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Cues used by shiny cowbirds (*Molothrus bonariensis*) to locate and parasitise chalk-browed mockingbird (*Mimus saturninus*) nests

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Abstract Unlike other birds, shiny cowbirds (*Molothrus bonariensis*) must locate host nests where to lay their eggs and then decide whether to parasitise them. They should also synchronise their laying with that of the host to increase the survival of parasite egg and young. Shiny cowbirds can discover nests using host behaviour as a cue, or by searching the habitat without need for the presence of a host. Besides, they can synchronise parasitism with host laying by monitoring nests during building and laying, or directly by assessing the degree of development of embryos through the puncture of host eggs. Alternatively, synchronization can arise by lower nest attentiveness during host laying. We determined the extent of synchronization between laying of shiny cowbirds and chalk-browed mockingbirds (*Mimus saturninus*) and estimated if parasitism was negatively associated with host nest attentiveness. We also conducted an experiment to test if host activity was necessary to locate nests, and if puncture of host eggs was a cue for deciding parasitism. Shiny cowbirds synchronised parasitism with host laying in 75% of the cases and synchronization was not explained by lower host nest attentiveness during laying. Shiny cowbirds located nests without need for presence of a host, but the decision of parasitising the nest depended on host activity at the nest. The information that shiny cowbirds could obtain through egg punctures was not necessary for deciding parasitism. Our results indicate that shiny cowbirds rely on the precise timing of their eggs and avoid laying in unsuitable nests.

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Introduction

Obligate avian brood parasites, like the cuckoos and cowbirds, lay eggs in nests of other species, the hosts, which incubate the parasitic eggs and raise their chicks (Ortega 1998; Rothstein and Robinson 1998; Davies 2000). Unlike other birds, brood parasites must find nests in where to lay their eggs, and to do this, they can use host behaviour as a cue. For example, female common cuckoos (*Cuculus canorus*) locate nests by watching host's nest-building activities from visual vantage points in trees (Wyllie 1981; Honza et al. 2002) which results in that hosts breeding close to trees to suffer a higher risk of parasitism (Alvarez 1993; Moskát and Honza 2000). Similarly, brown-headed cowbirds (*Molothrus ater*) and shiny cowbirds (*Molothrus bonariensis*) spend morning hours on breeding grounds watching host behaviour (Friedmann 1929; Hann 1941; Norman and Robertson 1975; Wiley 1988) and use host activity during nest building as a cue for finding nests (Wiley 1988; Banks and Martin 2001). Female cowbirds may also locate host nests by using conspicuously noisy searching (i.e. flushing the host from its nest, Norman and Robertson 1975; Wiley 1988; Strausberger 1998). It has been suggested that cowbirds can also locate nests by using host nest-defence responses directed towards them, a "nesting cue hypothesis" (Carter 1986; Smith et al. 1984; Uyehara and Narins 1995), but Gill et al. (1997) and Clotfelter (1998) found no experimental support for this hypothesis. In addition to the use of host behaviour, cowbirds could discover nests by searching the habitat without need for presence of a host, but the evidence for the use of this strategy is scarce (Norman and Robertson 1975; Kattan 1997; Svagelj et al. 2003).

After locating a host's nest, parasites must decide whether to parasitise it. Cowbirds should lay at the time the chances of survival of the parasite egg and young are maximum. If the parasite egg is laid before hosts begin to lay, it is more likely to be rejected (Rothstein 1986; Sealy 1992, 1995). Likewise, if the cowbird egg is laid after the host has begun incubation, it may or may not hatch after the host eggs, thus decreasing the chances of the parasite chick of competing successfully against host chicks for food.

Recent studies using genetic parentage analysis indicate that realised female fecundity of brown-headed cowbirds is relatively low (Hahn et al. 1999; Alderson et al. 1999; Strausberger and Ashley 2003; Woolfenden et al. 2003) compared with previously published estimates (Payne 1976; Scott and Ankney 1980, 1983; Jackson and Roby 1992; Kattan 1993). In consequence, the reproductive value of each cowbird egg would be higher than previously supposed and therefore, there are likely to be strong selection pressures on cowbirds to synchronise their laying with that of the host and to avoid laying in unsuitable nests. In agreement with this view, some studies reported that cowbirds synchronise parasitism with host laying in 70–80% of the cases (Massoni and Reboreda 1998; Mermoz and Reboreda 1999), and they do not parasitise before the host begins laying or after the nest is abandoned (Strausberger 1998; Mermoz and Reboreda 1999, but see Sealy 1995; Kattan 1997 for reviews).

Synchronization between shiny cowbird laying and that of the host could simply arise by lower nest attentiveness during host laying. During this period, in hosts that begin incubation with the penultimate egg, females and males may spend more time away from the nest when foraging and when mate guarding (Moller and Birkhead 1991). Synchronization also might be the result of cowbirds monitoring nest activities during building and laying. Wiley (1988) reported that female shiny cowbirds closely monitor nest status with frequent visits that peak on the host's first day of laying. Similarly, Kattan (1997) described that females monitor nests during early and late nest building and during laying. In addition, it has been proposed that host egg punctures inflicted by shiny cowbirds when they visit host nests might allow them to assess the degree of development of the embryos and, using this information, decide whether to parasitise the nest (Massoni and Reboreda 1999). This behaviour would be particularly convenient when cowbirds find a nest with a complete clutch and therefore they lack information about the time elapsed since the host has begun incubation.

In this paper, we evaluated the extent of synchronization between parasitism and host laying and if parasitism is negatively associated with host attention within and among nests. In addition, we tested if shiny cowbirds use host activity to locate nests and information obtained through the puncture of host eggs to parasitise the nest. Previous studies have used parasitism as an evidence of nest finding, and therefore they were unable to discriminate between the location of a nest and the decision of parasitising that nest (Lowther 1979; Wiley 1988; Grieef and Sealy 2000, Robinson and Robinson 2001; but see Svagelj et al. 2003 for a review). In this study, we used the presence of punctures in host eggs as evidence that cowbirds had located host nests, which provided us the unique opportunity to distinguish between cues used for finding nests from parasitism decisions. To test the hypotheses, we conducted an experiment in one of its common hosts, the chalked-browed mockingbird (*Mimus saturninus*). In this experiment, we controlled for host activity (nests with or without activity) and for the information that shiny cowbirds could obtain through the puncture of host eggs (nests with natural or with plaster eggs). If cowbirds used host activity to locate nests, we would expect a higher frequency of egg punctures in nests with host activity. Regarding the decision of parasitising a nest, if shiny cowbirds used only host activity to decide parasitism, we would not expect differences in parasitism between active nests with natural or plaster eggs, whilst if they used also punctures, parasitism should be higher in active nests with natural eggs.

Materials and methods

Study site

The study was carried out near the town of Magdalena (35° 08′ S, 57° 23′ W) in the province of Buenos Aires, Argentina, from October 2002 to January 2003 and from October 2003 to January 2004. The study area is a nearly flat and marshy grassland, with implanted pastures and old and second growth stands dominated by Tala (*Celtis tala*) and Coronillo (*Scutia buxifolia*).

Study species

Chalk-browed mockingbirds breed from mid-September until mid-January. They build open nests, and the most favoured nest sites are the shrubs or trees with dense foliage. In our study area, most nests were built in Tala, Coronillo and Molle (*Schinus longifolius*) at a height of 1.5–2.5 m. The nest is a large open cup of twigs (outer diameter 20–25 cm) lined with fibres and horsehair. Mockingbirds lay 3–5 eggs (mean±SE: 3.6±0.09, n=49 clutches). Incubation starts with the laying of the penultimate egg and lasts 13–14 days. Chicks leave the nest when they are 12–14 days old and weigh 50–55 g. Adult weight is approximately 70–75 g. This species is commonly parasitised by shiny cowbirds (Fraga 1985; Sackmann and Reboreda 2003).

Timing of parasitism and egg punctures

We found 165 active mockingbird nests (i.e. nests where the host began laying), 74 during the first year and 91 during the second year. The frequency of parasitism was 73% (54 out of 74 nests) and 60% (55 out of 91 nests), for the first and second year, respectively, whilst the intensity of parasitism for each year was 2.4±0.21 (n=54 nests) and 2.0±0.16 (n=55 nests) cowbird eggs per parasitised nest. Frequency and intensity of parasitism did not differ significantly between years (frequency: chi-square test, χ^2=2.3, P=0.13; intensity: Mann–Whitney U test: U'=1670, Z=1.18, P=0.24).

We found nests by focusing on mockingbird activity and then inspecting potential nesting sites within the territory of the pair. We are confident that we found all mockingbird nests within our study area. Nests were visited daily or every other day during laying and incubation. Nest visits were conducted from 1100 to 1800 h. At each visit, we recorded the number of host and parasite eggs and the occurrence of punctures in them. Punctures made by shiny cowbirds result in one big usually triangular hole through the eggshell. Shiny cowbird punctures are very different to the ones made by house wrens, *Troglodytes aedon* (small punctures usually traversing the eggshell). We never observed wren-like punctures in eggs of either chalk-browed mockingbirds or shiny cowbirds.

We estimated the timing of parasitism from a sample of 180 parasite eggs laid in 130 nests found before mockingbirds began laying or during laying. In 47% of the cases, we could estimate directly the date of parasitism (i.e. the nest was visited in consecutive days and parasitism occurred between visits). In the cases where the nest was not visited in consecutive days (i.e. every other day), we assumed that in half of the cases, the egg was laid the day before and in the other half the same day we visited the nest. We calculated the average number of parasitic eggs laid per nest during each day of the nesting cycle by dividing the number of eggs laid at a given day by the number of nests that was active that day.

In the same sample of 130 nests, we also estimated the timing of egg punctures. In these nests, we recorded 137 puncture events. In 79 cases (58%), we observed the host egg punctured whilst in the other 58 cases (42%), we observed that one host egg had disappeared between visits. In these cases, we assumed that the disappearance of the egg was the result of host nest sanitation (Kemal and Rothstein 1988) after the egg was punctured by cowbirds. We consider unlikely that the disappearance of host eggs was the result of partial depredation of nests, as we did not observe partial depredation in 13 nests where the host eggs were replaced by plaster eggs (see below). In addition, most host eggs disappeared during the laying period (42 out of 58 cases), the time when 74% of parasitism occurred (see "Results"). We calculated the average number of host eggs that was punctured in a nest during each day of the nesting cycle by dividing the number of host eggs punctured at a given day by the number of nests that was active that day.

To estimate the temporal association between puncture and parasitic events within a nest, we used a sample of 37 nests that was single parasitised (in multiple-parasitised nests, it is not possible to assign puncture to parasitic events unambiguously). We assumed that in single-parasitised nests, the same female was involved in the parasitic and puncture events.

Nest attentiveness, parasitism and egg punctures

We estimated the proportion of time that the nest was attended through focal observations made from a blind located at least 30 m away from the nest and using 10×50 binoculars. Observations lasted from 55 to 90 min and were conducted from 0630 to 1100 h. Shiny cowbirds lay eggs from before sunrise until approximately 11.00 h (Hoy and Ottow 1964; Scott 1991; Kattan 1997), and they visit nests and puncture host eggs during the whole morning (M.E. Mermoz, personal communication). We registered the proportion of time that any member of the pair was less than 10 m away from the nest, as preliminary observations indicated that within this radius, the members of the pair were vigilant and responded to cowbirds approaching the nest.

To analyse if nest attentiveness varied during host laying, we did observations in 16 nests during the first half (days 0–1) and the second half (days 2–3) of laying (we considered as day 0 the day at which the first host egg was laid). In these nests, we also determined the number of parasite eggs laid and the number of host eggs punctured. To analyse whether nest attentiveness varied along laying and incubation, we did focal observations in nine additional nests during laying (days 0–1), early incubation (days 4–8) and late incubation (days 9–13).

Cues used by cowbirds to locate and parasitise host nests

We made an experiment to evaluate if: (1) host activity was used by female cowbirds to locate the nest, and (2) the information that cowbirds could gather through the puncture of host eggs was used to decide parasitism. We analysed parasitism and egg punctures during laying (days 0–3) in four groups: (1) nests at which there was host activity and where the parasite could obtain information by puncturing host eggs (nests with natural eggs), (2) nests with host activity and where the parasite could not obtain information by puncturing host eggs (nests with plaster eggs), (3) nests without host activity and with natural eggs, and (4) nests without host activity and with plaster eggs.

For the two groups with host activity, we used nests that were in laying. In one of the groups (natural eggs), we left in the nest the eggs laid by the host. In the other group, we replaced each host egg for a plaster egg as soon as it was laid, thus not giving shiny cowbirds the opportunity to puncture natural eggs. The removed eggs were kept at room temperature in a laboratory at our study site. Once we completed the experiment (day 3), the eggs were returned to their original nest. This manipulation did not produce any noticeable effect on host behaviour (the mockingbird female continued laying and began incubation) or on the survival or hatching success of the eggs. The only measurable effect was to extend by 1 day the incubation period of the host. For the two groups without host activity, we used mockingbird nests that had been previously deserted. The nests were removed from their original places and located outside mockingbird territories in places that resemble nest sites of this species (i.e. similar tree species, height and cover). Nests were left in the new place for 1 day and after that, we simulated host laying by adding one egg per day during three consecutive days. Eggs were added between 0900 and 1030 h, the time at which mockingbirds lay. In one of the groups, we added natural eggs whilst in the other group, we added plaster eggs. These eggs were made of plaster of Paris and painted with acrylic paint to simulate the appearance of mockingbird eggs. Plaster eggs were 27.9 mm in length and 19.3 mm in width. Natural eggs were 28.6±0.3 in length and 20.4±0.2 in width (n=13 clutches). Natural eggs were obtained from nests that had been deserted during laying or early incubation. In the last case, the eggs were emptied, filled with white of chicken eggs and the hole sealed with paraffin.

For each group, we determined the number of parasitic eggs laid during days 0–3, the number of days elapsed until the laying of the first parasite egg, the number of host eggs punctured during days 0–3, and the numbers of days elapsed until the first host egg was punctured. Punctures in plaster eggs were detected as distinguishable marks in the painted surface (i.e. the marks were similar to the ones observed in plaster eggs pecked by captive cowbirds).

Statistical analysis

For the analyses, we used non-parametric statistics due to lack of normality of the data. Statistical tests were performed using StatView 5.0 (SAS Institute Inc. 1998) with P<0.05. Values reported are means±SE.

Results

Timing of parasitism and egg punctures

The frequency and intensity of shiny cowbird parasitism in chalk-browed mockingbird nests were 66% (109 out of 165 nests) and 2.23±0.13 eggs per nest (n=109 nests), respectively. The frequency of mockingbird nests with egg punctures was 62% (103 out of 165 nests). Parasitised nests had a higher frequency of punctures than unparasitised ones (parasitised 80 out of 109, unparasitised 23 out of 56, chi-square test, χ^2=15.1, P<0.001). On average, parasitised nests lost more host eggs as a result of punctures than unparasitised ones (parasitised: 1.03±0.1, n=81; unparasitised: 0.55±0.18, n=29; Mann–Whitney U test: U'=1,555, Z=−2.75, P=0.006). Most punctured eggs were removed by the host within 24 h after puncture.

We detected a total of 333 cowbird eggs, 243 (73%) were laid in 109 active nests (i.e. nests where the host begun laying), 38 (11%) in 21 nests where the host completed building but did not begin laying, and 26 (8%) in 19 nests that had been abandoned at the time the cowbird egg was laid (18 1 day, and nine 2 or 3 days after nest abandonment). Another 26 eggs (8%) were laid the same day the nest was deserted. In these cases, we were unable to determine if cowbird eggs were laid before or after nest abandonment. The majority of the nests (74%) that received cowbird eggs the same day or 1 or 2 days after abandonment were deserted during the laying period of the host.

We estimated the timing of parasitism at a population level from a sample of 180 parasite eggs laid in 130 nests found before mockingbirds began laying or during laying. In these nests, most parasitic events occurred during laying (days 0–3, Fig. 1a). The average number of parasite eggs laid per nest during this period (considering parasitised and unparasitised nests) was 1.22 (74% of the eggs); whilst during incubation (days 4–16), it was 0.59 (23% of the eggs). The number of cowbird eggs laid in these nests before the host began laying was 0.08 (3% of the eggs). Likewise in parasitism, most punctures in host eggs occurred during laying (days 0–3, Fig. 1b). The average number of host eggs punctured during this period was 0.92 (74%) whilst during incubation (days 4–16), it was 0.55 (26%).

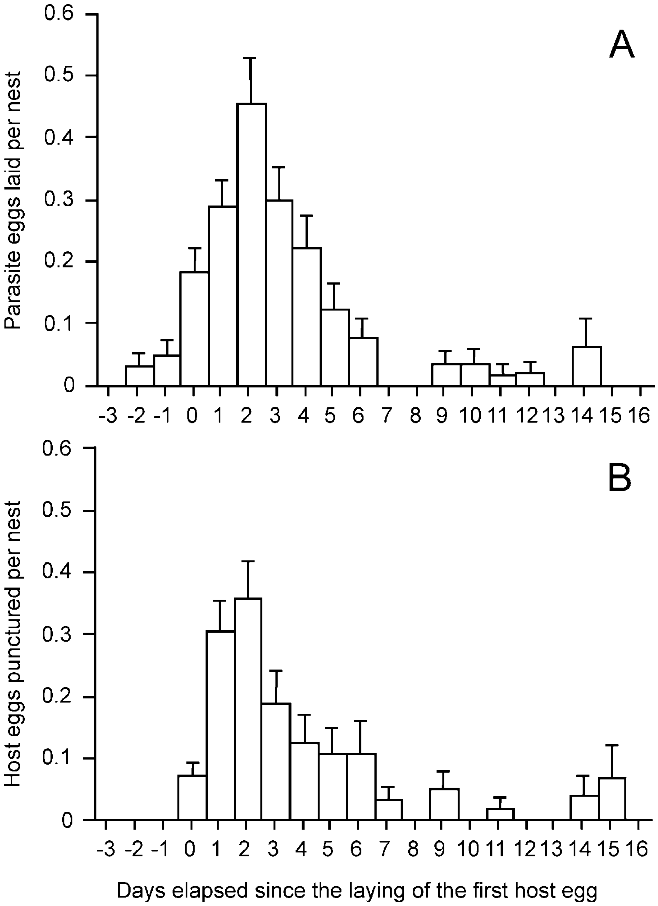

Fig. 1 *Bars* indicate the average number of cowbird eggs laid (**a**), and the average number of host eggs punctured (**b**) in a mockingbird nest along pre-laying, laying and incubation. Day 0 corresponds to the laying of the first host egg. The numbers of nests observed during days −3 to 16 were: 51, 67, 82, 127, 122, 106, 91, 81, 74, 66, 64, 65, 61, 57, 57, 54, 52, 48, 43 and 21

We estimated the association between punctures and parasitism at an individual level from a sample of 37 nests that was single parasitised. In 22 of these nests (59%), we observed punctures associated with parasitism. In 17 out of 22 cases, the puncture event occurred the same day of parasitism, in two out of 22 cases 1 day before and in two out of 22 cases 2 days before. Only in one case that the puncture event occurred after parasitism (it was the following day). In the other 15 parasitised nests, we did not observe puncture events. We also observed 21 events of egg punctures in 16 unparasitised nests.

Nest attentiveness, parasitism and egg punctures

We analysed if there was an association between the proportion of time that a nest was attended and: (1) the number of parasitic eggs that it received, and (2) the number of host eggs that was punctured. We did this analysis during laying because most parasitic and puncture events occurred at this time (Fig. 1). We measured the proportion of time that the nest was attended during the first half (days 0–1) and the second half (days 2–3) of laying. Although the proportion of time that a nest was attended varied broadly among nests, it was relatively similar within nests (Spearman rank correlation between first and second half of laying; r_s=0.62, Z=−2.4, P=0.02). On average, nest attentiveness did not differ between periods (days 0–1: 0.61±0.06, days 2–3: 0.64±0.06, n=16 nests, Wilcoxon signed rank test: Z=−0.52, P=0.6). Therefore, to evaluate whether there was an association between nest attentiveness and the number of parasitic and puncture events occurred during laying, we used the average value of the proportion of the time that the nest was attended during the first and the second half of laying. We did not detect any significant association between nest attentiveness and the number of parasitic eggs that the nest received (Spearman rank correlation; r_s=0.11, Z=0.42, P=0.67), or the number of host eggs that was punctured (Spearman rank correlation; r_s=0.39, Z=1.5, P=0.13).

We also measured how nest attentiveness varied along laying and incubation. For this analysis, we used an independent sample of nine nests followed from nest building to late incubation. The percentage of time that the nest was attended differed between laying and incubation. During the first 2 days of laying (before incubation had began), the proportion of time that the nest was attended was 0.63±0.1, whilst during early (days 4–8) and late (days 9–13) incubation, it was attended 0.86±0.04 and 0.84±0.04, respectively (Friedman test, χ^2=9.2, P<0.01).

Cues used by cowbirds to locate and parasitise host nests

Table 1 presents the results of frequency, intensity and latency of parasitism and egg punctures in the four experimental groups (nests with host activity and natural or plaster eggs, and nests without host activity and natural or plaster eggs). The frequency of parasitism differed between groups (Fisher exact test, P<0.001). Nests without host activity were not parasitised at all, whereas approximately 80% of the nests with host activity were parasitised. Nests with host activity and natural or plaster eggs did not differ in frequency (Fisher exact test, P>0.99) and intensity (Mann–Whitney U test: U'=246.5, Z=−0.81, P=0.42, Table 1) of parasitism. The latency until the first parasitic event was shorter in the group with natural eggs than in the one with plaster eggs (Mann–Whitney U test: U'=333.5, Z=−2.92, P=0.004, Table 1). A similar result was obtained when we considered only the parasitized nests where punctures did take place (natural eggs: 1.19±0.19, n=27; plaster eggs: 2.0±0.26, n=6; Mann–Whitney U test: U'=122, Z=−2.0, P=0.045).

We evaluated if nests (with or without host activity) were visited by cowbirds throughout the presence of punctures in mockingbird eggs (or marks in the case of plaster eggs). The proportion of nests with punctured eggs did not differ between groups (chi-square test, χ^2=4.75, P=0.19, Table 1). Similarly, the number of host eggs punctured and the latency until the first host egg was punctured did not differ between groups (Kruskal–Wallis tests, H=1.3, df=3, P=0.73 for the number of host eggs punctured, and H=3.4, df=3, P=0.34 for the latency to first egg punctured, Table 1).

Table 1 Frequency, intensity and latency of parasitism and egg punctures (mean±SE) in nests with or without host activity and with natural or plaster eggs

Host activity	Egg type	Percentage of nests parasitised	Number of parasitic eggs per nest	Latency of parasitism (days)	Percentage of nests with egg punctures	Number of punctured eggs per nest	Latency of egg punctures (days)
Present	Natural	79.6 (49)	1.97±0.2 (39)	1.1±0.15 (39)	65.3 (49)	1.63±0.12 (32)	1.47±0.17 (32)
Present	Plaster	84.6 (13)	1.64±0.28 (11)	2±0.19 (11)	46.2 (13)	1.5±0.34 (6)	1.67±0.33 (6)
Absent	Natural	0 (11)	–	–	54.5 (11)	1.67±0.42 (6)	2±0.37 (6)
Absent	Plaster	0 (12)	–	–	33.3 (12)	1.25±0.25 (4)	2.25±0.48 (4)

Sample sizes (nests) indicated in parenthesis

Discussion

Timing of parasitism and egg punctures

Most parasitism by shiny cowbirds occurred in active mockingbird nests. In these cases, cowbirds synchronised 75% of their laying with that of the host. When cowbirds laid in non-active nests, laying occurred 1 or 2 days after the nest had been deserted, or 1 or 2 days before the host should have begun laying (the nest cup was already lined with fibres and horsehair, which normally occurs 1 or 2 days before laying). These results indicate that in most cases, cowbirds avoid laying in unsuitable nests and synchronise their laying with that of the host. Similar results were previously reported in yellow-winged blackbirds, *Agelaius thilius* (Massoni and Reboreda 1998), and in brown-and-yellow marshbirds, *Pseudoleistes virescens* (Mermoz and Reboreda 1999). In these hosts, between 70 and 80% of parasitism occurred during host laying, and the proportion of eggs laid before the host begun laying or in abandoned nests was very low. On the contrary, Kattan (1997) found that only 47% of cowbird parasitism in active nests of house wrens (*T. aedon*) occurred during laying. This author also found that cowbirds laid a high proportion of eggs in nests that were abandoned by wrens before laying. The discrepancy between these and our results could be the consequence of differences between studies in the number of host nests that was available for laying. If the number of host nests available per cowbird female ready to lay eggs is low, it would be expected that there is an increase in the intensity (and consequently the frequency) of parasitism and a decrease in the synchronization between parasitism and host laying. The latter would be the result of a higher probability of absence of nests in laying at the time there are cowbirds laying. Consistent with this interpretation, the intensity of parasitism in Kattan's study was 4.6 eggs/nest whilst in the other studies, it was 1.2 (Massoni and Reboreda 1998), 2.1 (Mermoz and Reboreda 1999) and 2.2 (this study).

With regard to host egg puncture, at a population level, its intensity was strongly associated with intensity of parasitism. Similarly, at the level of individual nests, 60% of the parasitic events were associated with the puncture of mockingbird eggs. In 95% of these cases, egg punctures occurred the same day, or 1 or 2 days before parasitism. However, approximately 40% of the parasitic events were not associated to puncture events. In these nests, parasitism was also synchronised with host laying which would indicate that in some cases, cowbirds do not need to puncture host eggs to synchronise parasitism (see below).

Nest attentiveness, parasitism and egg punctures

We did not find an association between the proportion of time that a mockingbird nest was attended during laying and the number host eggs that was punctured or the number of parasite eggs that was laid during that period. Similarly, although nest attentiveness was 20–25% lower during laying than during incubation, parasitism during laying was more than three times higher than during incubation. These results indicate that synchronisation between parasitism and host laying is not solely a by-product of lower nest attentiveness during host laying.

Cues used by cowbirds to locate and parasitise host nests

It has been suggested that female cowbirds can locate host nests by searching the habitat without need for the presence of adult hosts (Norman and Robertson 1975; Wiley 1988). Yet, previous experimental studies (i.e. Lowther 1979; Wiley 1988; Grieef and Sealy 2000; Robinson and Robinson 2001, but see Svagelj et al. 2003 for a review) used parasitism as an evidence of nest finding and therefore, they were unable to distinguish between cues used for finding nests from parasitism decisions. In this study, we found that nests with or without host activity had similar frequency and intensity of egg punctures. This result indicates that shiny cowbirds are able to locate nests even when there is no host activity associated to them. On the contrary, host activity was a necessary cue for eliciting parasitism, as none of the nests without host activity was parasitised. This result indicates that the laying sequence by itself was not a cue for eliciting parasitism and suggests that shiny cowbirds need to observe the adult hosts close to the nest before parasitising it.

We did not find differences in the frequency and intensity of parasitism between active nests with natural or plaster eggs. This result is not consistent with the prediction of Massoni and Reboreda (1999), as female shiny cowbirds synchronised parasitism with egg laying without the possibility to use information gathered by egg punctures. However, it is interesting to mention that although the latency until the first host egg was punctured was similar in nests with natural and plaster eggs, the latency until the first parasitic event was longer in the latter. Our results suggest that in nests with host activity and a normal sequence of laying, the information that cowbirds may gather through the puncture of host eggs is not necessary for deciding parasitism. Yet, we cannot rule out the possibility that cowbirds use egg punctures to decide parasitism when they find a nest with a complete clutch, and they lack information about the time elapsed since the host began to incubate as suggested by Massoni and Reboreda (1999). In addition, egg punctures may have other benefits, like to reduce the competition in the nest between parasite and host chicks (Hoy and Ottow 1964, Sealy 1992, Soler et al. 1997, Peer 2006). This function is particularly important for shiny cowbirds when they parasitise hosts that are larger in size than themselves (Fraga 1985, Lichtenstein 1998, Sackmann and Reboreda 2003, Astié and Reboreda 2006).

In summary, our results indicate that shiny cowbirds synchronise parasitism with host laying and that synchronization is not totally explained by lower host nest attentiveness during laying or by the puncture of host eggs. Shiny cowbirds can locate host nests without need for the presence of adult hosts but they rely on host activity for deciding parasitism.

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