The majority of multiply parasitized nests were parasitized by more than one female. Females that lay white eggs did not avoid parasitizing brown-and-yellow marshbird nests. Egg pecking by cowbird females resulted, on average, in one egg lost per parasitic event and the probability of being broken was greater for host eggs when host and parasitic eggs where both in the nest.

Obligate avian brood parasitism is a breeding strategy in which females lay eggs in the nests of other species, the hosts, which incubate the eggs and provide the remaining parental care for the successful rearing of the chicks.

Brood parasites face two major problems in order to avoid wasting their reproductive effort. They should synchronize their laying with the laying of hosts to ensure the successful incubation of their egg and the rearing of their chicks, and to elude intraspecific competition, they should avoid laying eggs in already parasitized nests (Payne 1977; Rothstein 1990; Kattan 1997).

In most parasitic cuckoos (Cuculinae), the female defends territories with potential host nests from other females, and therefore, multiply parasitized nests are rare (Gill 1983; Davies & de Brooke 1988; Brooker & Brooker 1989; Øien et al. 1996). Female cuckoos usually parasitize a discrete group of hosts (Davies & de Brooke 1989a; Brooker & Brooker 1990), the nests of which they monitor throughout the breeding season to synchronize laying with the host (Davies & de Brooke 1988; Brooker & Brooker 1990). Laying and removal of one host egg takes cuckoos only ca. 10 s, thus minimizing the chance of detection by the host (Brooker et al. 1988).

In contrast to the specialization observed in cuckoos, both the parasitic shiny cowbird, *Molothrus bonariensis*, and the brown-headed cowbird, *M. ater*, are extreme generalists as they use more than 200 species as hosts (Friedmann & Kiff 1985). Similarly to cuckoos, cowbird females have developed rapid egg laying (mean 40 s; Sealy et al. 1995). They may also peck or remove an egg in the nest they parasitize but these behaviours do not always occur simultaneously with parasitism, and therefore, cowbird females must visit the nest more than once (Hudson 1874; Friedmann 1929; Fraga 1985; Scott et al. 1992; Sealy 1992; Hill & Sealy 1994). Cowbird eggs do not usually match host eggs (Rothstein 1975; Mason & Rothstein 1987). In some cowbird populations, parasitism is not synchronized with the laying of the host and there are high frequencies of multiply parasitized nests (Elliott 1978; Zimmerman 1983; Fraga 1985; Freeman et al. 1990; Sealy 1992; Scott & Lemon 1996; Kattan 1997). It has been suggested that, because of their high fecundity (females can lay from 40 to 120 eggs in a breeding season; Scott & Ankney 1980; Kattan 1993), these species would

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follow a ‘shotgun strategy’ whereby parasitic females achieve reproductive success through their high fecundity rather than selecting high-quality hosts and synchronizing their egg laying with them (Rothstein 1990; Kattan 1997).

In this paper, we study the laying behaviour of shiny cowbirds while parasitizing one of their common effective hosts, the brown-and-yellow marshbird, *Pseudoleistes virescens* (Hudson 1874; Gibson 1918; Mermoz & Reboreda 1994). Shiny cowbirds were historically confined to open grasslands of South America and it is assumed that the centre of their distribution was the so-called ‘pampas’ (Hudson 1874; Friedmann 1929). More recently, this species expanded its range to the Antilles and Florida (Cruz et al. 1985; Post et al. 1993). Brown-and-yellow marshbirds inhabit marshes and humid grassland in the ‘pampas’ and neighbouring areas of southern Brazil. Its distribution is totally within the historic distribution of the shiny cowbird (Ridgely & Tudor 1989). In the ‘pampas’, shiny cowbirds show egg polymorphism, which allows eggs to be classified into one of three distinct morphs based on their maculation pattern: spotted, white immaculate and intermediate (Hudson 1920; Mason 1986b). Spotted eggs are the most abundant, but in some areas up to 50% of eggs can be white immaculate (Hudson 1920; Fraga 1978). It is assumed that each female lays eggs of only one morph (Mason 1980; Fraga 1985; Lyon 1997). Artificial parasitism experiments indicate that brown-and-yellow marshbirds eject approximately 95% of the shiny cowbird’s white egg morph and that most ejections take place within 24 h after the parasitic event (Mermoz 1996). Spotted eggs are not ejected, while intermediate eggs are ejected in roughly half of the instances (Mermoz 1996). The observed frequency of the shiny cowbird’s white egg morph in brown-and-yellow marshbird nests is very low (Orians 1985; Mermoz & Reboreda 1994). This low frequency could be the consequence of one of two phenomena: (1) shiny cowbird females that lay the white egg morph do not avoid parasitizing brown-and-yellow marshbirds, and host ejection is the cause of the low observed frequency; (2) shiny cowbird females that lay the white egg morph avoid parasitizing brown-and-yellow marshbirds because this host ejects the white egg morph (Friedmann et al. 1977).

The brown-and-yellow marshbird is the most abundant shiny cowbird host in our study area. Other hosts that nest in marshes close to brown-and-yellow marshbirds are: yellow-winged blackbird, *Agelaius thilius* (frequency of parasitism 36.6%; Massoni & Reboreda 1998), chestnut-capped blackbird, *Agelaius ruficapillus* (frequency of parasitism 48%; Lyon 1997), and scarlet-headed blackbird, *Amblyramphus holoseriseus* (frequency of parasitism 14.3%, Mermoz & Fernández 1999). In grasslands and woodlands near our study area, there are nests of rufous-collared sparrows, *Zonotrichia capensis*, firewood gathers, *Anumbius annumbi*, chalk-browed mockingbirds, *Mimus saturninus*, rufous horneros, *Furnarius rufus*, bay-winged cowbirds, *Molothrus badius*, and rufous-bellied thrushes, *Turdus rufiventris*. All of these species are effective hosts (Friedmann & Kiff 1985) and accept shiny cowbird eggs of any morph except the chalk-browed mockingbirds (Fraga 1985) and the rufous-bellied thrushes (P. Sackmann & J. C. Reboreda, unpublished data).

We investigated the egg-laying behaviour of shiny cowbirds while parasitizing brown-and-yellow marshbirds to determine whether female cowbirds synchronize parasitism with the laying of this host and avoid laying in already parasitized nests. In addition, we studied the temporal association between the events of parasitism and egg pecking to determine whether egg-pecking behaviour is affected by the presence of other parasitic eggs. Finally, we determine whether shiny cowbirds females that lay the white egg morph avoid parasitizing brown-and-yellow marshbirds, which eject the white egg morph.

METHODS

Study Area and General Methodology

The study was carried out near the town of General Lavalle (36°26′S, 56°25′W) in the province of Buenos Aires, Argentina, during the 1992–1994 breeding seasons (October–December). The study area is part of the so-called ‘flooding pampas’, a flat and low region with little of the land rising more than 4 m above sea level. It includes marshes and humid grasslands with scattered patches of native woodland trees (*Celtis tala* and *Jodina rhombifolia*) at higher elevations. The climate is temperate subhumid with a mean monthly temperature of 23°C in summer (January) and 13°C in winter (July), and ca. 1000 mm of annual rainfall (Soriano 1991). Brown-and-yellow marshbird nests are open and cup-shaped, and most of them are built on thistles (*Cynara cardunculus*, *Carduus* spp.) ca. 0.5–1.5 m above ground (Mermoz & Reboreda 1998). Nests were found mainly along the sides of an unpaved road parallel with Canal 2, an artificial drainage canal. We tagged each nest inconspicuously with a number placed in the supporting plant and we flagged the location of each nest with a coloured marker placed more than 10 m from the nest. For each nest, we assigned an initiation date corresponding to the laying of the first brown-and-yellow marshbird egg. Most nests were checked daily or every other day until they either fledged young or failed. In less than 10% of the cases (most of them during the 1992 breeding season), nests were checked at intervals of 5–7 days. Eggs were marked with waterproof ink on the first visit to the nest, and on subsequent visits, they were checked for cracks or punctures. Eggs were individually removed from the nest for better handling. Egg manipulation lasted approximately 30 s and nest visits lasted less than 2 min. The times for visiting the nests were at random. In all cases we approached the nest walking very slowly. In those cases in which the female was at the nest, she left the nest when we were at 2–3 m away. During laying and incubation, females spend approximately 15–35% and 50–70% of the time at the nest, respectively (Mermoz 1996). Therefore, the proportion of visits in which we could have disturbed the birds is probably similar to those percentages. In preliminary observations of focal nests females resumed incubation between 5 and 10 min after we left the immediate vicinity of the nest. There was no evidence that our nest visits affected nesting success as nests checked at intervals of 1–2 days did not have higher rates of mortality than nests checked weekly (Mermoz & Reboreda 1998). The rate of nest failure during our study was approximately 85%. Main causes of nest failure were predation and desertion after the loss of several eggs due to punctures inflicted by parasitic shiny cowbirds. Previous work also indicates that this species suffers high rates of nest predation and desertion (Orians et al. 1977). We considered as parasitized those nests that had cowbird eggs or nestlings at any stage of the host nesting cycle. We assigned each parasitic egg to one of the following categories (according to Mason 1986b): white immaculate, spotted and intermediate.

Timing of Egg Laying by the Parasite

We analysed the relationship between the availability of brown-and-yellow marshbird nests in laying stage and the number of parasitic events. As a consequence of predation or desertion, egg laying in 35% of brown-and-yellow marshbird nests is not completed (Mermoz & Reboreda 1998). Therefore, to estimate the actual availability of host nests in laying stage, we used nest-days as the unit of measure, where 1 nest-day is equal to 1 day of nest activity (Mayfield 1975). For example, if one nest was active for 4 days, we considered that there were 4 nest-days. This would be equivalent to two nests that were active for 2 days each, or four nests that were active 1 day each. Because some nests were not checked daily, we were unable to date some parasitic events without error. Therefore, we divided the breeding season into 5-day periods, and for each period, we determined the number of parasitic events per nest-day availability. For this analysis we excluded the 1992 data because we checked nests less frequently that year.

We considered that shiny cowbirds parasitized active nests during building, laying or incubation when parasitic eggs were laid before the first host egg, simultaneously with the laying of host eggs or after the host had completed egg laying, respectively. We considered that parasitism took place in inactive nests when the eggs were laid during the building stage in nests at which the host did not lay any eggs, or after the nest had been deserted or lost to predation.

Avoidance of Intraspecific Competition by the Parasite

In multiply parasitized nests, parasite eggs could have been laid by one or several shiny cowbird females. We assumed that each shiny cowbird female lays eggs of one colour morph (Mason 1980; Fraga 1985; Lyon 1997). In nests parasitized with different egg morphs, we estimated the number of shiny cowbird females as the number of different morphs observed. In nests parasitized with eggs of the same morph, we estimated the number of laying shiny cowbirds as the maximum number of parasitic eggs laid in 1 day. Although the use of differences in ground coloration and spotted pattern could have increased the estimation of the number of parasitic females involved, this technique is not always reliable (Sick 1958). For the estimation of the number of females that laid in multiply parasitized nests, we used nests that were checked daily during laying and early incubation (N=60 nests).

To test whether cowbird females avoided laying in nests that were already parasitized, we compared the observed frequencies of shiny cowbird eggs per nest with the number of eggs expected under a Poisson distribution (Mayfield 1965; Orians et al. 1989). Because nonparasitized nests could have been more difficult for cowbirds to detect than parasitized nests, we repeated the analysis excluding the nonparasitized nests. In this case, we compared the observed frequencies with the frequencies expected using a truncated Poisson distribution (Orians et al. 1989). We compared observed and expected frequencies with a χ^2 goodness-of-fit test. To control for a possible temporal effect, we analysed the frequencies of parasitic eggs per nest in the early to midbreeding season (October–November) and in the late breeding season (December) separately.

Frequency of White Eggs: Parasite Avoidance or Host Ejection?

The low frequency of parasitic white eggs in brown-and-yellow marshbird nests could be the result of either the host ejecting eggs of this morph (Mermoz & Reboreda 1994) or shiny cowbird females that lay white eggs avoiding this host. To discriminate between these two hypotheses we compared the frequency of white cowbird eggs in nests that had been deserted recently, as a control for the effect of the host behaviour, with the frequency in active nests. If shiny cowbird females that lay the white egg morph avoid this host, the frequency of parasitism in deserted nests should be lower than the frequency observed in nests of host species that accept the white egg morph.

Egg-pecking Behaviour

We estimated the time elapsed between the events of egg pecking and laying of the parasite egg in nests parasitized with one cowbird egg that were monitored daily from 1 day before parasitism occurred. We also included in our analysis those multiply parasitized nests in which all the parasitic events occurred on the same day.

Because 50% of parasitized brown-and-yellow marshbird nests were multiply parasitized (see Results), a shiny cowbird female is likely to have the opportunity to peck eggs of the host, of the other parasite, or both. To determine whether pecking was at random or whether there were preferences for eggs of any species, we compared the proportion of host and parasitic eggs that were pecked using a Fisher's exact test (Daniel 1978). For this analysis, we only considered nests that had host and parasitic eggs 24 h before the event of egg pecking.

Table 1. Shiny cowbird parasitism in brown-and-yellow marshbird nests

Year	Nests	Parasitism (%)	Parasite eggs
1992	73	74.3	1.9±0.16 (53)
1993	129	69.7	2.1±0.32 (90)
1994	216	62.0	1.93±0.11 (133)

Number of nests found per year, percentage of parasitized nests and mean±SE of shiny cowbird eggs per parasitized nest. Number of parasitized nests in parentheses.

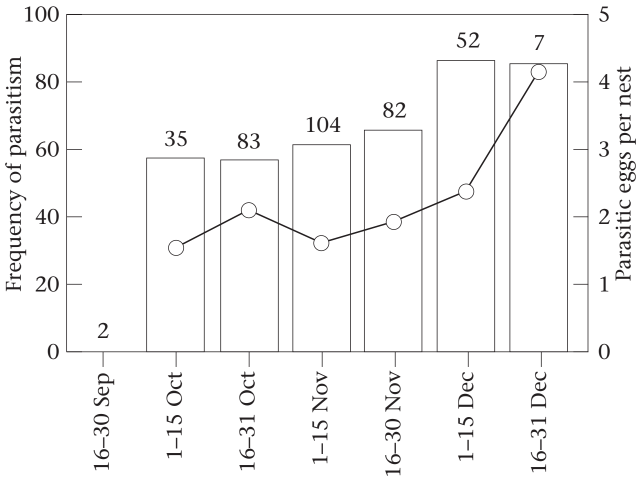

Figure 1. The frequency of parasitism in brown-and-yellow marshbird nests throughout the breeding season (□) and the mean number of shiny cowbird eggs laid per parasitized nest (○). Numbers above bars indicate the number of nests. The data correspond to 345 nests found during the 1993–1994 breeding seasons.

Results are presented as means ± SE. All statistics are two tailed.

RESULTS

Incidence of Parasitism

The frequency of shiny cowbird parasitism in brown-and-yellow marshbird nests was 66.5%. There were no differences among years either in the proportion of parasitized nests (Table 1; χ^2 test of heterogeneity for year: $\chi^2_2=4.5$, NS), or in the number of shiny cowbird eggs per parasitized nest (Kruskal–Wallis test for year: $H_2=2.01$, NS). The number of shiny cowbird eggs per parasitized nest was 2.09 ± 0.14 (range 1–8; $N=110$ nests found during building or laying that reached the incubation stage). In 52.4% of the parasitized nests, there were two or more cowbird eggs. We observed an increase in the proportion of parasitized nests and in the number of cowbird eggs per nest as the breeding season progressed (Fig. 1; proportion of parasitized nests: χ^2 test of heterogeneity for month: $\chi^2_2=12.78$, $P<0.01$; number of cowbird eggs: Kruskal–Wallis test for month: $H_2=9.36$, $P<0.01$; post hoc contrasts $P<0.05$; Siegel & Castellan 1988).

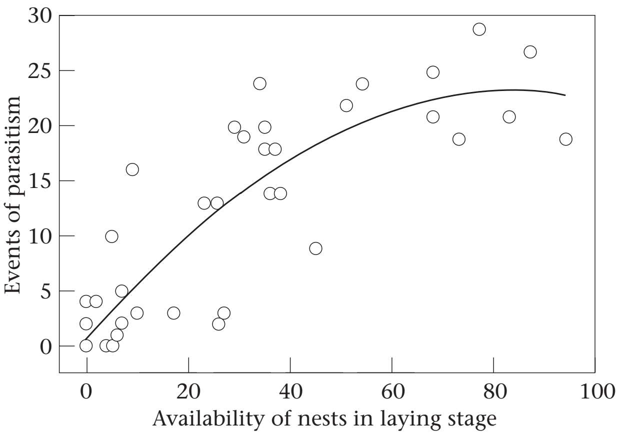

Figure 2. Events of parasitism (in 5-day periods) as a function of the availability of brown-and-yellow marshbird nests in laying stage. Nest availability was measured in nest-days. The data correspond to 38 periods of 5 days during the 1993–1994 breeding seasons. The events of parasitism with zero availability correspond to those that took place in inactive nests or in active nests during the building or incubation stages. The adjusted function was $Y=0.52+0.54X+0.0032X^2$.

Timing of Egg Laying by the Parasite

We analysed the relationship between the availability of brown-and-yellow marshbird nests in the laying stage and the number of parasitic events with a polynomial regression (Zar 1996). The number of parasitic events fitted a quadratic function of the availability of nests during laying (Fig. 2; regression analysis: $R^2=0.72$, $F_{2,35}=46.8$, $P<0.0001$; quadratic term: $t_{35}=-2.8$, $P<0.01$; linear term: $t_{36}=5.47$, $P<0.0001$; intercept: $t_{36}=0.33$, NS).

Shiny cowbirds parasitized brown-and-yellow marshbird nests more frequently before the start of full incubation (laying of the penultimate egg). We were able to assign unequivocally the timing of parasitism within 1 day of the host nesting cycle in 119 cases. In 78% of these cases, parasitism took place during the host laying period (Fig. 3). In addition, there were another 244 cases for which we only knew whether the nest was active or inactive when it was parasitized. Parasitism occurred before the host had started egg laying in only nine of these 363 cases (the nine cases occurred in three nests). Similarly, only 20 of 363 parasitic events occurred in nests that had been deserted or depredated ($N=10$ nests).

Avoidance of Intraspecific Competition by the Parasite

Shiny cowbird females did not avoid parasitizing nests that were already parasitized by other females. Among the 60 multiply parasitized nests that were observed daily during egg laying and early incubation, at least 35 (58.3%) were parasitized by more than one female because they received more than one parasitic egg per

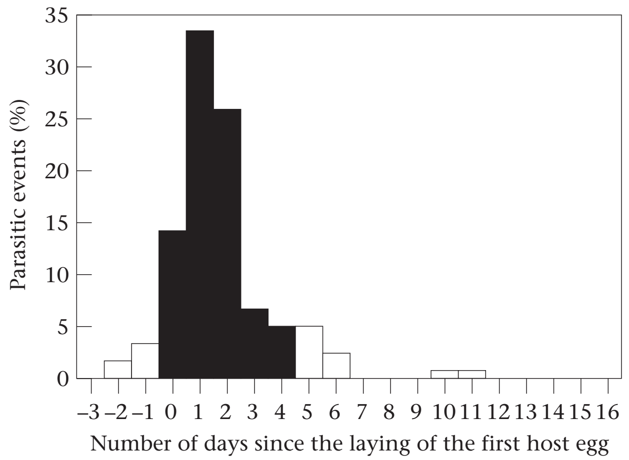

Figure 3. Frequency distribution of parasitic events (*N*=119) at different stages of the nesting cycle of brown-and-yellow marshbirds. The black bars indicate the laying period of the host. Day 0 corresponds to the laying of the first brown-and-yellow marshbird egg. In this species, clutch size is four to five eggs, and the incubation starts with the laying of the penultimate egg and lasts 13–15 days.

day, or were parasitized with more than one egg morph. Among these 35 nests, 28 were parasitized by at least two females, six by at least three females and one by at least four different females.

To test whether shiny cowbird females avoid laying in already parasitized nests, we compared the observed frequencies of parasitic eggs per nest with those expected under a random (Poisson) distribution. Because the proportion of parasitized nests and the number of cowbird eggs per nest increased towards the end of the breeding season (December), we analysed separately the frequencies of parasitic eggs per nest in the early to midbreeding season (October–November) and in the late breeding season (December). During October–November, we observed a higher number of nonparasitized nests and nests with more than five parasitic eggs than expected by chance (Fig. 4a; χ^2 goodness-of-fit test for October and November with nests having five and more than five eggs combined: Poisson χ^2_4=19.9, P<0.0001). However, at the end of the breeding season (December), when the availability of host nests declined, the observed frequencies did not differ from those expected under a Poisson distribution (Fig. 4b; χ^2 goodness-of-fit test for December with nests having five and more than five eggs combined: χ^2_4=7, NS). We repeated the analysis excluding the nonparasitized nests, as they could have been more difficult for parasitic females to detect. In this case, the observed frequencies differed from those expected under a truncated Poisson distribution in both October–November and December (Fig. 4a, b). Again, we observed a higher number of singly parasitized nests and nests with more than five parasitic eggs than expected by chance (χ^2 goodness-of-fit test with nests having five and more than five eggs combined: October and November: χ^2_3=17.9, P<0.0001; December: χ^2_3=11, P<0.02).

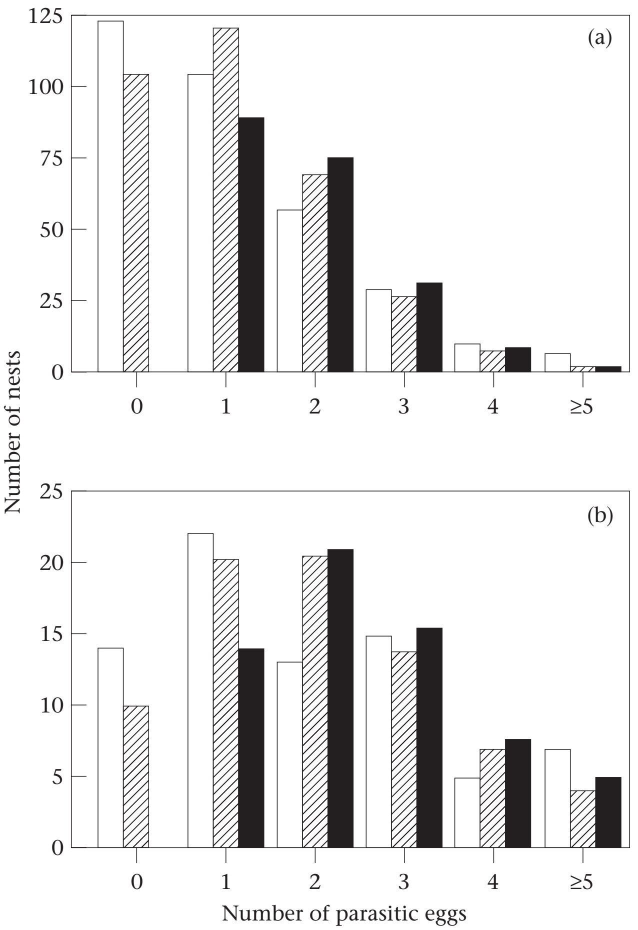

Figure 4. Frequency distribution of shiny cowbird eggs in brown-and-yellow marshbird nests during (a) the early to midbreeding season (October–November) and (b) the late breeding season (December). The bars correspond to the observed distribution (□), the distribution expected by chance (Poisson: ▨) and the distribution expected by chance taking into account only parasitized nests (truncated Poisson: ■).

Frequency of White Eggs: Parasite Avoidance or Host Ejection?

During the study we recorded 541 events of parasitism. Ninety per cent (486/541) of the parasitic eggs were spotted, 6% (33/541) were white and 4% (22/541) were intermediate. The frequency of white eggs in nests that were attended by the host (active nests) was lower than in nests that were unattended (inactive nests). Only 4.6% (15/335) of shiny cowbird eggs that were laid in active nests were white, while the frequency in inactive nests was 24% (7/29; Fisher's exact test: P=0.002). The percentage of white eggs in inactive nests was similar to the percentage recorded in nests of yellow-winged blackbirds, *Agelaius thilius*, a host that accepts white shiny cowbird eggs. In a parallel study conducted in the same area (Massoni & Reboreda 1998), 20.4% (20/98) of the parasitic eggs observed in nests of yellow-winged blackbirds were white (Fisher's exact test: P=0.79).

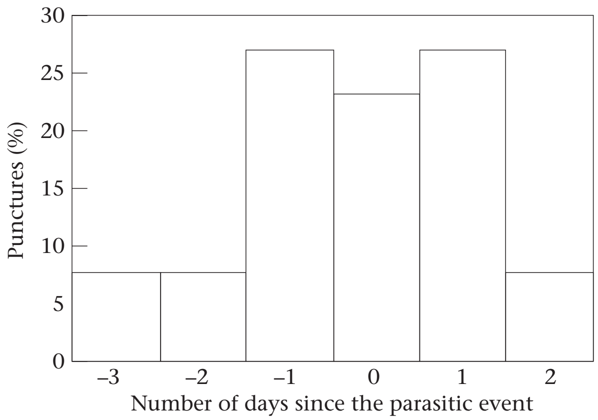

Figure 5. Frequency distribution of puncture events as a function of the number of days elapsed since the parasitic event. Negative values correspond to those cases in which egg pecking preceded parasitism.

Egg-pecking Behaviour

We determined the temporal association between the laying of the parasitic egg and the pecking of eggs in 18 parasitized nests that were followed daily since the building stage (14 nests were singly parasitized and four were multiply parasitized the same day). If we assume, like Sealy (1992), that the female that laid in a nest was the same one that pecked or removed eggs in that nest (see Discussion), pecking took place from 1 day before to 1 day after the parasitic event in 76.8% of the instances (Fig. 5). To avoid underestimating host egg losses associated with parasitism, we used data from parasitized nests that were under observation during this 2-day interval. We used data from all singly parasitized nests that were active and observed daily during that interval and all multiply parasitized nests that were monitored since the day before the first parasitic event until 1–2 days after the last parasitic event.

Hosts lost fewer eggs in singly parasitized nests than in multiply parasitized nests (0.83 ± 0.21 and 1.55 ± 0.18 eggs, respectively; Mann–Whitney *U* test: $U'=574$, $N_1=23$, $N_2=36$, $P<0.001$). However, when we considered egg losses per parasitic event, these differences were no longer significant (host egg losses/parasitic eggs laid: 0.83 ± 0.21 versus 0.60 ± 0.07; Mann–Whitney *U* test: $U'=433$, $N_1=23$, $N_2=36$, NS). We detected losses of shiny cowbird eggs in 58% (21/36) of the multiply parasitized nests as well as in 13% (3/23) of singly parasitized nests. Losses of cowbird eggs were higher in multiply than in singly parasitized nests (0.13 ± 0.07 eggs versus 0.78 ± 0.14 eggs; Mann–Whitney *U* test: $U'=597.5$, $N_1=23$, $N_2=36$, $P<0.001$). The differences still held when shiny cowbird egg losses were standardized to the number of parasitic events (parasite egg losses/parasite eggs laid: 0.13 ± 0.07 versus 0.28 ± 0.04, respectively; Mann–Whitney *U* test: $U'=561$, $N_1=23$, $N_2=36$, $P<0.001$).

To determine whether shiny cowbird females show a preference for pecking host or parasitic eggs, we compared the proportion of host and parasitic eggs that were punctured by shiny cowbird females in nests that had eggs of both species ($N=54$). Host eggs had a higher probability of being punctured than parasitic eggs (host eggs: 46/147, 31.3%; parasitic eggs: 14/111, 12%; Fisher's exact test: $P=0.0003$). Brown-and-yellow marshbirds usually remove punctured eggs within 24 h. However, some cases in which we did not observe the punctured egg could have been the result of partial predation (see Discussion). Therefore, to be more conservative, we repeated the previous analysis excluding the cases in which we did not observe a punctured egg. Again, host eggs had a higher probability of being punctured than parasitic eggs (host eggs: 24/67, 35.8%; parasitic eggs: 4/54, 7.4%; Fisher's exact test: $P=0.004$). The higher frequency of punctures of host eggs was also observed in nests in which more than one shiny cowbird female laid eggs (i.e. nests parasitized with different egg morphs or that received more than one parasitic egg per day). In those nests, the percentage of host and parasitic eggs pecked or removed was 45.4 (20/44) and 8.9 (4/45), respectively (Fisher's exact test: $P<0.001$).

DISCUSSION

Incidence of Parasitism

The frequency of parasitism on brown-and-yellow marshbird observed in this study is similar to the range of 60–78% recorded for other hosts in areas of the shiny cowbird's historical distribution (Sick 1958; King 1973; Fraga 1978, 1985; Salvador 1984; Cruz et al. 1990). However, two blackbird species nesting in the same area were parasitized less frequently during the 1994 breeding season (48% in the chestnut-capped blackbird, Lyon 1997; 36.6% in the yellow-winged blackbird, Massoni & Reboreda 1998). This apparent higher incidence of shiny cowbird parasitism in brown-and-yellow marshbird nests could indicate a preference for this host. Neither of these blackbird species ejects shiny cowbird eggs of either morph, and when parasitized, they can successfully rear shiny cowbird chicks (Friedmann & Kiff 1985; Massoni & Reboreda 1998). In contrast, brown-and-yellow marshbirds eject white eggs laid after their own eggs and also eject most eggs of any morph laid before their own eggs (Mermoz 1996). Thus, shiny cowbirds would not be expected to show a preference for brown-and-yellow marshbirds except for this host's high capability for rearing cowbird chicks (they can rear up to four cowbird fledglings per nest; Mermoz 1996). Alternatively, the higher frequency of parasitism in brown-and-yellow marshbird nests could occur because it is easier for shiny cowbirds to find and parasitize their nests.

Timing of Egg Laying by the Parasite

The positive relationship between the number of parasitic events and the number of nests in the laying stage indicates that shiny cowbird females respond to the availability of nests in laying stage. This result could have arisen either because there was an increase in the number of females involved in the parasitic events or because each female laid more eggs.

Shiny cowbird females synchronized their laying with the laying of brown-and-yellow marshbirds in approximately 80% of the cases. Both the high degree of synchronization and the low frequency of parasitism in inactive nests or nests during the building stage would indicate that shiny cowbird females monitored the nests before parasitizing them. It is unlikely that the low frequency of parasitism that we observed during the building stage can be attributable to undetected events of parasitism because we started monitoring nests that were later parasitized 3–5 days before the start of the laying by the host. However, because most shiny cowbird eggs are laid before the host eggs are ejected (Mermoz 1996) we may not have detected all parasitic events.

The high degree of laying synchrony between shiny cowbirds and brown-and-yellow marshbirds is similar to that observed in yellow-winged blackbirds (Massoni & Reboreda 1998), but it is not consistent with data from other hosts. In a study with house wrens, *Troglodytes aedeon*, conducted in Colombia, only 33% of parasitism events by shiny cowbirds were synchronized with laying by the host, while in 55 and 12% of the cases, parasitism took place during building or incubation, respectively (Kattan 1997). Kattan suggested that for this host, a better synchronization is precluded because of the difficulties that shiny cowbirds have in gaining access to cavity nests with small entrances. Others have described shiny cowbirds as brood parasites that 'waste their eggs' because they do not synchronize their laying with that of the host, but results from these studies could also be biased by inclusion of data of hosts with doomed nests (Hudson 1874, 1920; Friedmann 1929; Hoy & Otow 1964). Our results indicate that when shiny cowbirds can ascertain the stage of the nest, they can synchronize parasitism with laying of the host. However, as hosts differ widely in nesting behaviour and antiparasitic responses, it would be unlikely that shiny cowbirds could synchronize their laying with the laying of the host in all cases. Thus, shiny cowbirds could be 'shotgun' or 'selective layers' depending on the host species or nest type.

Avoidance of Intraspecific Competition by the Parasite

We found a high proportion of multiply parasitized nests that received more than one egg morph or more than one egg per day. This result indicates that shiny cowbird females: (1) did not avoid nests that were already parasitized by other females; and (2) they did not effectively defend host nests from other females. This is the first study of shiny cowbirds that presents direct evidence of several females parasitizing the same nest. In a previous study, Lyon (1997) estimated that all cases of multiple parasitism in chestnut-capped blackbird nests involved more than one female. However, in that study the number of different females laying in a nest was estimated by differences in the pattern of egg coloration and morphology. It is important to point out that, because of the criteria we used (see Methods), our estimation of the number of females that laid in a nest is rather conservative and that the real value could be even larger.

Shiny cowbird females did not avoid parasitizing already parasitized brown-and-yellow marshbird nests. The distribution of shiny cowbird eggs per nest was random, and even clumped in contrast to that expected had females avoided previously parasitized nests. When we excluded nonparasitized nests, because they may have been more difficult for the parasite to detect, the distribution of cowbird eggs remained clumped. Shiny cowbird females that laid white eggs did not appear to avoid parasitizing brown-and-yellow marshbird nests (see below). Therefore, the recorded number of nonparasitized nests could have been larger than the number expected at random because we may not have detected many or most nests that were only parasitized with white (ejected) eggs. However, this putative bias cannot explain the high number of nests parasitized with more than four shiny cowbird eggs. In addition, the clumped pattern of parasitism has also been reported in shiny cowbirds parasitizing acceptor hosts like the chestnut-capped blackbird (Lyon 1997) and the house wren (Kattan 1997). The clumped pattern could arise if some nests are defended less or are detected more easily and therefore have a higher probability of parasitism (Kattan 1997), or if shiny cowbird females search for nests in groups (Wiley 1988). In our study area, we observed shiny cowbird females searching for nests either alone, followed by a male, a female or by several individuals (males and/or females). Alternatively, the nonrandom pattern could arise if some females parasitize the same nest repeatedly, although Lyon (1997) suggested that shiny cowbird females never lay more than one egg per nest.

Lack of Host Selection by Females that Lay White Eggs

Host selection has evolved in some parasitic species like the common cuckoo, *Cuculus canorus* (Davies & de Brooke 1989a, b). Among the most generalist parasitic cowbirds, individual female brown-headed cowbirds parasitize multiple host species (Fleischer 1985). This species does not appear to select hosts as it does not avoid parasitizing species that eject their eggs nor does it avoid low-quality hosts (Rothstein 1976; Scott 1977; Briskie et al 1990; Neudorf & Sealy 1994). There is no information about how many hosts shiny cowbirds use. Shiny cowbirds differ from brown-headed cowbirds in that shiny cowbirds show egg polymorphism. Although some hosts eject the shiny cowbird's white egg morph other hosts accept any morph (no host accepts the white eggs and rejects spotted eggs). Only three species, the brown-and-yellow marshbird, the chalk-browed mockingbird and the rufous-bellied thrush, eject the white egg morph, while another 15 hosts tested accept any morph (Fraga 1978, 1985; Mason 1986a, b; Mermoz & Reboreda 1994; Lyon 1997; Massoni & Reboreda 1998; P. Sackmann & J. C. Reboreda, unpublished data). Shiny cowbird females that laid white eggs did not avoid parasitizing brown-and-yellow marshbird nests despite the fact that white eggs are ejected by this host. If shiny cowbirds use more than one host during their lifetime and do not selectively choose hosts, as a matter of chance, the majority of their eggs would be laid in nests of acceptor species. Shiny cowbird females can lay up to 100 eggs in a breeding season (Kattan 1993). Although the low energy content of the eggs (Kattan 1995) and the low number of rejecting hosts could ameliorate the selective pressure for the evolution of host selection in shiny cowbirds, a decrease would be expected in the frequency of the white egg morph if females that lay these eggs do not selectively choose their hosts. It has been suggested that the maintenance of white eggs could be explained without assuming an adaptive value of that trait. Shiny cowbird females that lay white eggs could be 'hybrids' of two strains of the spotted morph, and may be incapable of producing egg pigmentation because of a genetic incompatibility in the loci responsible for colour formation (Lyon 1997).

Egg-pecking Behaviour

The frequency of egg pecking by shiny cowbirds depends on the host studied, and in some populations egg pecking is totally absent (Post & Wiley 1977; Wiley & Wiley 1980; Kattan 1997). Female cowbirds should peck eggs before parasitizing the nest to avoid breaking their own eggs accidentally. In brown-headed cowbirds, pecking or egg removal occurs after the parasitic event in 46% of the instances (Sealy 1992). In our study, pecking preceded parasitism in 64.5% of the cases. However, there are alternative explanations for the events of puncture that occurred after parasitism. Some of these punctures could have been made by females that laid white eggs. As we mentioned above, these eggs are quickly ejected, and therefore, we could have missed the event of parasitism. In addition, not all puncture events are necessarily followed by parasitism. In the yellow-winged blackbird, 30.2% of the nests with egg punctures were not parasitized (Massoni & Reboreda 1998). As this species accepts all shiny cowbird eggs, this result indicates that there are cases in which punctures are not followed by parasitism. Finally, some authors (Hudson 1874; Friedmann 1963; Hoy & Otow 1964) have suggested that shiny cowbird males may also peck eggs.

In nests in which host and parasitic eggs were present when the event of pecking occurred, host eggs were punctured more frequently than parasitic eggs. This apparent 'selective' pecking would be adaptive if all the parasitic eggs were laid by the same female, and would imply that shiny cowbird females recognize their own eggs. Egg recognition by shiny cowbird females may be selected to minimize the accidental breakage of their own eggs when egg pecking occurs after parasitism. Shiny cowbird eggs of the spotted morph and brown-and-yellow marshbird eggs are very similar in appearance, and this host cannot distinguish between them (Mermoz & Reboreda 1994). Therefore, we cannot expect that the parasitic females, which are more briefly in contact with their eggs and do not have the opportunity to see their eggs together, to have developed a better discrimination than the host (Brooker & Brooker 1990). A more parsimonious interpretation of our results is that events of egg pecking are a by-product of differences between their resistance of eggs to breakage by punctures. Shiny cowbird eggs are more spherical than brown-and-yellow marshbird eggs (length/width: 1.25 ± 0.005, N=121 versus 1.36 ± 0.004, N=302, respectively; t test: $t_{421}=14.8$, $P<0.001$), and although they are smaller (Mermoz & Reboreda 1994), their eggshells are thicker (Schönwetter 1984). Both characteristics could make them more resistant to breakage (Picman 1989). Other indirect evidence against the hypothesis of egg discrimination by shiny cowbird females is that we also observed a higher proportion of host eggs with punctures in nests parasitized by more than one female. This is not what would be expected if parasitic females could recognize their own eggs. In this case, the best strategy for shiny cowbird females would be to puncture any parasitic egg in the nest. Because these eggs have a shorter incubation period than the host eggs (Mermoz & Reboreda 1994; Mermoz 1996), they will be the first eggs to hatch and therefore, the main competitors in the nest.

Brown-and-yellow marshbirds usually remove the punctured eggs within 24 h (Mermoz 1996). According to some authors, shiny cowbirds also remove eggs from host nests (Hoy & Ottow 1964). Although these behaviours could explain the disappearance of host and parasitic eggs, we cannot rule out that some cases in which we did not observe the punctured egg could have been the result of partial predation. If partial predation were an important cause of egg losses, parasitized and nonparasitized nests should lose eggs at the same rate (Sealy 1992). However, although there is no difference in clutch size between nonparasitized and parasitized nests, at the end of incubation, nonparasitized nests have on average 1.5 more eggs than parasitized nests (Mermoz 1996). Therefore, we assumed that egg losses that occurred in nests in which we did not observe the punctured eggs were caused either by host removal of eggs pecked by shiny cowbirds or egg removal by shiny cowbirds.

There are several hypothesis about the possible adaptive value of egg pecking and removal by cowbirds (Scott et al. 1992; Sealy 1992; McMaster & Sealy 1997). The breakage of host eggs could increase the success of shiny cowbird nestlings, as it reduces the number of potential competitors. This effect should not be very important in brown-and-yellow marshbird nests because, as mentioned above, shiny cowbird females synchronize parasitism with host laying in near 80% of the instances. Furthermore, the incubation period of shiny cowbird eggs is, on average, 2 days shorter than that of this host. Although, at the time of hatching, brown-and-yellow marshbird chicks are 20% heavier than shiny cowbird chicks, these differences disappear if the host hatches 1 day after the parasite (Mermoz 1996). Therefore, hatching 2 days in advance provides parasitic nestlings with a clear advantage over host chicks because they will be the biggest chicks in the nest during the nestling period. Of the 85 shiny cowbird nestlings we observed, only eight died by starvation and seven of these cases occurred in nests that had between two and four shiny cowbird chicks.

Another explanation for selective advantages associated with egg removal is that it improves incubation efficiency of the parasitic egg (Brown & Brown 1988; Lombardo et al. 1989; Rothstein 1990; Lerkelund et al.

1993). Nevertheless, undamaged shiny cowbird eggs did not have a higher hatchability in brown-and-yellow marshbird nests at which the number of eggs was decreased by pecking than in nests without removals (Mermoz 1996).

Shiny cowbirds are opportunistic brood parasites that interact with a large number of hosts. Therefore, it is likely that the behaviour of shiny cowbirds is modulated by an 'average host' in a kind of 'diffuse interaction'. Thus, certain behaviours that do not appear to be appropriate for a given host, like egg pecking, could be appropriate for others.

CONCLUSIONS

Some characteristics of egg laying by shiny cowbirds supports the hypothesis that they are 'selective layers' while others favour the hypothesis of a 'shotgun strategy'. Shiny cowbirds synchronized parasitism with host laying in near 80% of the instances and they seldom parasitized nests that were deserted or nests at which the host did not lay. However, they did not avoid laying in already parasitized nests as more than one female laid in at least 60% of the multiply parasitized nests. Similarly, females that laid white eggs did not appear to select hosts, as they did not avoid parasitizing brown-and-yellow marshbird nests despite the fact that this host ejects white eggs. Egg pecking by shiny cowbirds preceded parasitism and resulted, on average, in one egg lost per parasitic event. In nests in which host and parasitic eggs were present when shiny cowbirds pecked, host eggs had a higher probability of being broken. The thicker eggshell and the spherical form of the parasitic eggs may protect them from conspecific punctures.

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