

Egg puncture allows shiny cowbirds to assess host egg development and suitability for parasitism

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Parasitic cowbirds and cuckoos generally reduce the clutch size of the hosts they parasitize by removing or destroying some of their eggs. Shiny cowbirds (*Molothrus bonariensis*) puncture their hosts' eggs both when parasitizing the nests and also when they do not parasitize them. We propose that, by puncturing the host's eggs, shiny cowbirds gain an informational benefit. They assess the degree of development of the host's embryos and so avoid laying in nests that would not provide enough incubation time for the parasitic eggs to hatch. Two predictions follow: (i) punctures should occur in advance or immediately before parasitic events, and (ii) the occurrence of parasitism should depend on the degree of development of the host's embryos when punctures occurred, i.e. on the stage of incubation. Both predictions are supported by our data of shiny cowbirds parasitizing yellow-winged blackbirds (*Agelaius thilius*). Egg punctures are not used to reset the host's nesting attempt when shiny cowbirds do not parasitize the nests. We discuss the potential mechanisms implicated in egg development assessment and propose a critical experiment to test this hypothesis.

Keywords: brood parasitism; shiny cowbirds; yellow-winged blackbirds; egg punctures; egg synchronization

1. INTRODUCTION

Brood parasitism is a reproductive strategy of several avian species in which parasites lay eggs in the nests of other birds, the hosts, who incubate and provide food for the parasite as they do with their own brood (see the review by Rothstein & Robinson (1998)).

Parasitic cowbirds show egg and behavioural adaptations including (i) high fecundity, which allows them to parasitize over extended breeding seasons (Scott & Ankney 1983; Jackson & Roby 1992; Kattan 1993), (ii) thick, round eggshells, which may counter egg ejection by the host (Blankespoor *et al.* 1982; Spaw & Rohwer 1987; Rahn *et al.* 1988; Picman 1989), (iii) a short incubation period, which furnishes their eggs with a hatching advantage and benefits their chicks in competition with foster siblings (Briskie & Sealy 1990; Kattan 1995), and (iv) partial destruction of the host clutch, which reduces overcrowding (Sealy 1992). By destroying or removing some of the host's eggs at nests they parasitize, cowbirds might gain incubation efficiency for their remaining eggs and reduce future competition for the cowbird chick (Sealy 1992).

The shiny cowbird (*Molothrus bonariensis*) is an obligate brood parasite that lays eggs in the nests of *ca.* 200 host species (Friedmann & Kiff 1985) and normally reduces the reproductive success of its hosts (Post & Wiley 1977; Fraga 1978, 1985; Massoni & Reboreda 1998; Mermoz &

Reboreda 1998). One of the main costs suffered by parasitized hosts is the loss of eggs through punctures made by the parasite (Hudson 1874; Hoy & Ottow 1964; Fraga 1978; Lichtenstein 1998). However, shiny cowbirds also puncture eggs at nests they do not parasitize (Massoni & Reboreda 1998). This apparently pointless behaviour of puncturing eggs has not, to our knowledge, been analysed before.

We propose that, by puncturing the eggs, shiny cowbirds can assess the degree of development of the host's embryos and, using this information, decide whether or not to parasitize the nest. According to this hypothesis, we predict that cowbirds who find hosts' nests in an advanced state of incubation will puncture some eggs but will then abstain from parasitizing them and so avoid wasting eggs that will not receive enough incubation time for their chicks to hatch. This behaviour should result in shiny cowbirds synchronizing their laying with the host. This idea was considered by Livesey (1936) in relation to egg-eating behaviour by common cuckoos (*Cuculus canorus*). However, as Sealy (1992) pointed out, cuckoos lay their own egg before eating the host egg, thus precluding any potential advantage of the egg-testing behaviour.

The yellow-winged blackbird (*Agelaius thilius*) is a suitable host for testing this hypothesis. It shows a low incidence of shiny cowbird parasitism (26.5%), most of it single parasitism, so we can safely assume the same female is involved in puncture and parasitic events at a given nest. In addition, this host does not reject any of the

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egg colour morphs—white or spotted—laid by shiny cowbirds in our study area (Massoni & Reboresda 1998), so we can ascertain that egg punctures at non-parasitized nests do not result from undetected parasitic events. Previous studies have shown that shiny cowbirds puncture yellow-winged blackbird eggs when parasitizing their nests, but some of the punctured nests are not subsequently parasitized (Massoni & Reboresda 1998). Colonies with no records of parasitism, i.e. no cowbird eggs in any nest, showed no sign of egg punctures (V. Massoni and J. C. Reboresda, unpublished results).

The egg-testing hypothesis makes two clear predictions: (i) cowbird punctures to the host's eggs must precede the parasitic event, and (ii) the occurrence of parasitism must depend on the degree of development of the host's embryos at the time punctures occur, i.e. on the stage of incubation.

2. MATERIAL AND METHODS

The study was conducted in flat, low and marshy areas alongside an artificial drainage canal (canal 2) near the town of General Lavalle in the province of Buenos Aires, Argentina (36°30' S, 57°01' W) from early October to late December 1994.

We found 213 active nests (81 during construction, 42 during laying, 80 during incubation and ten after the chicks had hatched). All these nests were built on cattails (*Typha* sp.) and we tagged them inconspicuously at the base of the plant. The mean clutch size of yellow-winged blackbirds was 3.4 eggs and in *ca.* 90% of the nests incubation started after the laying of the second egg. Adult individuals of *A. thilius* are smaller than shiny cowbirds and average 35 g in weight, 10–15 g less than adult shiny cowbirds (V. Massoni and J. C. Reboresda, unpublished results). The parasitism frequency estimated in 117 nests found in construction and early laying was 26.5% and 70% of these parasitic eggs were laid during the egg-laying period of the host (Massoni & Reboresda 1998).

To test our hypothesis we used a subgroup of nests that complied with the following criteria: (i) we knew the date the first blackbird egg was laid, (ii) the nest showed parasitism and/or punctures of one or more eggs, and (iii) through daily visits to the nest, we determined the date of punctures and/or parasitic events to the nearest day. These nests were distributed throughout the breeding season.

We recorded 51 puncture events at 47 nests, i.e. four nests suffered two puncture incidents. Second puncture events at those nests occurred four to seven days after the first one. Because of the latency between punctures and parasitic events (see below), we felt confident in including them as independent cases. Nonetheless, the exclusion of these four cases did not affect our results.

Punctures followed by disappearance of the host's eggs could be interpreted as cowbird egg-removal behaviour or host sanitation following cowbird egg punctures (Kemal & Rothstein 1988). We never observed shiny cowbirds removing yellow-winged blackbird eggs but we detected punctures before eggs were removed from the nest in 73% of the cases. It could be argued that shiny cowbirds were returning to the nests to remove the punctured eggs. However, we believe that host removal of broken eggs during regular sanitation of the nest is a more parsimonious explanation for this pattern than extra visits made by shiny cowbirds to remove the punctured eggs. Nonetheless, as according to our data, egg removal occurs *a posteriori* of

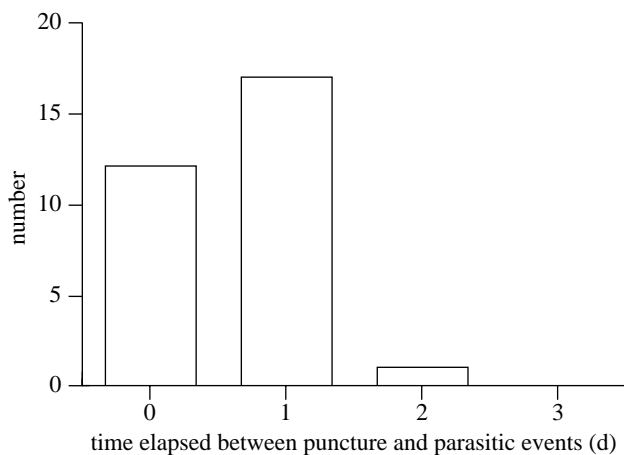


Figure 1. Distribution of parasitic events as a function of the number of days elapsed since the puncture event. There were no cases of parasitic events preceding puncture events.

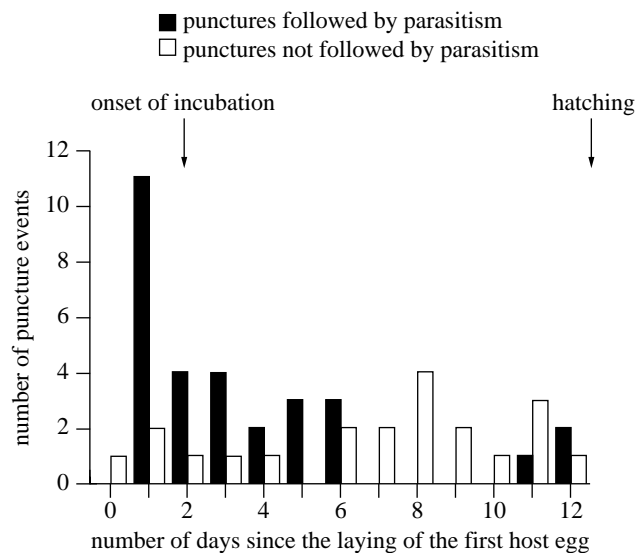


Figure 2. The bars show puncture events relative to the day of first host egg laying. The black and white bars indicate the number of punctured nests that were subsequently parasitized and non-parasitized, respectively.

the egg-testing behaviour, the predictions of our hypothesis remain unchanged.

3. RESULTS

The dates on which puncture events occurred were determined for 51 cases. In 30 cases, punctures were followed by parasitism. The time elapsed between puncture and parasitic events at parasitized nests supported our first prediction as all punctures preceded parasitism (figure 1).

To test our second prediction we performed a logistic regression between the occurrence of parasitism and incubation day at the time of host egg puncture. The result showed a decline in the cowbird's egg-laying frequency when the host's eggs were punctured at an advanced developmental stage ($\chi^2 = 9.57$, d.f. = 1 and $p = 0.0019$; figure 2).

It is important to note that, during the egg-laying period of the host, when full incubation has not yet begun and nests are less attended, both punctures and parasitism could be easier to achieve by parasites. Punctures followed by parasitism during that period would bias the result in favour of our hypothesis. Therefore, we repeated the analysis including only events that occurred at nests where full incubation had begun, i.e. nests where two or more days had elapsed since the laying of the first host egg. In spite of the reduction in sample size, the result was highly significant ($n=37$ nests, $\chi^2=6.81$, d.f.=1 and $p=0.009$).

Shiny cowbirds could attempt to reset the host when they find nests too old to be parasitized successfully, i.e. force the host to renest by destroying most of the nest contents. If cowbirds were resetting the advanced nests they do not parasitize, we should find a higher number of eggs punctured at those nests than at the freshly laid nests that they do parasitize. We found no support for this hypothesis as punctured–parasitized nests lost on average the same number of eggs as punctured–non-parasitized nests (mean \pm s.e.: parasitized nests 1.5 ± 0.15 and $n=30$ and non-parasitized nests 1.76 ± 0.18 and $n=21$; $t=1.11$ and $p=0.27$).

4. DISCUSSION

Puncturing host's eggs might benefit shiny cowbirds in several ways. As discussed above, the destruction of some of the host's eggs at parasitized nests might prevent overcrowding. The extra egg could decrease the incubation efficiency of the enlarged clutch (Davies & Brooke 1988). However, evidence in support of this hypothesis is not conclusive (Lerkelund *et al.* 1993; McMaster & Sealy 1997; Wood & Bollinger 1997). In addition, a complete clutch would represent a competitive environment for the cowbird chick unless some of the host eggs were destroyed (Scott 1977; Blankespoor *et al.* 1982). We do not dispute the potential advantages of egg-puncturing behaviour at parasitized nests. However, these benefits do not predict or explain the occurrence of punctured eggs at nests not subsequently parasitized.

Shiny cowbirds puncture when they parasitize a nest, but also puncture eggs in nests they do not parasitize. We proposed that the latter phenomenon reflects the decision made by parasites not to parasitize unsuitable nests containing well-developed host embryos that will soon hatch. If shiny cowbirds use this egg-laying synchronization behaviour, we would expect this pattern to be detected at the nests of other hosts.

Our results are consistent with our predictions. First, we showed that punctures occurred the same day or the day previous to parasitism, indicating that shiny cowbirds could use the information gained through punctures before committing their eggs to the nest. Second, we found that the frequency of parasitism decreased when the nest contents were punctured at an advanced state of incubation, indicating that shiny cowbirds do not parasitize nests that will not provide enough incubation care for their egg to hatch.

When shiny cowbirds do not immediately parasitize nests with fresh eggs, they must return to those nests to parasitize them. Such requirement of spatial memory

might be related to the larger hippocampus, a brain structure involved in spatial memory processing, which is found in parasitic cowbirds in comparison with their non-parasitic relatives (Sherry *et al.* 1993; Reboreda *et al.* 1996).

Shiny cowbirds do not use punctures to reset yellow-winged blackbirds nesting attempts as was suggested for brown-headed cowbirds (Arcese *et al.* 1996; Peer & Sealy 1999). The number of punctured eggs was no higher in long-incubated, non-parasitized nests than the number of punctured eggs at newly incubated parasitized nests, as would be expected if cowbirds were attempting to force their hosts to renest.

Obligate brood parasites like shiny cowbirds delegate incubation, feeding and early protection of their young to foster parents. For this reproductive strategy to persist over time they have to (i) select hosts that provide appropriate incubation and nutrition for their chicks, and (ii) synchronize egg laying with those hosts, thus enhancing the probability of their eggs surviving the nesting period. Shiny cowbirds parasitize several appropriate hosts species (Mason 1986; Wiley 1988) and egg synchronization with their hosts is usually found (Massoni & Reboreda 1998; Mermoz & Reboreda 1999; but see Kattan 1997).

Shiny cowbirds might use another strategy to adjust their egg laying to that of their hosts. Females have been seen searching for prospective nests, closely following the nest building behaviour of their hosts (Wiley 1988). Given the opportunity to witness nest construction, female cowbirds should use the information to parasitize the nest on time. Nonetheless, different cowbird females multiply parasitized other hosts in our study area, indicating that cowbirds cannot monopolize the host resource (Lyon 1997; Mermoz & Reboreda 1999). When cowbirds find a nest with a complete clutch, a probable event if they do not hold exclusive territories nor know the host's nest location in advance, they lack information about the time elapsed since the host began to incubate. Host egg testing through punctures would allow female cowbirds to decide instantaneously whether to parasitize the nest or not.

We can only speculate about the mechanism involved in assessing the eggs by puncturing them. It could be mediated by visual, taste or tactile cues. For example, the majority of the birds possess sensible and flexible bills (Zusi 1984) which bend at the nasofrontal hinge (Gill 1995). One possibility is that, during punctures, bending of the bill could allow shiny cowbirds to detect differences between the softness of the white and yolk of a newly laid egg and the hardness of a well-developed embryo. However, other mechanisms could be in use.

A critical experiment for testing this hypothesis would consist of a clutch translocation between fresh egg-laid nests and close-to-hatching, old nests. We would expect parasitism to follow punctures at old nests containing fresh eggs, but not at new nests containing old eggs. This experiment would discriminate between the nest monitoring and egg testing mechanisms of egg synchronization between shiny cowbirds and their hosts.

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