The Auk 123(1):23–32, 2006
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COSTS OF EGG PUNCTURES AND PARASITISM BY SHINY COWBIRDS (*MOLOTHRUS BONARIENSIS*) AT CREAMY-BELLIED THRUSH (*TURDUS AMAUROCHALINUS*) NESTS

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Abstract.—Most studies on cowbird parasitism have focused on its effects on parasitized nests, whereas few have considered the costs at nests that cowbirds visit but at which they do not lay eggs. Shiny Cowbirds (*Molothrus bonariensis*) peck and puncture host eggs both in nests where they lay eggs and in unparasitized nests. We analyzed the effect of egg punctures in unparasitized and parasitized nests of a large host, the Creamy-bellied Thrush (*Turdus amaurochalinus*; hereafter "thrush"), as well as the costs of Shiny Cowbird eggs and chicks in this host's nests. We determined thrush egg survival, hatching success, and chick survival in successful nests, and nest survival during the egg and nestling stages. Frequency of parasitism was 60%, and its intensity 1.6 ± 0.1 eggs nest^{-1}. Number of host eggs punctured was positively associated with intensity of parasitism. The host's eggs were frequently punctured in parasitized nests (71%) and in unparasitized nests (42%). Egg punctures reduced the number of eggs at hatching in 23% and 49% of unparasitized and parasitized nests, respectively. Nests with egg punctures had a lower survival rate than nests without them, but nest survival was not associated with parasitism. Presence of a Shiny Cowbird egg was associated with a decrease in the hatching success of host eggs, but presence of a Shiny Cowbird chick did not have any detrimental effect on either the survival and growth rate of host chicks in successful nests or the survival of the whole nest. Our results show that egg punctures were the primary determinant of thrush reproductive success. Consequently, comparison of unparasitized and parasitized nests gives an incomplete estimation of the effects of Shiny Cowbirds on host reproductive success, because the cost of egg punctures is also important in nests where there is no Shiny Cowbird egg laying. *Received 26 January 2004, accepted 8 June 2005.*

Key words: brood parasitism, Creamy-bellied Thrush, egg punctures, *Molothrus bonariensis*, Shiny Cowbird, *Turdus amaurochalinus*.

Costos de la Perforación de Huevos y el Parasitismo por *Molothrus bonariensis* en Nidos de *Turdus amaurochalinus*

Resumen.—La mayoría de los estudios sobre el parasitismo de los tordos se ha focalizado en el impacto producido por éstos en nidos parasitados, pero pocos trabajos han tratado los costos producidos en los nidos que los tordos visitan pero donde el parásito no pone huevos. *Molothrus bonariensis* pica y perfora los huevos del hospedador en nidos donde pone sus huevos, pero también en nidos no parasitados. En este estudio analizamos el impacto de las perforaciones de huevos en nidos no parasitados y parasitados de un hospedador grande, *Turdus amaurochalinus* así como los costos producidos por huevos y pichones de tordo en nidos de este hospedador.

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Se determinó la supervivencia de huevos, el éxito de eclosión y la supervivencia de pichones de zorzal en nidos exitosos, y la supervivencia de los nidos durante los estadíos de huevos y pichones. La frecuencia de parasitismo fue 60% y su intensidad 1.6 ± 0.1 huevos/nido. El número de huevos del hospedador con perforaciones estuvo positivamente asociado con la intensidad de parasitismo. Los huevos del hospedador fueron frecuentemente perforados en nidos parasitados (71%) así como en nidos no parasitados (42%). Las perforaciones de huevos disminuyeron el número de huevos antes de la eclosión en 23% y 49% en nidos no parasitados y parasitados respectivamente. Los nidos con huevos perforados tuvieron una menor supervivencia que los nidos con huevos sin perforaciones, pero la supervivencia de los nidos no estuvo asociada al parasitismo. La presencia de un huevo de tordo estuvo asociada con un descenso del éxito de eclosión de los huevos del hospedador, pero la presencia de un pichón de tordo no tuvo efectos negativos sobre la supervivencia y el crecimiento de los pichones del hospedador en nidos exitosos, o sobre la supervivencia del nido. Nuestros resultados muestran que la perforación de huevos fue el determinante primario del éxito reproductivo de los zorzales. Consecuentemente, comparar nidos no parasitados y parasitados brinda una estimación incompleta del impacto que *M. bonariensis* produce sobre el éxito reproductivo del hospedador ya que el costo de perforación de huevos es también importante en nidos donde no se hay puesta de huevos del parásito.

Brood parasitic cowbirds (*Molothrus* spp.) lay eggs in nests of other birds (hosts), which care for the parasitic offspring (Ortega 1998, Rothstein and Robinson 1998). Cowbird parasitism can reduce the reproductive success of the host in several ways: (1) cowbirds can remove (Sealy 1992, Payne and Payne 1998, Clotfelter and Yasukawa 1999) or puncture (Hoy and Ottow 1964, Post and Wiley 1977) the host's eggs; (2) cowbird eggs or chicks can reduce the hatchability of the host's eggs (Carter 1986, Petit 1991); (3) cowbird chicks can outcompete the host's chicks for food, lowering growth rates and promoting brood reduction (King 1973, Marvil and Cruz 1989); and (4) raising parasitic chicks can reduce the postfledging survival of the host's young (Payne and Payne 1998) or reduce the host's future reproductive value (Rothstein and Robinson 1998). In addition, cowbird parasitism can increase the probability of nest failure during the egg stage (Petit 1991, Clotfelter and Yasukawa 1999, Smith et al. 2003; but see Hill and Sealy 1994) or the chick stage (Massoni and Reboreda 1998, Dearborn 1999).

Most studies have focused on the effect produced by cowbirds at parasitized nests, and few have dealt with the costs inflicted by cowbirds at nests they visit but where they do not lay eggs. For example, Arcese et al. (1992, 1996) and Arcese and Smith (1999) reported a reduction in the success of unparasitized Song Sparrow (*Melospiza melodia*) nests when Brown-headed Cowbirds (*M. ater*) were present. Arcese et al. (1996) suggested that parasitism and predation are often linked because cowbirds depredate nests discovered late in the host's nesting cycle to enhance future opportunities for parasitism.

The Shiny Cowbird (*M. bonariensis*) uses multiple hosts, and collectively the species has parasitized more than 200 hosts (Friedmann and Kiff 1985, Ortega 1998). One cost associated with parasitism by Shiny Cowbirds is the puncture of host eggs at parasitized nests (Post and Wiley 1977; Fraga 1978, 1985; Massoni and Reboreda 1998). Punctured eggs also occur at unparasitized nests (Hudson 1874, Hoy and Ottow 1964, Nakamura and Cruz 2000), but until recently (Massoni and Reboreda 2002), the effect of egg punctures on host reproductive success was not analyzed in detail.

In the grassland regions of Argentina and Uruguay, Shiny Cowbirds lay either white (unspotted) or spotted eggs (Hudson 1874, Friedmann 1929). Some hosts accept both egg morphs, whereas others accept only spotted eggs (Mason 1986). One difficulty in estimating the cost of egg punctures by Shiny Cowbirds at unparasitized nests is that several of the hosts studied, like the Chalk-browed Mockingbird (*Mimus saturninus*; Fraga 1985, Sackmann and Reboreda 2003), the Rufous-bellied Thrush (*Turdus rufiventris*; Lichtenstein 1998, Sackmann and Reboreda 2003), or the Brown-and-yellow Marshbird (*Pseudoleistes virescens*; Mermoz and Reboreda 1994, 1998, 1999, 2003), reject white cowbird eggs. Therefore, some nests recorded as unparasitized may have been parasitized with white eggs that were subsequently rejected by the host before their detection by observers.

The Creamy-bellied Thrush (*T. amaurochalinus*; hereafter "thrush") has been reported as a host of the Shiny Cowbird (Friedmann and Kiff 1985), but the interactions between these species have not been studied. We measured the effects that Shiny Cowbirds have on (1) thrush egg survival, hatching success, and chick survival at unparasitized and parasitized successful nests and (2) nest survival during the egg and nestling stages in unparasitized and parasitized nests. Thrushes do not reject Shiny Cowbird eggs of the spotted morph, but they reject eggs of the white morph in ~60% of cases (Astié and Reboreda 2005). However, because our study was conducted in an area where the frequency of Shiny Cowbirds of the white morph was very low, we were able to estimate the costs produced by Shiny Cowbird egg-puncturing behavior in unparasitized and parasitized nests.

Methods

Study site and data collection.—The study was carried out at Guaymallén, Mendoza Province, Argentina (32°51′S, 68°42′W) during the 1999–2002 breeding seasons (September–December).

We followed the fates of 237 thrush nests (18 nests in 1999, 90 in 2000, 91 in 2001, and 38 in 2002). Sixty-one of these nests were found during construction, 38 during egg laying, 120 during incubation, and 18 after the chicks had hatched. Because we did not band the birds in our study, we cannot exclude the possibility that some nests were renesting attempts for failed nests. However, taking into account the location and laying date of each nest, we estimate that the proportion of nests that could have been renesting attempts of the same pair was <15%.

We found thrush nests mostly by focusing on alarm calls. Most nests were built in vineyards and olive and poplar groves, at heights of 1–10 m (mean ± SE: 2.42 ± 0.11 m; n = 158 nests). Nests were visited every 1–2 days until the chicks fledged or the nest failed. During visits, we recorded the numbers of host and Shiny Cowbird eggs and chicks and the occurrence of punctured eggs. After hatching, chicks were marked on the tarsus with waterproof ink and weighed on Pesola scales to the nearest 0.5 g.

Punctures made by Shiny Cowbirds result in one big, usually triangular, hole poked through the eggshell. Punctures made by House Wrens (*Troglodytes aedon*) result in several small punctures, usually traversing the eggshell. We never observed House Wren punctures in thrush eggs.

We assumed that the disappearance of host eggs at either unparasitized or parasitized nests was the result of host nest-sanitation (Kemal and Rothstein 1988) after the eggs had been punctured by Shiny Cowbirds. We consider this assumption parsimonious, because in 65% of the cases (n = 55) in which we observed that a host egg had disappeared, we found that the egg had been punctured within the previous 24 h. In addition, disappearance of eggs was higher during the laying period of the host, at which time 63% of parasitic events occurred.

Data analysis.—We estimated clutch size only from nests found during construction and visited daily until the clutch was complete. We used this criterion because Shiny Cowbirds often punctured host eggs shortly after they were laid, and to include nests found after clutch initiation could therefore have resulted in underestimation of clutch size. We assumed that the clutch was complete when the number of host eggs remained constant for at least two consecutive days.

To estimate the frequency and intensity (Shiny Cowbird eggs per nest) of parasitism, we considered only nests found during construction or laying and at which the host completed laying. We used this criterion because most parasitism by Shiny Cowbirds in thrush nests occurred during the laying period of the host. Therefore, inclusion of nests found during later stages could underestimate the frequency of parasitism if nest failure during the egg stage was associated with parasitism.

We analyzed separately the effects of Shiny Cowbird egg-puncturing behavior and parasitism on (1) number of host eggs before hatching, number of host hatchlings, and hatching success; and (2) nest survival during the egg stage (laying and incubation). Similarly, we analyzed the effect of parasitism on (1) host chick survival and growth rate and (2) nest survival during the nestling stage. To analyze the effect of parasitism during the egg stage, we considered clutches that received Shiny Cowbird eggs during laying or incubation to be parasitized. To analyze the effect of parasitism during the nestling stage, we considered as parasitized only those nests from which Shiny Cowbirds hatched.

We considered negligible the probability that nests were falsely recorded as unparasitized because of undetected host rejection of white eggs. Artificial parasitism experiments showed that thrushes eject white Shiny Cowbird eggs in ~60% of cases ($n = 28$ nests; Astié and Reboreda 2005). However, our study was conducted in an area where white eggs were uncommon. We found no white Shiny Cowbird eggs in 19 parasitized nests of a host known to accept them (the Rufous-collared Sparrow [*Zonotrichia capensis*]), and we found only 2 white eggs (out of 232 Shiny Cowbird eggs) in 137 parasitized thrush nests.

We recorded the number of host eggs present before the first host egg hatched and the numbers of chicks hatched and fledged. To estimate the number of eggs before hatching and the number of chicks hatched, we considered only nests found during construction, laying, or incubation that hatched either host or Shiny Cowbird chicks ($n = 126$). For estimating the number of chicks fledged, we considered only nests found in construction, laying, or incubation that fledged either host or Shiny Cowbird chicks ($n = 47$). We calculated hatching success as the number of hatchlings divided by the number of eggs present in the nest at the time of hatching. We determined chick survival as the number of fledglings divided by the number of hatchlings.

We also measured the effect of parasitism on host chick growth by comparing growth rate of chicks in unparasitized and parasitized nests. We estimated growth rate from the slope of a linear regression of weight versus chick age for chicks one to eight days old (hatching day = age 0). During this period, growth rate was almost linear ($F = 1295$, df = 1 and 7, $P < 0.001$, $r^2 = 0.995$). To avoid pseudoreplication, we used the means for each brood growth. To calculate the mean growth rate of the brood, we did not consider data from chicks that starved within the first 1–3 days after hatching, primarily because we did not have enough measurements to estimate their growth rate. Brood reduction was common in this species, affecting 69% of nests ($n = 35$) from which two or more (up to five) thrush or Shiny Cowbird chicks hatched, and 89% of nests ($n = 19$) from which three or more thrush or Shiny Cowbird chicks hatched.

We estimated daily nest mortality rate using Mayfield's exposure method (Mayfield 1975). Nest mortality was estimated as the number of nests lost divided by the total number of days those nests were under observation. The variance of daily mortality rate (V) was estimated as $V = [(\text{nest days} - \text{nest losses}) \times \text{nest losses}] / \text{nest days}^3$ (Johnson 1979). When we did not know the exact day of the nest loss, we assumed that it occurred at the midpoint between our visits (Mayfield 1975). Daily mortality rate was calculated for unparasitized and parasitized nests at two stages: eggs and nestlings. We also calculated daily mortality rate during the egg stage for nests with and without egg punctures. We compared specific daily mortality rates using the program CONTRAST (Hines and Sauer 1989). Nest survival at each nest stage was calculated as $(1 - DMR)^t$, where DMR is the daily mortality rate and t is the length in days per stage.

Statistical analysis.—For most analyses, we used nonparametric statistics because of lack of normality of the data. Statistical tests were performed using STATVIEW 5.0 (SAS Institute 1998) with $P < 0.05$. Values reported are means ± SE.

Results

Frequency of parasitism and egg punctures.—First thrush nesting attempts occurred during the second half of October, peaked during late November, and ended in late December. The frequency of Shiny Cowbird parasitism was 60% (56 of 94 nests), and its intensity was 1.6 ± 0.1 eggs. Thirty-nine percent of the parasitized nests received more than one Shiny Cowbird egg (22 of 56 nests, range: 2–4 eggs).

The average clutch size of thrushes was 3.1 ± 0.07 eggs ($n = 35$ nests, range: 3–4 eggs). Host eggs were punctured in both unparasitized and parasitized nests, but the frequency of nests with egg punctures was higher in the latter group (40 of 56 vs. 16 of 38, $\chi^2 = 6.9$, df = 1, $P < 0.01$). In addition, there was a negative association between the number of parasitic eggs and number of host eggs remaining at hatching (Spearman rank correlation, $\rho = -0.30$, $Z = -4.8$, $P < 0.001$; Fig. 1).

Effects of egg punctures and parasitism on egg survival, hatching success, and chick survival.—We analyzed separately the effects of egg punctures and parasitism on the host's egg survival and hatching success. For this analysis, we grouped the nests as unparasitized or parasitized, with or without punctured eggs. Number of eggs at time of hatching differed among groups (Kruskal-Wallis test, $H = 53.8$, df = 3, $P < 0.001$; Fig. 2A). Egg survival was higher in nests without egg punctures than in nests with egg punctures, for both unparasitized and parasitized nests ($P < 0.01$; Fig. 2A). Egg punctures decreased the number of eggs at hatching in 23% and 49% of unparasitized and parasitized nests, respectively. Number of eggs at time of hatching did not differ between unparasitized and parasitized nests without egg punctures, but was higher for unparasitized than for parasitized nests with egg punctures ($P < 0.01$; Fig. 2A). Similarly, number of chicks hatched was higher in nests without egg punctures than in nests with them, for both unparasitized and parasitized nests (Kruskal-Wallis test, $H = 52$, df = 3, $P < 0.001$, contrasts $P < 0.01$; Fig. 2B). Unparasitized nests with or without egg punctures had a higher number of hatchlings than parasitized nests with or without egg punctures ($P < 0.01$; Fig. 2B). Number of chicks that fledged was higher in unparasitized than in parasitized nests (U-test, $Z = 2.1$, $P < 0.05$; Fig. 2C), though the proportion of fledged chicks per egg laid was relatively low in both groups (unparasitized nests: 0.58, parasitized nests: 0.44).

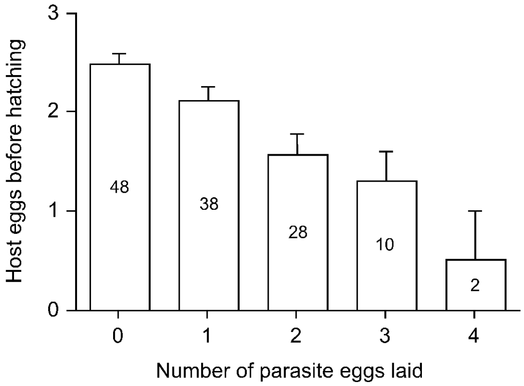

Fig. 1. Number (mean ± SE) of host eggs at time of hatching as a function of the number of Shiny Cowbird eggs. Sample sizes (nests) are indicated inside each bar.

To evaluate whether Shiny Cowbird eggs decreased the efficiency of host incubation, we estimated hatching success (number of host hatchlings divided by number of host eggs at hatching). There were significant differences in hatching success between groups (Kruskal-Wallis test, $H = 8.3$, df = 3, $P < 0.05$; Fig. 3A). Unparasitized nests with or without punctured eggs had higher hatching success than parasitized nests with or without punctured eggs ($P < 0.05$; Fig. 3A). Parasitized nests had more

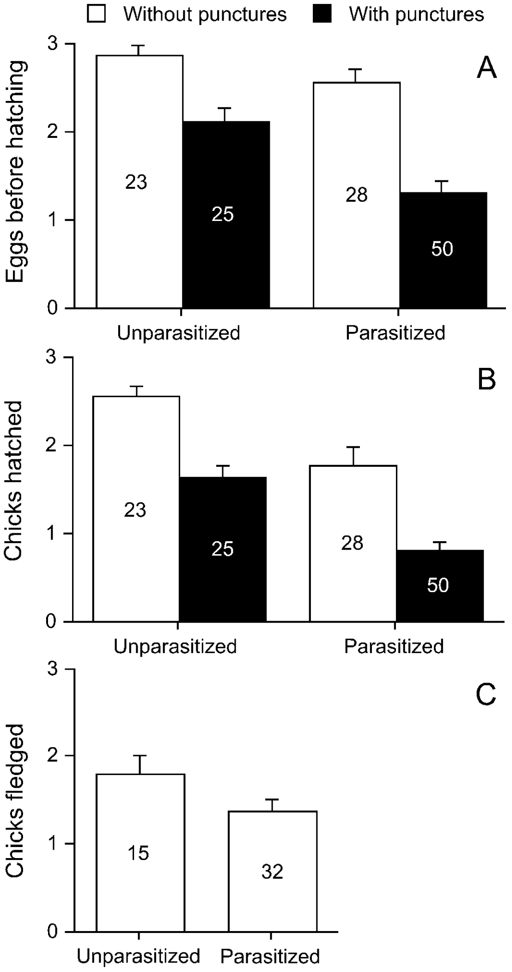

Fig. 2. Number (mean ± SE) of (A) host eggs at the time of hatching, (B) chicks hatched, and (C) chicks fledged, for unparasitized and parasitized Creamy-bellied Thrush nests. In (A) and (B), solid and empty bars are values for nests with and without egg punctures, respectively. Sample sizes (nests) are indicated inside each bar.

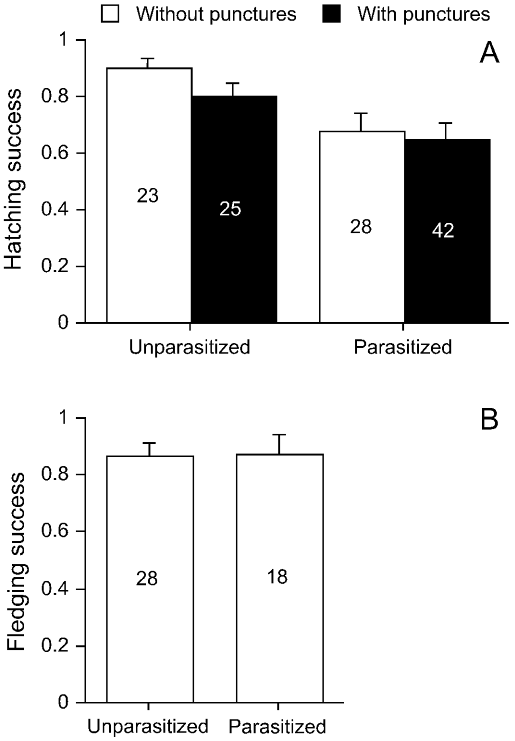

Fig. 3. (A) Proportions (mean ± SE) of chicks hatched among unparasitized and parasitized Creamy-bellied Thrush nests. Solid and empty bars are values in nests with and without egg punctures, respectively. (B) Proportion of chicks that fledged for unparasitized and parasitized nests. Sample sizes (nests) are indicated inside each bar.

eggs at hatching than unparasitized ones (parasitized: 3.32 ± 0.12, range: 1–5 eggs, $n = 78$ nests; unparasitized: 2.48 ± 0.11, range: 1–4 eggs, $n = 48$ nests; U-test, $Z = 4.25$, $P < 0.001$), and there was a negative association between number of eggs in the nest and host hatching success (Spearman rank correlation, $\rho = 0.19$, $Z = -2.1$, $P < 0.05$).

We also evaluated whether Shiny Cowbird chicks decreased the survival or growth rate of host chicks. For this analysis, we considered as parasitized only those nests where Shiny Cowbird chicks hatched. Thrush chicks were, on average, 25% larger than Shiny Cowbird chicks at hatching (thrush: 4.6 ± 0.07 g, $n = 58$; Shiny Cowbird: 3.7 ± 0.13 g, $n = 23$). Parasitized nests had more hatchlings (counting thrush and Shiny Cowbird chicks) than unparasitized nests (parasitized: 3.11 ± 0.24, $n = 18$ nests; unparasitized: 1.89 ± 0.2, $n = 28$ nests; U-test, $Z = 3.6$, $P < 0.001$), and there was a positive association between number of hatchlings and brood reduction (logistic regression, $\chi^2 = 12.1$, df = 1, $P < 0.001$). However, because for most of the parasitized nests, brood reduction involved Shiny Cowbird but not thrush chicks, host chick survival did not differ between unparasitized and parasitized nests (U-test, $Z = -0.6$, $P = 0.58$; Fig 3B). In addition, hatching of Shiny Cowbird chicks did not affect host growth. Host growth was 4.85 ± 0.25 g day^{-1} in nests with two host chicks ($n = 13$ nests) and 4.7 ± 0.25 g day^{-1} in nests with one host and one Shiny Cowbird chick (U-test, $Z = -0.7$, $P = 0.47$; $n = 8$ nests,), whereas it was 4.8 ± 0.25 g day^{-1} in nests with three host chicks ($n = 8$ nests) and 4.43 ± 0.32 g day^{-1} in nests with two host and one Shiny Cowbird chick (U-test, $Z = -0.26$, $P = 0.8$; $n = 6$ nests).

Effects of egg punctures and parasitism on nest survival.—Daily nest mortality during the egg stage differed among groups ($\chi^2 = 14.1$, df = 1, $P < 0.001$; Fig. 4A). Mortality was higher in parasitized nests with egg punctures than in parasitized nests without them ($\chi^2 = 10.7$, df = 1, $P < 0.001$), but it did not differ between unparasitized nests with and without egg punctures ($\chi^2 = 2.4$, df = 1, $P < 0.12$; Fig. 4A). Nest mortality rate did not differ between unparasitized and parasitized nests with or without egg punctures ($\chi^2 = 0.21$, df = 1, $P = 0.64$; $\chi^2 = 2.0$, df = 1, $P = 0.16$, respectively; Fig. 4A). Considering the effects of egg punctures and parasitism independently, nest mortality was higher in nests with egg punctures than in nests without them (0.068 ± 0.007 vs. 0.035 ± 0.007; $\chi^2 = 9.8$, df = 1, $P < 0.01$). However, mortality for unparasitized and parasitized nests did not differ (0.059 ± 0.006 vs. 0.074 ± 0.008; $\chi^2 = 0.27$, df = 1, $P = 0.6$). Daily nest mortality during the nestling stage did not differ between unparasitized and parasitized nests ($\chi^2 = 0.48$, df = 1, $P = 0.49$; Fig. 4B). Considering that incubation averaged 13.5 days and the nestling stage lasted 12.5 days, survival for unparasitized and parasitized nests during the egg stage was 0.44 and 0.48; whereas during the nestling stage, it was 0.30 and 0.36, respectively.

Discussion

Egg puncturing by Shiny Cowbirds was the main cause of reproductive loss in thrushes. Number of thrush eggs punctured was positively associated with intensity of parasitism,

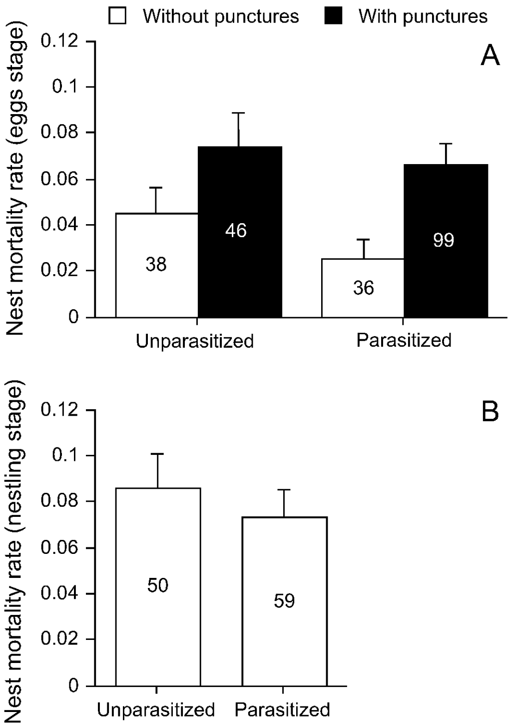

FIG. 4. (A) Daily mortality rates (mean ± SD) during egg stage (laying and incubation) for unparasitized and parasitized Creamy-bellied Thrush nests. Solid and empty bars are mortality rates in nests with and without egg punctures, respectively. (B) Daily mortality rates during the nestling stage for unparasitized and parasitized nests. Sample sizes (nests) are indicated inside each bar.

and although egg punctures were more frequent in parasitized nests, they were also common in unparasitized nests. Egg punctures were also associated with greater nest failure during the egg stage.

Arcese et al. (1996) proposed that Brown-headed Cowbirds act as nest predators (i.e. cause nest failure by destroying entire clutches or broods) when they discover unparasitized nests late in the host's nesting cycle. We found no support for this hypothesis, given that failure at nests with punctured eggs did not differ between unparasitized and parasitized nests during the egg stage. Similarly, there were no differences for the failure of unparasitized and parasitized nests during the nestling stage. More recently, Smith et al. (2003) analyzed whether Brown-headed Cowbirds cause Song Sparrow nests to fail by lowering clutch size below a threshold where the host deserts (cowbird-induced desertion) or by destroying entire clutches or broods (cowbird predation). They found that cowbird-induced desertion had a greater effect on nest failure than cowbird predation. Likewise, our results suggest that Shiny Cowbird punctures induced thrush nest-desertion by lowering clutch size.

In addition to the effect of egg puncturing at both unparasitized and parasitized nests, we also observed that Shiny Cowbird eggs reduced host egg hatching success. An explanation for this effect is that the efficiency of incubation was reduced in parasitized nests (Scott and Lemon 1996, McMaster and Sealy 1998). Although Shiny Cowbirds punctured host eggs, the number of thrush eggs destroyed was lower than the number of Shiny Cowbird eggs added per nest. Therefore, parasitized nests had larger clutches (counting thrush and Shiny Cowbird eggs) than unparasitized ones. Alternatively, the reduced hatching success could reflect the earlier hatching of Shiny Cowbirds, which disrupts the incubation behavior of the host. We consider this explanation unlikely, because in 76% of cases ($n = 34$), Shiny Cowbird chicks hatched between one day before and one day later than thrush chicks.

We did not detect an effect of Shiny Cowbird chicks on either thrush chick survival or growth rate. This is consistent with other studies of relatively large hosts that did not find any effect of Shiny Cowbird chicks on survival or growth of host chicks (Mermoz and Reboreda 2003, Sackmann and Reboreda 2003). Similarly, several studies of Brown-headed Cowbirds have shown that larger hosts are less sensitive to parasitism than smaller hosts (Trine et al. 1998, Lorenzana and Sealy 1999, Hauber 2003).

Nests that hatched Shiny Cowbirds did not have lower nest survival than nests without Shiny Cowbird chicks, as found among Yellow-winged Blackbirds (*Agelaius thilius*; Massoni and Reboreda 1998). As mentioned above, Shiny Cowbird and host chicks often hatched synchronously. Because thrush chicks were, on average, ~25% larger than Shiny Cowbird chicks at hatching, they outcompeted Shiny Cowbird chicks for food (in ~56% of cases, the Shiny Cowbird chick died 1–3 days after hatching). Considering that they spent so few days in the nest in most cases, it is unlikely that Shiny Cowbird chicks increased the risk of nest predation through higher begging activity or frequency of parental visits to the nest.

Our results indicate that punctures were the primary cause of reproductive loss among thrushes. Egg punctures affected unparasitized and parasitized nests, but because parasitized nests had a higher frequency of egg punctures and a lower hatching success, they produced approximately 20–25% fewer fledglings than unparasitized nests. Survival among unparasitized and parasitized nests did not differ during the egg and nestling stages. Had we not considered egg puncturing, our results would have led us to conclude that Shiny Cowbirds had a minimal effect on the reproductive success of thrushes. Such comparison of unparasitized and parasitized nests would miss the costs of egg puncturing by Shiny Cowbirds at unparasitized host nests. To better estimate the effects of Shiny Cowbirds, host reproductive success at unparasitized nests without punctures should be compared with reproductive success in the other groups. Alternatively, a removal experiment like that conducted by Smith et al. (2003) would provide comparative data.

Egg-puncturing behavior has been reported in other cowbirds, such as the Screaming Cowbird (*M. rufoaxillaris*; Fraga 1998) and the Bronzed Cowbird (*M. aeneus*; Friedmann 1929, Carter 1986, Peer and Sealy 1999). Similarly, Brown-headed Cowbirds reduce hosts' clutches in parasitized and unparasitized nests through egg removal (Sealy 1992). Therefore, destruction of host eggs appears to be a common cost produced by cowbirds, whose effects on unparasitized and parasitized nests need to be studied in more detail.

Acknowledgments

We thank M. E. Mermoz and two anonymous reviewers for helpful comments on a previous version of this manuscript. A.A.A. was supported by a fellowship from the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). J.C.R. is a Research Fellow of CONICET. This work was supported by CONICET (grant PID 0798/98), University of Buenos Aires (grant X158), and Agencia Nacional de Promoción Científica y Tecnológica (grant 01-09237).

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Associate Editor: K. Yasukawa