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A NEGLECTED COST OF BROOD PARASITISM: EGG PUNCTURES BY SHINY COWBIRDS DURING INSPECTION OF POTENTIAL HOST NESTS

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Abstract. Parasitized hosts of the Shiny Cowbird (*Molothrus bonariensis*) suffer several costs, and among the most important is the loss of eggs through egg punctures inflicted by the parasite. Unparasitized nests also have eggs damaged by cowbirds, but researchers usually ignore these losses. To quantify this cost we compared three groups of nests of the Yellow-winged Blackbird (*Agelaius thilius*): parasitized and unparasitized nests from an area used by Shiny Cowbirds, and unparasitized nests from an area not used by the parasite. Because cowbirds puncture eggs as soon as the first host eggs are laid, we calculated the clutch size only for those nests found during construction. Unparasitized nests in the area used by cowbirds had lower egg survival rate and hatching success and higher probability of nest desertion than unparasitized nests in the cowbird-free area. Our results indicate that one must consider egg punctures at unparasitized nests to avoid underestimating the impact of parasitism.

Key words: Agelaius thilius, *brood parasitism, costs of parasitism, egg punctures,* Molothrus bonariensis, *Shiny Cowbird, Yellow-winged Blackbird.*

Un Costo Ignorado del Parasitismo de Cría: Perforación de Huevos por *Molothrus bonariensis* durante la Inspección de Potenciales Nidos de Hospedadores

Resumen. Los hospedadores de *Molothrus bonariensis* sufren varios costos, entre los que se destaca la pérdida de huevos debida a perforaciónes hechas por el parásito. Los nidos no parasitados también tienen huevos perforados por *M. bonariensis*, pero estas pérdidas son normalmente ignoradas. Para cuantificar este costo comparamos tres grupos de nidos de *Agelaius thilius*: nidos parasitados y no parasitados de un área usada por *M. bonariensis*, y nidos no parasitados de un área no utilizada por el parásito. Como los parásitos perforan los huevos del hospedador tan pronto como éstos son puestos, el tamaño de puesta se calculó utilizando únicamente los nidos encontrados durante su construcción. Los nidos no parasitados del área visitada por los parásitos tuvieron menor supervivencia de sus huevos durante la incubación, menor éxito de eclosión y mayor probabilidad de ser abandonados que los nidos no parasitados del área libre de parásitos. Los resultados obtenidos indican que deben considerarse las perforaciones de huevos en nidos no parasitados para evitar subestimar el impacto del parasitismo.

INTRODUCTION

Brood parasites, such as cowbirds and cuckoos, induce other birds to incubate and feed their chicks, thereby reducing the reproductive success of their hosts (Ortega 1998, Rothstein and Robinson 1998). Cowbird parasitism may reduce the host's reproductive success in several ways: (1) cowbirds can puncture or remove one or more host eggs when laying their own eggs (Hoy and Ottow 1964, Post and Wiley 1977, Sealy 1992, Payne and Payne 1998); (2) cowbird eggs or chicks can reduce the viability of the host eggs (Carter 1986, Petit 1991); (3) cowbird chicks can outcompete the host's chicks for food, causing brood reduction (King 1973, Marvil and Cruz 1989); and (4) raising parasitic chicks can reduce the post-fledging survival of the host chicks (Payne and Payne 1998) or the host's future reproductive value (Rothstein and Robinson 1998). In addition, cowbird parasitism can increase the probability of nest desertion (Petit 1991, Clotfelter and Yasukawa 1999), and the presence of cowbird chicks can increase the probability of nest predation (Massoni and Reboreda 1998).

Most studies have focused on the costs inflicted by cowbirds at parasitized nests. Few studies

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have dealt specifically with the costs inflicted by cowbirds at unparasitized nests. As an example of the latter, Arcese et al. (1992, 1996) and Arcese and Smith (1999) have reported a reduction in the nesting success of unparasitized nests when Brown-headed Cowbirds (*Molothrus ater*) were present. Similarly, Clotfelter and Yasukawa (1999) found that the proportion of Red-winged Blackbird (*Agelaius phoeniceus*) nests parasitized by Brown-headed Cowbirds was negatively correlated with the proportion of unparasitized nests that succeeded. Arcese et al. (1996) proposed that Brown-headed Cowbirds remove eggs from unparasitized nests to force renesting and gain new opportunities for parasitism, and provided evidence in support of the ''cowbird predation hypothesis.'' Other authors (Rogers et al. 1997, McLaren and Sealy 2000) did not find support for this hypothesis.

The Shiny Cowbird, (*Molothrus bonariensis*), is a generalist brood parasite that reduces the reproductive success of its hosts (King 1973, Post and Wiley 1977, Fraga 1978, 1985). One of the main costs of Shiny Cowbird parasitism is the puncture of host eggs at parasitized nests (Lichtenstein 1998, Massoni and Reboreda 1998, Mermoz and Reboreda 1999). Egg punctures also occur at unparasitized nests (Hudson 1874, Hoy and Ottow 1964, Mermoz and Reboreda 1994), but have not been studied in detail until recently (Massoni and Reboreda 1999). Our data indicate that egg puncturing has not necessarily evolved as a means of forcing hosts to renest, but rather occurs when Shiny Cowbirds are searching for nests to parasitize, allowing the parasites to assess host egg development and suitability for parasitism (Massoni and Reboreda 1999).

Previous studies on Shiny Cowbird interactions with hosts have not considered the costs of the exploratory behavior of cowbirds at nests of potential hosts. Therefore, the impact of the parasite on the reproductive success of the host might be seriously underestimated. The aim of this study was to quantify this cost. To do so, we compared several measures of host reproductive success among three groups of colonial Yellow-winged Blackbirds (*Agelaius thilius*). One of the groups was a colony without evidence of Shiny Cowbird activity in the area, while the other two groups belonged to a colony in which 33% of the nests were parasitized. If the exploratory behavior of Shiny Cowbirds reduces the reproductive success of unparasitized nests, we expect to find significant differences between these nests and those belonging to the colony of Yellow-winged Blackbirds not visited by the parasites.

METHODS

STUDY AREA

The study was conducted in two areas: a marshy area at the Estancia ''El Campillo'' (36°32′S, 56°55′W) where we have never seen adult Shiny Cowbirds or parasitic eggs, and a marsh surrounding an artificial drainage canal (36°29′S, 57°00′W) where adult Shiny Cowbirds and their eggs were present (Massoni and Reboreda 1998). Data were collected from early October to late December 1998 in the cowbird-free area and from early October to late December 1994 in the parasitized area. The distance between the study areas is 10 km, and they are connected by an almost uninterrupted sequence of marshes and flooded land. Clutch size and nest failure rates did not differ between areas. We believe that the presence of cowbirds in the latter area may be associated with differences in host communities. In the cowbird-free area we found no other hosts available for the parasite, while in the area with cowbirds we found several other hosts of Shiny Cowbirds, such as the Brown-and-Yellow Marshbird (*Pseudoleistes virescens*; Mermoz and Reboreda 1999), the Chestnut-capped Blackbird (*Agelaius ruficapillus*; Lyon 1997), and the Rufous-collared Sparrow (*Zonotrichia capensis*; VM, pers. obs.).

DATA COLLECTION

We conducted intensive nest surveys at each site. In the cowbird-free area we found 43 nests: 6 during construction, 10 during egg laying, 22 during incubation, and 6 after the chicks had hatched. In the area visited by cowbirds, we found 213 nests: 81 during construction, 42 during egg laying, 80 during incubation and 10 after the chicks had hatched. We numbered nests with flagging tape placed nearby, and we visited them daily until they either fledged or failed. In each visit we recorded the number of host and parasite eggs and chicks, and the occurrence of cracks or punctures in eggs. Host and parasite eggs were marked with waterproof ink.

DATA ANALYSIS

We assumed that the clutch was complete when the number of host eggs remained constant for at least two consecutive days. We considered as parasitized those clutches that had cowbird eggs or nestlings at any stage of the nesting cycle. To estimate the frequency of parasitism, however, we considered only those nests that were found in the building, laying, and early incubation stages and for which the host completed laying. We believe these criteria better estimate the frequency of parasitism than including nests found during the late incubation or nestling periods. The inclusion of nests found during later stages could create a systematic underestimation of parasitism rates because (1) most parasitism by Shiny Cowbirds occurs during the laying period of the host (Massoni and Reboreda 1998, Mermoz and Reboreda 1999) and (2) nest desertion during the egg stages is associated with parasitism.

We estimated the number of eggs laid (clutch size) from two different subsamples of nests: (1) nests found during construction (hereafter clutch size A) and (2) nests found during construction, egg laying, or early incubation (clutch size B). We consider clutch size A a better estimate of the real number of eggs laid by Yellow-winged Blackbirds than clutch size B because nests found during egg laying or early incubation could have lost eggs before we found them.

We calculated the egg survival rate as the proportion of eggs laid by the host that were present in the nest at hatching. Similarly, we calculated hatching success as the number of hatched eggs over the total number of eggs present in the nest at the time of hatching, and fledging success as the number of chicks fledged over the number of nestlings that hatched, for all nests found during construction, egg laying, or early incubation.

Nests were considered deserted if the eggs were cold to the touch for two consecutive days and no Yellow-winged Blackbirds attended the nest, and depredated if all the eggs or chicks disappeared between two consecutive visits.

We used nonparametric statistics due to small sample size. Data are presented as means ± SE. Statistical tests were performed using StatView 5.0 (SAS Institute Inc. 1998) with $P < 0.05$.

RESULTS

Average clutch size of Yellow-winged Blackbirds was the same in both colonies. Clutch size for nests found during construction (clutch size A) was not different among the three groups (Fig. 1). The cost of the cowbird presence became apparent when clutch size was calculated using nests found during construction, egg laying, and early incubation (clutch size B). It was larger in the area without cowbirds than in the area with cowbirds (for either unparasitized or parasitized nests, Kruskal-Wallis test, $H = 40.5$, df = 2, $P < 0.001$, and contrasts $P < 0.01$; Fig. 1). Clutch size B did not differ between unparasitized and parasitized nests in the parasitized colony.

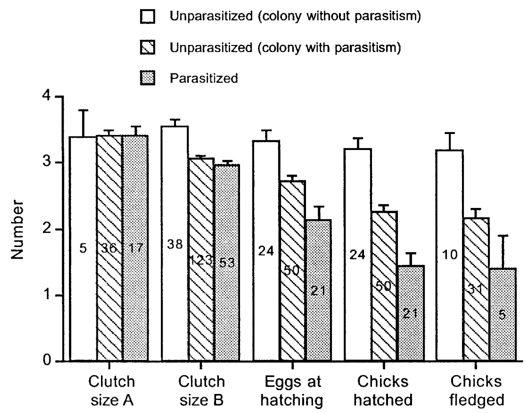

FIGURE 1. Number (mean ± SE) of eggs laid, eggs in the nest at the time of hatching, chicks that hatched and chicks that fledged in unparasitized nests of Yellow-winged Blackbirds from two colonies, one without Shiny Cowbird parasitism and one with parasitism. Clutch size A was estimated only from nests found during construction, while clutch size B was estimated from nests found during construction, egg laying, or early incubation. Sample sizes (nests) are indicated at bar centers.

The number of eggs surviving to the time of hatching was significantly different among the three groups ($H = 21.2$, df = 2, $P < 0.001$, and contrasts $P < 0.01$; Fig. 1). We also observed significant differences among the three groups when we analyzed the number of chicks that hatched and fledged ($H = 31.7$, df = 2, $P < 0.001$, and contrasts $P < 0.01$; $H = 12.4$, df = 2, $P < 0.01$, and contrasts $P < 0.01$, respectively; Fig. 1).

In areas visited by cowbirds, clutch size B underestimated the real clutch size. However, we used this criterion to calculate the egg survival rate because for the cowbird-free colony, few nests found during construction reached the nestling stage. The egg survival rate at the cowbird-

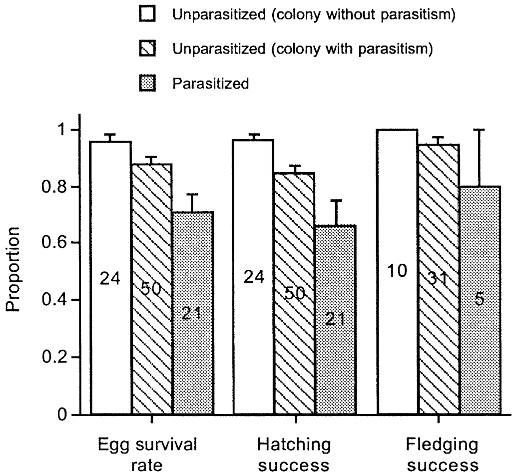

FIGURE 2. Proportions (mean ± SE) of eggs that survived until the time of hatching, chicks that hatched, and chicks that fledged in two Yellow-winged Blackbird colonies, one without Shiny Cowbird parasitism and one with parasitism. Sample sizes (nests) are indicated at bar centers.

free area was higher than in unparasitized or parasitized nests in the colony visited by cowbirds. The latter groups also differed significantly in this respect ($H = 13.9$, df = 2, $P < 0.001$, and contrasts $P < 0.01$; Fig. 2). Had we been able to use clutch size A, the difference in egg survival rate would have been even more pronounced and the effect of cowbird visits to the area would have been more evident.

We also found differences in hatching success between nests from the colony without cowbirds and unparasitized and parasitized nests from the colony with cowbirds ($H = 9.7$, df = 2, $P < 0.01$, and contrasts $P < 0.01$; Fig. 2), but not between unparasitized and parasitized nests from the colony with cowbirds (Fig. 2). Finally, we found no significant differences in fledging success among the groups ($H = 1.9$, df = 2, $P > 0.5$).

Nest desertion was significantly lower at the colony without cowbird visits (14%) than either unparasitized or parasitized nests in the colony visited by cowbirds (33% and 42%, respectively, $G = 8.7$, $P < 0.05$).

DISCUSSION

Our results show that (1) the egg survival rate and hatching success of nests in areas without Shiny Cowbirds is higher than in unparasitized nests in areas with parasites, and (2) nest desertion in areas without Shiny Cowbirds is lower than nest desertion of unparasitized nests in areas with parasites. These differences are attributable to egg-puncturing by Shiny Cowbirds during inspection visits to nests that they may not later parasitize. These costs are usually not considered because most studies compare the costs of parasitism between parasitized and unparasitized nests in areas with cowbirds. In addition, because the parasite punctures the host eggs as soon as they are laid, nests that are found after egg laying has started may produce an underestimate of clutch size in both parasitized and unparasitized nests.

Host-egg destruction by Shiny Cowbirds at parasitized nests has been reported as egg eating, egg removal, and egg puncture. Egg eating was briefly mentioned but not quantified by Hudson (1874). Similarly, Hoy and Ottow (1964) speculated about the potential use of eggs as nourishment, but found only punctured or missing host eggs and did not report egg eating. Egg removal by Shiny Cowbirds is, to our knowledge, no better documented than egg eating. We believe that the reduced clutch size of parasitized nests compared to unparasitized nests is not proof of egg removal by cowbirds, as there are no well-documented cases of cowbirds carrying eggs. Clutch reduction may result from two different behaviors: egg removal by cowbirds or, more likely, from host nest sanitation after the eggs have been damaged (Kemal and Rothstein 1988). In most studies the nests are not checked daily, which reduces the probability of finding punctured eggs before their removal. The disappearance of host eggs at parasitized nests may then be attributed to the parasite. Through daily visits to the nests, however, we were able to detect punctures in more than 70% of eggs that later disappeared from the nests (Massoni and Reboreda 1999). Because we do not expect Shiny Cowbirds to puncture host eggs and make another visit to carry them away, the most parsimonious explanation is removal of the egg by the host instead of the parasite.

Host-egg puncture by Shiny Cowbirds at parasitized nests is well documented and has been mentioned by several authors (Hoy and Ottow 1964, Post and Wiley 1977, Fraga 1978, 1985), who reported that it is one of the most important costs of brood parasitism, either through reduced number of fledglings or nest abandonment after egg breakage. Host-egg punctures by Shiny

Cowbirds at unparasitized nests have also been reported (Lichtenstein 1998, Nakamura and Cruz 2000), but not included in the calculations of the costs suffered by the hosts.

Egg puncturing by Shiny Cowbirds appears to be common throughout the species' range (Hoy and Ottow 1964, Post and Wiley 1977, Fraga 1978, Cruz et al. 1990). The frequency of its occurrence differs among studies, and this can be attributed to (1) differences in the density of either hosts or parasites (Post and Wiley 1977); (2) differences in the way data were collected (frequency of nest inspections); and (3) behavioral differences among populations (Post and Wiley 1977). Shiny Cowbirds have invaded the West Indies and are expanding their distribution across North America, raising the alarm about their settling on stable populations (Post et al. 1993, Cruz et al. 1998). If the Shiny Cowbird, a generalist species that already parasitizes 214 hosts (Ortega 1998), does become established in these areas, their new hosts will have to bear the cost of nest inspections by the parasite.

The reduction of the host's clutch by Brown-headed Cowbirds in parasitized and unparasitized nests is mainly achieved through egg removal (Sealy 1992, Arcese et al. 1996), but some studies also report egg punctures (Rogers et al. 1997). Other brood parasites like the Screaming Cowbird (*Molothrus rufoaxillaris*) and the Bronzed Cowbird (*Molothrus aeneus*) regularly puncture eggs at parasitized nests (Carter 1986, Fraga 1998, Peer and Sealy 1999). Therefore, the puncture or removal of host eggs is a widespread behavior in parasitic cowbirds whose impact on unparasitized nests needs to be addressed in more detail.

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