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BROOD PARASITISM OF THE SHINY COWBIRD, *MOLOTHRUS BONARIENSIS*, ON THE BROWN-AND-YELLOW MARSHBIRD, *PSEUDOLEISTES VIRESCENS*[1]

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Abstract. We studied the relationship between a generalist brood parasite, the Shiny Cowbird (*Molothrus bonariensis*) and one of its hosts, the Brown-and-Yellow Marshbird (*Pseudoleistes virescens*). Seventy-four percent of the nests found were parasitized. Although the parasite lays both white and spotted eggs, most of the cowbird eggs found in the nests of this host were spotted. Artificial parasitism experiments showed that the host rejected the cowbird white eggs. Shiny cowbird parasitism reduced the nesting success of the Brown-and-Yellow Marshbird mainly by punctures or cracks of the host eggs. The reduction of the nesting success of the parasite was due mostly to the loss of eggs in multiple parasitized nests. Shiny cowbird chicks were not outcompeted for food although they are smaller than the host chicks. The Brown-and-Yellow Marshbird appears to be a very good host, capable of rearing up to four cowbird chicks in a nest. We compared the nesting success of the Shiny Cowbird in Brown-and-Yellow Marshbird nests with its nesting success in the other sympatric hosts studied.

Key words: Brood parasitism; nesting success; Shiny cowbird; Brown-and-Yellow Marshbird; Molothrus bonariensis; Pseudoleistes virescens.

INTRODUCTION

Interspecific brood parasitism is a breeding system in which the parasite lays its eggs in the nest of another species, the host, which performs all the parental care. It is found in about 1% of bird species in seven different taxa. Those taxa are two subfamilies of cuckoos (Cuculinae and Neomorphinae), two types of finches (*Anomalospiza imberbis* and whydahs in the Viduinnae), the honeyguides (Indicatoridae), the Black-headed Duck (Anatidae), and the cowbirds (Icterinae) (Payne 1977, Rothstein 1990).

Within the cowbirds, the Shiny Cowbird, *Molothrus bonariensis,* is one of the most ubiquitous species. It is widespread through most of South America, with major gaps in the Amazonian forests, High Andes and the south of Patagonia (Friedmann 1929, Fraga 1985, Wiley 1985). Its eggs have been found in the nests of 201 bird species and at least 53 of them have reared its chicks successfully (Friedmann and Kiff 1985).

However, the impact of Shiny Cowbird parasitism on the nesting success of its hosts has only been studied in detail in four species: the Rufous-collared Sparrow, *Zonotrichia capensis* (Sick 1958; King 1973; Fraga 1978, 1983), the Chalk-browed Mockingbird, *Mimus saturninus* (Salvador 1984, Fraga 1985), the Yellow-shouldered Blackbird, *Agelaius xanthomus* (Post and Wiley 1977) and the Yellow-hooded Blackbird, *Agelaius icterocephalus* (Cruz et al. 1990).

The Brown-and-Yellow Marshbird, *Pseudoleistes virescens* (Icterinae), inhabits marshes and moist grasslands in the east–northeast of Argentina, Uruguay and adjacent areas of Brazil and it is sympatric with the Shiny Cowbird in all its distribution (Ridgely and Tudor 1989). Although Brown-and-Yellow Marshbirds have been mentioned as highly parasitized by the Shiny Cowbird (Gibson 1918, Hudson 1920, Orians 1985), there are no reports of this species rearing cowbird chicks successfully.

In eastern Argentina, southeast of Brazil and Uruguay, Shiny Cowbird eggs can be either white-immaculate or spotted (Hudson 1874, Friedmann 1929). Spotted eggs have a white, pale gray or pale blue background color and a variable pattern of gray and reddish-brown spots. Brown-and-Yellow Marshbird eggs have also reddish-brown spots, similar to the Shiny Cowbird's spotted morph. It has been suggested that this host accepts the spotted cowbird eggs but rejects

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the white ones (Hudson 1874, Friedmann et al. 1977, Orians 1985).

In this paper, we estimate the incidence of Shiny Cowbird parasitism on the Brown-and-Yellow Marshbird and analyze its effect on the nesting success of the host. We also analyze the nesting success of the Shiny Cowbird in Brown-and-Yellow Marshbird nests and compare it with the nesting success in the other sympatric hosts studied.

METHODS

The study was performed near General Lavalle (36°25′ South, 56°55′ West), in the province of Buenos Aires, Argentina from October to December 1992. This is a flat, low, marshy region, with little of the land rising more than 10 m above sea level. The native vegetation is composed of short grass species with scattered patches of woodland of *Celtis tala* and *Jodina rhombifolia* trees in the higher areas.

We followed the fates of 74 Brown-and-Yellow Marshbird nests. Sixty-six nests were found during the building or egg stage and eight during the nestling stage. The nests were found mainly along the sides of an unpaved road parallel with an artificial drainage canal (Canal 2). They were built in thistles (*Cynara cardunculus, Carduus* sp.), black rushes (*Juncus acutus*), pampa grasses (*Cortaderia selloana*) and cat-tails (*Typha* sp.) between 0.5 and 1.5 m in height. In most cases, nests were not in close proximity to one another. We marked the nests with a coded tag and we visited them every other day when possible. The eggs were checked for cracks or punctures, marked with water proof ink and measured with calipers (long and wide) to the nearest 0.1 mm. The chicks were marked with waterproof ink or color bands and were weighed with Pesola scales to the nearest 0.5 g until they fledged. All the nests were checked until they either fledged young or failed.

We considered as parasitized those nests that had cowbird eggs or nestlings at any stage. A parasite egg was considered as accepted if it hatched or if it stayed in the nest at least five days. On the other hand, it was considered as rejected if it disappeared from the nest without any sign of disturbance (e.g., a new parasitic egg, disappearance of another egg, etc.).

Brown-and-Yellow Marshbirds have helpers at the nest (Orians et al. 1977). We did not make direct observations of nest-provisioning activities but we considered that the nest had helpers if more than two adults performed active mobbing during our visits to the nest. As the nests were not in clumps, it is unlikely that our activities elicited mobbing behavior by close neighbors.

In the artificial parasitism experiments, a natural cowbird white egg was added to complete clutches (3–6 host eggs) and was considered as accepted if it remained in the nest for at least five days after the experimental introduction (Rothstein 1975). Values with means are standard error of the means.

RESULTS

The incidence of Shiny Cowbird parasitism on the Brown-and-Yellow Marshbird was 74.3% (55 out of 74 nests were parasitized). Twenty-two out of the 47 nests found during the egg stage were multiple parasitized (10 with 2 cowbird eggs, 7 with 3, 3 with 4 and 2 with 5). On average, the number of eggs laid in parasitized nests was 1.87 ± 0.17. Most of the cowbird eggs found were spotted. We observed white cowbird eggs in only 3 of 47 nests and in one of these nests the white egg disappeared later. The percentage of white eggs in the 47 nests was 4.5 (4 of 88 eggs). To test if this low percentage could be the result of host rejection, we made artificial parasitism experiments with white eggs in nests that had been naturally parasitized with spotted eggs. In five out of six cases, the white egg was rejected (in three cases before 24 hr and in the other two between the fourth and the fifth day), but in all the cases the spotted egg remained in the nest. There were no differences in width and length between the white introduced eggs and the spotted eggs that were in the nest.

We did not detect any cases of rejection of spotted eggs and they were accepted although parasite eggs were shorter (22.7 ± 0.082 mm, $n = 121$ vs. 25.96 ± 0.07, $n = 302$, t-test $P = 0.001$) and narrower (18.07 ± 0.05 mm, $n = 121$ vs. 19.09 ± 0.04, $n = 302$, t-test $P = 0.001$) than the host eggs.

The main factor which affected the nesting success of Brown-and-Yellow Marshbirds was predation. Only 22 (4 non-parasitized and 18 parasitized) out of 74 nests (29.7%) produced fledglings. The other 52 nests were abandoned and/or depredated during the egg ($n = 42$) or nestling ($n = 10$) stage. There was no difference in the percentage of abandonment and/or pre-

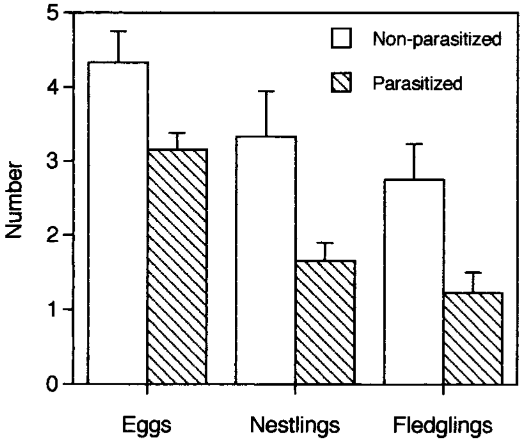

FIGURE 1. Number (mean ± SEM) of Brown-and-Yellow Marshbird eggs at the time of hatching, chicks hatched and fledglings produced in non-parasitized (white bars) and parasitized (stripped bars) nests. Sample sizes for the non-parasitized group are 6, 6, and 4 nests and for the parasitized group are 26, 26, and 18 nests.

dation between parasitized and non-parasitized nests.

Although the number of eggs laid by Brown-and-Yellow Marshbirds did not differ between parasitized and non-parasitized nests (3.88 ± 0.14, n = 33 vs. 4.25 ± 0.3, n = 12, Mann-Whitney two-tailed test, P = 0.26), the number of eggs present in the nest at the time of hatching was smaller in parasitized nests (Mann-Whitney two-tailed test, P = 0.029). Similarly, the number of chicks that hatched and the number of fledglings produced was smaller in parasitized nests (Mann-Whitney two-tailed tests, P = 0.017 and P = 0.032 respectively) (Fig. 1). Hatching failures in non-parasitized and parasitized nests were 21.1% and 43.1% respectively (Mann-Whitney two-tailed tests, P = 0.17).

Parasitism took place mainly during the laying period of the host (21 out of 28 cases). Shiny Cowbird chicks hatched after 11–13 days of incubation compared to 14–15 days for the host chicks. Consequently, in most cases (18 out of 22), cowbird chicks hatched before host chicks. The nestlings of the host and the parasite are clearly different in their general aspect. Brown-and-Yellow Marshbird nestlings have flesh-colored skin with scattered tufts of yellowish down, being these particularly conspicuous above the eyes. The oral flanges are white and the mouth lining is reddish. Shiny cowbird nestlings have flesh-colored skin too, but with scattered tufts of blackish down. The oral flanges range from white to yellow and the mouth lining is reddish. The host and the parasite chicks stayed in the nest during 11–13 days and their mass at day nine was 45.1 ± 1.24 (range 33–58, n = 23) and 38 ± 1.2 g (range 31.5–47, n = 14) respectively. The mass of an adult Brown-and-Yellow Marshbird is approximately 80 g whereas the mass of an adult Shiny Cowbird (*Molothrus bonariensis*) is: males = 55.5 ± 0.88 g (n = 21), females = 45.6 ± 0.69 g (n = 31).

The main factors that affected the nesting success of the parasite in the 18 parasitized nests that produced fledglings were the loss of eggs in multiple parasitized nests and the failure of some eggs to hatch. The number of eggs at the time of hatching, the number of chicks that hatched and the number of fledglings produced were smaller than the number of eggs laid ($P < 0.05$, Friedman test and multiple comparisons). There was no difference between the number of chicks that hatched and the number of chicks that fledged (Fig. 2). Hatching failures were similar to the observed for the host eggs in non-parasitized nests (20.6%).

We observed brood reduction in five out of 18 parasitized nests and in two out of six non-parasitized nests. Brood reduction always took place before the fifth day after hatching. Therefore, to analyze brood reduction we considered the nests that had not been depredated up to that day and where at least two chicks had hatched. In the parasitized nests brood reduction affected mainly the host chicks. All five parasitized nests lost host chicks (9 out of 10 chicks) but only one nest lost parasite chicks (2 out of 11 chicks) (Fisher Exact two-tailed test, $P < 0.001$).

Eight of 22 nests (2 non-parasitized and 6 parasitized) had helpers at the nest. Nests with helpers produced more fledglings (host and parasite) than the ones without helpers (3.25 ± 0.37, n = 8 vs. 2 ± 0.36, n = 14, Mann-Whitney two-tailed test, P = 0.04). All the nests in which we observed brood reduction did not have helpers.

DISCUSSION

Several studies have analyzed the host selection by Shiny Cowbirds (Mason 1986b, Wiley 1988) and the quality of its hosts (Sick 1958; King 1973; Post and Wiley 1977; Fraga 1978, 1985; Wiley 1985, 1986; Mason 1986a).

In the area where we worked, other hosts that have been previously studied are the Rufous-collared Sparrow and the Chalk-browed Mockingbird. The incidence of parasitism in the Brown-and-Yellow Marshbird (74.3%) was similar to that reported for the Rufous-collared Sparrow (72.5%, Fraga 1978) and the Chalk-browed Mockingbird (72.5%, Fraga 1985). However, our value is probably an underestimate because some nests recorded as non-parasitized could have been parasitized with white eggs that were quickly rejected.

The 4.5% of cowbird white eggs that we found in Brown-and-Yellow Marshbird nests was clearly smaller than the 50% observed in nests of the Rufous-collared Sparrow, a species that accepts both morphs (Fraga 1978). The rejection of white eggs shown by the Brown-and-Yellow Marshbird could account for this result. However, we cannot exclude the possibility that the low percentage of white eggs found in the nests of this host was also due to the fact that the Shiny Cowbird females that lay white eggs avoid parasiting this host, as suggested by Friedmann (Friedmann et al. 1977). We did not observe white cowbird eggs in the ground near the nests as mentioned by Hudson (1920). The percentage of cowbird white eggs in Brown-and-Yellow Marshbird nests was similar to the one observed in nests of the Chalk-browed Mockingbird (4.9%, Fraga 1985), another rejecter of the cowbird white eggs (Fraga 1985, Mason 1986).

The rejection of cowbird eggs by Brown-and-Yellow Marshbird was apparently elicited by the difference in color between its eggs and the eggs of the parasite. As noted above Brown-and Yellow Marshbird eggs are spotted, similar to the Shiny Cowbird spotted morph. Cowbird spotted eggs were accepted although they were shorter and narrower than the host eggs. This suggests that Brown-and-Yellow Marshbirds do not discriminate by size as does the Rufous Hornero, *Furnarius rufus* (Mason and Rothstein 1986). We recorded only one case of rejection of a spotted egg in one nest in which the host female laid eggs with few, pale brown spots. In this nest, the hosts accepted one cowbird white egg.

Several studies have shown that cowbird parasitism reduces the nesting success of the host. The female can remove or puncture one or more eggs of the host (Payne 1977, Rothstein 1990, Sealy 1992). They also have a thicker egg shell than their host (Spaw and Rohwer 1987, Rahn et al. 1988) and therefore its eggs could crack the eggs of the host during the laying or the incubation (Blankespoor et al. 1982, Røskaft et al. 1990). In addition, parasitic eggs could reduce the hatching success of the host and parasitic chicks may outcompete some or all the host nestlings for food.

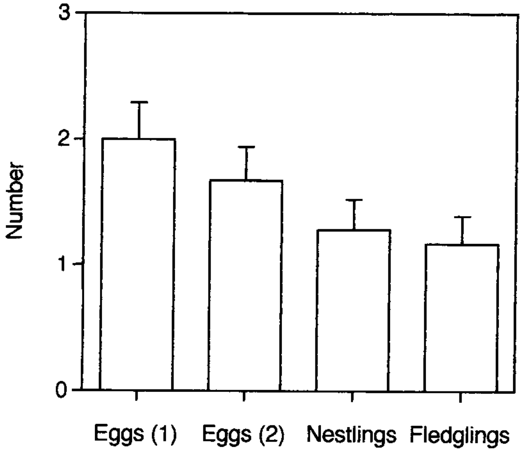

FIGURE 2. Number (mean ± SEM) of Shiny Cowbird eggs laid (Eggs 1), eggs at the time of hatching (Eggs 2), chicks hatched and fledglings produced in the 18 parasitized Brown-and-Yellow Marshbird nests that reached the fledgling stage.

The reduction of the nesting success of the Brown-and-Yellow Marshbird by Shiny Cowbird parasitism was mainly due to loss of eggs in parasitized nests. These losses could be a consequence of either the removal of intact eggs by the parasite or the removal by the host of eggs that had been punctured or cracked by the parasite. We did not detect any effect of parasitism on either the hatching success of the remaining host eggs or the fledgling success of the host chicks. Although brood reduction in parasitized nests affected mainly the host chicks, we also observed brood reduction in non-parasitized nests. Therefore, brood reduction appears to happen independently of parasitism and could be related to the presence of helpers at the nests.

The Brown-and-Yellow Marshbird appears to be a very good host, capable of rearing up to four cowbird chicks in a nest. The main reduction of the nesting success of the parasite was due to the loss of eggs, probably by punctures of other cowbirds in multiple parasitized nests. It is interesting to point out that, although cowbird chicks

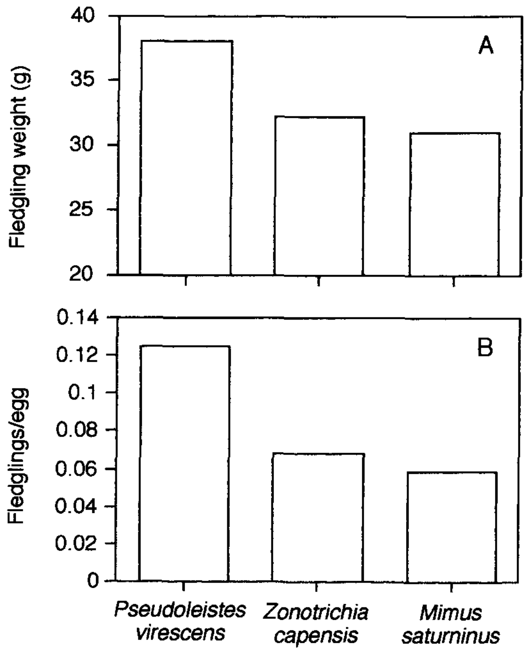

FIGURE 3. Mean weight of Shiny Cowbird chicks at day nine (A) and number of fledglings produced per Shiny Cowbird egg laid (B) in three hosts, the Brown-and-Yellow Marshbird *Pseudoleistes virescens,* the Rufous-collared Sparrow *Zonotrichia capensis* (data from Fraga 1978), and the Chalk-browed Mockingbird *Mimus saturninus* (data from Fraga 1985).

were smaller than Brown-and-Yellow Marshbird chicks, they were not outcompeted for food as it happens in nests of the Chalk-browed Mockingbird (Fraga 1985). We only observed two cowbird chicks that starved and that happened in a nest which had five chicks, two of the host and three of the parasite. In the other nests that produced fledglings all the cowbird chicks fledged. This result contrasts with that reported for the other sympatric cowbird hosts that have been studied. Starvation of cowbird chicks is common in the nests of both, Rufous-collared Sparrow and Chalk-browed Mockingbird (Fraga 1978, 1985). In the nests of these species the weight of the cowbird nestlings at day nine (asymptotic weight) is smaller than in the nests of the Brown-and-Yellow Marshbird (Fig. 3a). The nesting success of cowbirds, measured as fledglings produced per egg laid, is higher in the nests of the Brown-and-Yellow Marshbird than in the nests of the Rufous-collared Sparrow or the Chalk-browed Mockingbird (Fig. 3b). Thus, the Brown-and-Yellow Marshbird has a higher "host value" for cowbirds than the other sympatric hosts studied. The high quality as a host could be related to the presence of helpers at the nests that would allow the Brown-and-Yellow Marshbird to rear successfully both, the host and the parasitic chicks.

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