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Costs of brood parasitism and the lack of defenses on the yellow-winged blackbird - shiny cowbird system

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Abstract The shiny cowbird (*Molothrus bonariensis*) is a generalist brood parasite that lays either white-immaculate or spotted egg morphs in eastern Argentina and Uruguay. Some hosts accept both morphs, others accept spotted eggs and reject the white morph, but no host has been found to accept white eggs and reject spotted ones. It has been suggested that the yellow-winged blackbird (*Agelaius thilius*) may be that type of host. The finding of a white acceptor-spotted rejector species would help to explain the occurrence and maintenance of the parasite egg polymorphism. We studied the incidence of shiny cowbird parasitism on this host, its costs for their reproductive success and the presence of antiparasitic defenses in the yellow-winged blackbird - shiny cowbird system. The parasite affected the reproductive success of the host in two ways. Cowbirds punctured host eggs causing a reduction in clutch size, and yellow-winged blackbirds deserted their nests whenever they suffered high egg loss. In addition, parasitized nests suffered higher predation during the nestling stage, but not during egg stages, indicating that the difference found was related to the presence of the cowbird chick, and not to higher exposure of parasitized nests to both parasites and predators. Despite the costs imposed by the parasite, yellow-winged blackbirds have not evolved antiparasitic defenses. This host did not reject any egg morph of the shiny cowbird nor desert parasitized nests unless it had suffered high egg loss. Current explanations for the host lack of defenses, the "time lag" and the "equilibrium" hypothesis, are discussed.

Key words Brood parasitism · Shiny cowbirds · Yellow-winged blackbirds · *Molothrus bonariensis* · *Agelaius thilius*

Introduction

Obligate brood parasites depend on other species, the hosts, to raise their offspring. Brood parasitism usually reduces the reproductive success of the hosts (see Payne 1977; Rothstein 1990 for reviews), and its effects can be observed at different stages of the nesting cycle: (1) parasites can puncture or remove one or more host eggs when laying their own eggs (Hoy and Ottow 1964; Brooker et al. 1988; Davies and Brooke 1988; Sealy 1992); (2) parasite eggs or chicks can reduce the hatchability of host eggs (Blankespoor et al. 1982; Soler 1990; Petit 1991); (3) parasite chicks can outcompete the host's chicks for food and therefore cause brood reduction (Post and Wiley 1977; Marvil and Cruz 1989; Soler 1990); and finally, (4) raising parasite chicks may reduce the post-fledgling survival of the host chicks or the future reproductive success of the host parents, although these costs have not been measured in any species. Selection pressures arising from parasitism may result in the evolution of host defenses. Common antiparasite defenses include aggression towards the parasite, rejection of the parasitic eggs, and nest desertion (Rothstein 1990). While aggression towards the parasite may eliminate most costs of parasitism by decreasing its incidence (but see Robertson and Norman 1977), the latter two eliminate the effect of parasitism on host hatching and fledgling success.

The shiny cowbird (*Molothrus bonariensis*) is a generalist, obligate brood parasite that reduces the reproductive success of the majority of the hosts studied in detail (Post and Wiley 1977; Fraga 1978, 1985; Cruz et al.

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1990; Mermoz and Reboreda 1994). Throughout most of its distribution, shiny cowbird females lay spotted eggs. However, in the grasslands regions of Argentina and Uruguay, they lay both white-immaculate and spotted egg morphs (Friedmann 1929; Fraga 1978; Mermoz and Reboreda 1994; Lyon 1997), the frequency of the white morph varying from 20% (Mermoz 1996) up to 50% (Fraga 1978). Some host species accept both egg morphs while others accept only spotted eggs, but there are no known cases of species that reject the spotted eggs and accept the white ones (Mason 1986; Mermoz and Reboreda 1994; Lyon 1997).

The yellow-winged blackbird (*Agelaius thilius*) is one host of the shiny cowbird (Friedmann et al. 1977), and its distribution is enclosed within that of the parasite (Ridgely and Tudor 1990). This host is smaller in body size than the shiny cowbird (average adult weight: 35 g versus 50 g, respectively), which suggests relatively high costs of parasitism (Fraga 1978) and, consequently, increased selection pressure for the development of antiparasitic defenses. Yellow-winged blackbird eggs are creamy in color, lightly scrawled or spotted with blackish marks. Based on the light color of its eggs, and some parasitized nests that contained only cowbird eggs of the white morph, the yellow-winged blackbird has been suggested as a potential rejector of spotted eggs and acceptor of the white morph (Friedmann et al. 1977). The finding of a species with that pattern of egg rejection would help to explain the occurrence of the two egg morphs, as well as the maintenance of the parasite egg polymorphism. Nevertheless, this is the first in-depth study of the yellow-winged blackbird - shiny cowbird system.

The aim of this study was to: (1) determine the incidence of parasitism of shiny cowbirds on yellow-winged blackbirds; (2) estimate the cost of parasitism on the host reproductive success throughout the breeding cycle; and (3) determine whether yellow-winged blackbirds have developed antiparasitic defenses such as egg ejection or nest desertion against a particular egg morph of the shiny cowbird.

Methods

Study area

The study was conducted near the town of General Lavalle in the province of Buenos Aires, Argentina (36°25′S, 56°55′W) from early October to late December 1994. The area is flat, low and marshy, 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 on the higher ground. We conducted intense nest surveys in marshy areas close to an artificial drainage canal.

Data collection

We found 213 active nests (81 during construction, 42 during egg laying, 80 during incubation, and 10 after the chicks had hatched). Nests were numbered with flagging tape placed nearby and visited daily until either their chicks fledged or failed. We considered as parasitized those clutches that had cowbird eggs or nestlings at any stage of the host nesting cycle. In each visit we recorded the number of hosts and parasite eggs and the occurrence of cracks or punctures in eggs. Host and parasite eggs were marked with waterproof ink and measured with a caliper (length and breadth) to the nearest 0.01 mm. After hatching, chicks were marked on the tarsus with waterproof ink and weighed daily (except for 4 days scattered throughout the season) with 50-g Pesola spring balances to the nearest 0.5 g until they fledged. Nests were considered deserted if the eggs were cold to the touch for 2 consecutive days and no yellow-winged blackbirds tended the nest, and predated if all the eggs or chicks disappeared between 2 consecutive visits (days).

Artificial parasitism experiments

We performed artificial parasitism experiments on 14 yellow-winged blackbird nests. In each nest, we added one real cowbird egg during the first (12 cases) or the second day (2 cases) of egg laying. Cowbird eggs were collected from deserted nests of yellow-winged blackbirds or from nests of another host nesting in the study area, the brown-and-yellow marshbird (*Pseudoleistes virescens*). In eight nests we added one spotted cowbird egg (22.80 ± 0.22 mm in length and 18.00 ± 0.27 mm in breadth, mean ± SE) and in six nests one white-immaculate egg (22.82 ± 0.30 mm in length and 17.20 ± 0.33 mm in breadth, mean ± SE). Nests were artificially parasitized during early morning to simulate parasitism by shiny cowbirds (Hoy and Ottow 1964). Eggs were considered accepted if they remained in the nest for at least 5 days after the experimental introduction (Rothstein 1975) or if they remained for 4 days and the nest was found predated at day five (Sealy 1992).

Data analysis

Clutches were considered completed when the number of host eggs remained constant for at least 2 consecutive days. Incubation period for yellow-winged blackbird eggs was estimated as the time elapsed since the laying of the last egg and the hatching of the last nestling in clutches where all eggs hatched (Nice 1954). Incubation period for shiny cowbirds was estimated as the time elapsed from the commencement of full incubation of the host (usually just after laying the penultimate egg) to hatching (Briskie and Sealy 1990).

Weight data of host and parasitic chicks were analyzed according to the methodology proposed by Ricklefs (1967, 1968). Data were fitted to a logistic equation of the form:

$$W = A/1 + e^{-k(t-t_{50})}$$

where W is the weight of the bird in grams at age t, A is the approximate asymptote of the growth curve, K is the growth rate and t_{50} is the age in days where the growth rate reaches its maximum (the inflection point of the growth curve), which occurs at half the asymptotic weight on the logistic curve. Growth curves were linearized and their slopes, directly proportional to the growth rate (K), compared using a Student's t-test (Zar 1996).

We estimated clutch size of 53 yellow-winged blackbird nests (36 non-parasitized and 17 parasitized) found exclusively during construction and checked daily until the egg laying period ended without predation. The number of eggs before hatching and the number of chicks hatched were estimated from 71 nests (50 non-parasitized and 21 parasitized) that were found during construction, egg laying or early incubation and that reached the nestling stage. Finally, the number of host chicks fledged was estimated from 36 nests (31 non-parasitized and 5 parasitized) that were found during construction, egg laying, incubation or nestling stage and that fledged chicks. Hatching success (per nest) was calculated as the number of chicks hatched over the number of eggs before hatching (total clutch laid minus egg losses during incubation), and fledgling success (per nest) was calculated as the number of chicks fledged over the number of chicks hatched.

In the previous paragraph we explain the criteria by which, for each test and data category, we made use of the maximum number of nests possible. However, we carefully excluded those nests that could potentially bias the results. For example, as we mentioned before, some of the nests were found after incubation had begun. Shiny cowbirds usually damage the host's eggs in association with parasitic events, and the hosts subsequently remove broken eggs. In order to avoid underestimation of the incidence of brood parasitism and its effects on the host breeding success – a likely event if one or more cowbirds visited the nests and damaged eggs before we found them – we used a subset of nests found exclusively during construction and early laying stages. This sample ($n = 117$) was used only where the inclusion of all nests could have biased the results, as for the incidence of parasitism, nest desertion and predation tests.

We estimated the host quality of yellow-winged blackbirds by the number of shiny cowbirds chicks fledged per egg laid, and by the weight of parasitic chicks at the time to fledge.

Values are mean ± SE. All tests are two-tailed.

Results

Breeding biology of host and parasite

Nest attempts by yellow-winged blackbirds first occurred during mid-October and the latest during the third week of December. All active nests found were built in cattails (*Typha* sp.) at an average height from the base of the plant of 60.28 ± 1.23 cm ($n = 213$). On average, clutch size was 3.41 ± 0.07 eggs (32 nests with 3 eggs, 20 nests with 4 eggs and 1 nest with 5 eggs). There was no difference in clutch size between parasitized (3.41 ± 0.15 eggs, $n = 17$) and non-parasitized (3.42 ± 0.08 eggs, $n = 36$) nests (Mann-Whitney *U*-test, $z = 0.23$, $P = 0.79$). Because the size of eggs from the same clutch are not statistically independent, we calculated the mean value of egg length and egg breadth for each of the complete clutches and then calculated the overall average of the nest means. Eggs were 21.87 ± 0.13 mm in length and 16.03 ± 0.07 mm in breadth ($n = 53$ clutches). The average incubation period was 12.4 days (12 days in 15 cases, 13 days in 9 cases, and 14 days in 1 case). In 75% of the cases, incubation started after the laying of the second egg, and in the remaining cases it started after the laying of the first (12.5%) or the third (12.5%) egg.

Shiny cowbird eggs in yellow-winged blackbird nests first appeared during mid-October, coinciding with first nest attempts by this host. Of the 213 active nests 78 were parasitized with 98 cowbird eggs; 78 eggs (79.6%) were spotted and 20 eggs (20.4%) were white-immaculate. Spotted and white eggs were similar in length (22.66 ± 0.08 mm vs. 22.9 ± 0.14 mm, respectively) but spotted eggs (18.14 ± 0.08 mm) were significantly wider than white eggs (17.51 ± 0.17 mm; Mann Whitney *U*-test, $z = -3.72$, $P = 0.0002$). We recorded the laying date of 60 parasitic eggs. From those, 70% (42 of 60) were laid during the laying period of the host (days 0–3 in Fig. 1) and their incubation period was on average 11.6 days (11 days in 3 cases and 12 days in 5 cases). As a consequence of the synchronization between parasite and host egg laying, and the shorter incubation period of the parasite, in 84.2% of the cases (16 of 19), shiny cowbird chicks hatched before or simultaneously with the first host chicks (Fig. 2).

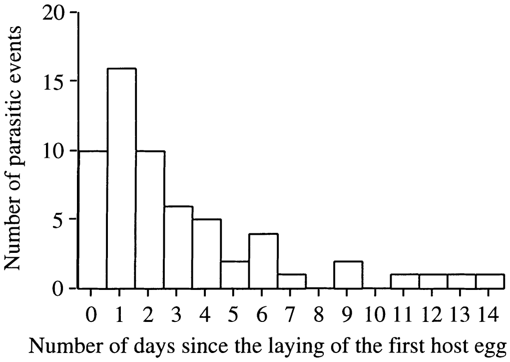

Fig. 1 Frequency distribution of the time at which shiny cowbirds laid their eggs in yellow-winged blackbird nests, relative to day of first host egg oviposition (total $n = 60$ parasitic events)

Incidence of parasitism, egg punctures and nest desertion

We estimated the incidence of parasitism from 117 yellow-winged blackbird nests found exclusively during construction and egg laying stages. In this way we avoided a possible underestimation of the rate of parasitism, for reasons explained in Methods, and because parasitized nests have a higher probability of being predated during the nestling stage. The overall incidence of parasitism was 26.5% (31 of 117 nests, Table 1). In 80.6% of these cases (25 of 31) the nests were parasitized once, while in the remaining 19.4% of the cases (6 of 31) they were parasitized twice and, based on the different color of the parasitic eggs, presumably by different females (Collias 1993; Lyon 1997).

Shiny cowbirds do not remove or eat the eggs of their hosts, but they puncture them (Hudson 1874; Hoy and Ottow 1964, Fraga 1978, 1985; Mermoz 1996; V. Massoni and J.C. Reboreda, unpublished work), and those eggs do not hatch. Punctured eggs were detected

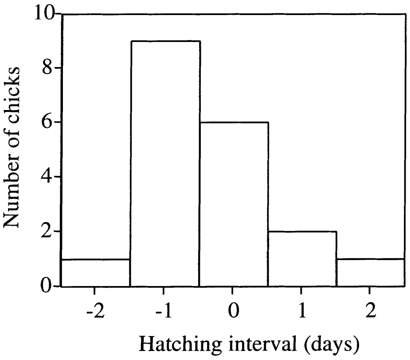

Fig. 2 Frequency distribution of the interval between the hatching of shiny cowbird chicks and the first yellow-winged blackbird chick hatched at the nests ($n = 19$ cases)

Table 1 Number of non-parasitized and parasitized nests that fledged chicks or that were deserted or predated at different stages of the nesting cycle. The number in brackets indicates the number of nests where we observed punctures of host eggs. All 117 nests were found during construction or early egg laying and were visited daily until either fledged chicks or failed

	Laying and incubation stage		Nestling stage			
	Deserted	Predated	Deserted	Predated	Successful	Total
Non-parasitized	20 (17)	40 (4)	2 (1)	9 (2)	15 (2)	86 (26)
Parasitized	10 (10)	11 (9)	0 (0)	9 (7)	1 (0)	31 (26)
Total	30 (27)	51 (13)	2 (1)	18 (9)	16 (2)	117 (52)

during daily visits to the nests and were lately removed by the hosts, irrespectively of whether the nest had received a cowbird egg or not. The appearance of punctures on the host eggs was associated with the presence of parasitic eggs, although a lower incidence of punctures was also found in non-parasitized nests. In 83.9% of parasitized nests (26 of 31) we observed punctures of host eggs, while in the non-parasitized nests we only observed punctures in 30.2% of the nests (26 of 86) ($\chi^2 = 26.55$, $df = 1$, $P < 0.0001$).

Nests that suffered egg punctures had a higher probability of being deserted. Of 52 nests 27 (51.9%) which had punctures of one or more host eggs were deserted, while only 3 of 65 nests (4.6%) which did not have punctures were deserted ($\chi^2 = 33.9$, $df = 1$, $P < 0.0001$). In nests with egg punctures, the number of eggs lost affected the rate of nest desertion. On average, nests with egg punctures that were deserted lost 2.77 ± 0.16 eggs ($n = 22$ nests) while non-deserted punctured nests lost on average 1.15 ± 0.27 eggs ($n = 13$ nests) (Mann-Whitney U-test, $z = -3.98$, $P = 0.0001$).

In 25.6% (30 of 117) of the cases, the nest was deserted during egg laying or incubation. In spite of the common occurrence of punctures at parasitized nests, nest desertion was not statistically different between parasitized (32.2%, 10 of 31) and non-parasitized nests (23.2%, 20 of 86), ($\chi^2 = 0.97$, $df = 1$, $P = 0.33$), probably because of the replacement role of cowbird eggs at those nests. Parasitized nests received 1.19 ± 0.07 cowbird eggs ($n = 31$ nests), and lost a very low number of them (0.17 ± 0.081, $n = 23$ nests, a total of 4 cowbird eggs) due to punctures. On average, then, punctured-parasitized nests had one more egg than punctured non-parasitized nests. Because of the addition of the cowbird egg, which yellow-winged blackbirds do not seem to distinguish from their own, and the host's tendency to desert when it suffered high egg loss, parasitized nests were probably less likely to be deserted than unparasitized nests that experienced a similar loss of host eggs.

Nest predation

Table 1 shows the number of parasitized and non-parasitized nests that were predated at different stages of the nesting cycle of yellow-winged blackbirds. The main cause of nest failure was predation (50.5% of the failures during the egg laying or incubation stages and 17.8% of the failures during the nestling stage). Potential predators in the area include chimangos caracara (*Mivalgo chimango*), long-winged harriers (*Circus buffoni*), barn owls (*Tyto alba*), opossums (*Didelphis* sp.), skunks (*Conepatus* sp.) and small snakes. During the nestling stage, parasitized nests experienced higher predation than non-parasitized nests, suggesting that the presence of the cowbird chick at the nest increased its chances of being predated upon. One explanation for this result could be that parasitized nests were intrinsically more detectable and, therefore, more susceptible to both parasitism and predation. However, if that is the rationale, predation of parasitized nests should be higher during the egg stages as well.

Predation during egg laying and incubation stages was similar for parasitized (35.4%, 11 of 31) and non-parasitized (46.5%, 40 of 86) nests, ($\chi^2 = 1.13$, $df = 1$, $P = 0.29$; Table 1), indicating that parasitized nests were not more detectable during those stages. Conversely, during the nestling stage, 90% of parasitized nests (9 of 10) were predated, against 34.6% of the non-parasitized nests (9 of 26) (Fisher's exact P-value = 0.004). Because of the small size of this sample, which includes only those nests found during construction or early egg laying stage, we repeated the analysis of nestling predation including those nests found during incubation. Once again, parasitized nests were more predated (69.6%, 16 of 23) than non-parasitized nests (36.8%, 21 of 57) ($\chi^2 = 3.06$, $df = 1$, $P = 0.008$). The association between parasitism and predation was highly significant during the nestling stage but not earlier, indicating that increased predation of parasitized nests is caused by the presence of parasitic chicks, and not by higher exposure of those nests.

On average, only 13.7% (16 of 117) of the yellow-winged blackbird nests fledged chicks. Nesting success of non-parasitized nests was 17.4%, while nesting success of parasitized nests was 3.2% (15 of 86 vs. 1 of 31 nests, Fisher's exact P-value = 0.07). These values underestimate the decrease in nesting success produced by shiny cowbirds because do not take into account those non-parasitized nests (i.e., without cowbird eggs) that were deserted as a result of egg punctures. Nesting success of the nests with no signs of the visit of shiny cowbirds (neither parasitic eggs nor host eggs with punctures) was 21.7%, while the nesting success of those nests with either parasitic eggs or punctures in host's eggs was 5.6% (13 of 60 vs. 3 of 57 nests, Fisher's exact P-value = 0.01).

Effect of parasitism on host eggs and chicks

The clutch size laid by yellow-winged blackbirds was similar in non-parasitized and parasitized nests, but the number of eggs at the time of hatching was significantly smaller in parasitized nests (Mann-Whitney U-test, $z = -2.71$, $P = 0.007$; Fig. 3). Parasitized nests also hatched fewer chicks (Mann-Whitney U-test, $z = -3.32$, $P = 0.0009$) and there was a tendency to produce fewer fledglings although it was not significant, probably because of the small sample size (Mann-Whitney U-test, $z = -1.58$, $P = 0.11$; Fig. 3). To evaluate whether reduced broods in parasitized nests resulted from egg punctures (more frequent in parasitized nests) or there were additional costs due to the presence of the parasitic egg or chick, we calculated the hatching and fledgling success in parasitized and non-parasitized nests.

According to the definitions given above, we decided to utilize a bigger sample size than the one used to analyze incidence of parasitism. Hatching success, the number of eggs hatched over number of eggs before hatching, is not affected by the stage at which the nests are found as far as no nests with nestlings are included. Similarly, the number of chicks fledged over the number of chicks hatched, or fledgling success, can be calculated using all nests found right before the hatching stage because what is being measured is the effect of parasitic nestlings over their foster siblings.

Although they were lower in parasitized nests, there was no significant effect of parasitism on either hatching success (non-parasitized nests: 0.84 ± 0.03, $n = 50$, parasitized nests: 0.66 ± 0.09, $n = 21$, Mann-Whitney U-test, $z = -1.56$, $P = 0.12$) or fledgling success (non-parasitized nests: 0.95 ± 0.03, $n = 31$, parasitized nests: 0.80 ± 0.20, $n = 5$, Mann-Whitney U-test, $z = -0.57$, $P = 0.57$). When the overall success (i.e., from egg to fledgling stages) is compared, no difference is found between parasitized and non parasitized nests (non-parasitized nests: 0.787 ± 0.045, $n = 29$, parasitized nests: 0.80 ± 0.20, $n = 5$, Mann-Whitney U-test, $z = -0.729$, $P = 0.466$).

Because parasitic chicks hatched before host chicks (Fig. 2), had a higher weight at hatching (shiny cowbirds: 3.58 ± 0.18 g, $n = 13$, yellow-winged blackbirds: 2.19 ± 0.05 g, $n = 83$, Mann-Whitney U-test, $z = -5.65$, $P = 0.0001$), and were heavier throughout the nestling stage (Fig. 4), they could outcompete the host chicks for food and therefore decrease host chick growth rate. We calculated the growth rate of yellow-winged blackbird chicks in non-parasitized and parasitized nests. Weights were fitted to a logistic equation (see Methods). The values for non-parasitized and parasitized nests were: growth rate, 0.62 and 0.50; t_{50}, 3.75 and 4.25 days; and days at the nest, 7.03 and 8.64, respectively. Growth curves were linearized ($r^2 = 0.995$ and 0.99 for the non-parasitized and parasitized groups) and their slopes were not significantly different (non-parasitized group: 0.16; parasitized group: 0.14; $t = 0.16$, $df = 16$, $P > 0.5$; Fig. 5).

Antiparasitic defenses of yellow-winged blackbirds

We did not record any case of egg rejection either in naturally parasitized nests (78 nests with 78 spotted eggs and 20 white eggs) or artificially parasitized nests (14 nests, 8 with spotted and 6 with white eggs). In seven of the eight nests experimentally parasitized with spotted eggs, the egg was accepted according to the criteria described above (see Methods), and in the other case the parasite egg remained 3 days after which the nest was predated. In a similar way, in five of the six nests parasitized with the white morph the egg was accepted, and in the other case it remained 2 days after which the nest

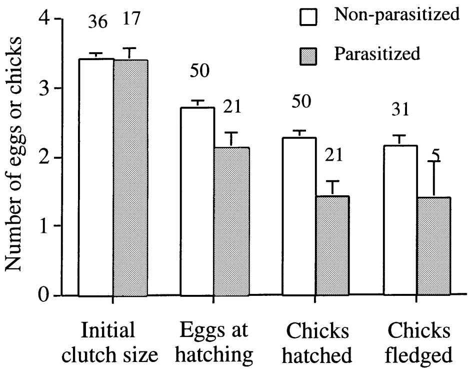

Fig. 3 Number (mean ± SE) of eggs laid, eggs in the nest at the time of hatching, chicks that hatched and chicks that fledged in non-parasitized and parasitized nests. *Sample sizes* (nests) are indicated above the *bars*

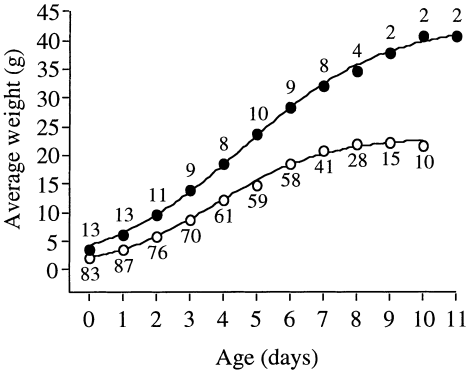

Fig. 4 Growth curves of shiny cowbirds (*filled circles*) and yellow-winged blackbirds (*open circles*). Sample sizes (chicks) for shiny cowbirds and yellow-winged blackbird weights are indicated *above* and *below* the symbols, respectively

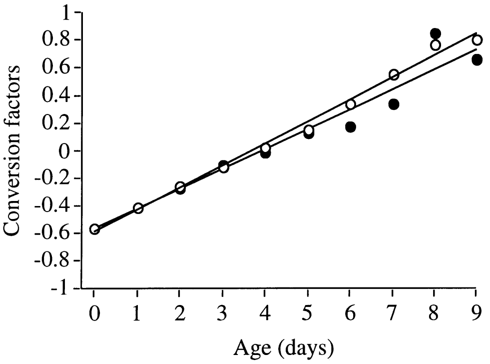

Fig. 5 Linearized growth curves of yellow-winged blackbird chicks in non-parasitized (*open circles*) and parasitized (*filled circles*) nests for days 0–9. Sample sizes for the non-parasitized group were 62, 69, 65, 56,50, 50, 47, 37, 24 and 12 chicks while for the parasitized group were 21, 18, 11, 14, 11, 9, 11, 4, 4 and 3 chicks

was predated. We did not observe any aggressive display of yellow-winged blackbirds towards male or female shiny cowbirds. We found no evidence of host discrimination at the time of feeding their own and the parasitic chicks: shiny cowbird chicks that hatched left the nest unless it was predated.

Host quality

From 37 cowbird eggs laid in the 31 yellow-winged blackbird parasitized nests of Table 1, there was 1 chick that fledged (2.7%). The main causes of parasite egg losses were nest predation, nest desertion and egg punctures. This host did not reject any parasite egg morph, and we did not detect any case of brood reduction affecting a parasite chick. The weight of the chick at fledging was 40 g.

Discussion

Impact of shiny cowbird parasitism on yellow-winged blackbird reproductive success

Shiny cowbird parasitism affected the reproductive success of yellow-winged blackbirds in several ways.

1. Yellow-winged blackbirds deserted 25% of their nests during egg laying or incubation. Nest desertion was the result of egg punctures inflicted to host eggs, which were associated with the laying of parasitic eggs. Yellow-winged blackbirds appear to monitor egg losses and desert the nest as a function of the amount of egg loss. Nest desertion would not be a real antiparasitic defense as it also occurs in non-parasitized nests that lost several eggs (Hill and Sealy 1994).

2. Parasitized nests had a higher rate of predation during the nestling stage than non-parasitized nests. As far as we know, this is the first study in which this cost has been shown. One possible explanation for this observation could be that shiny cowbird chicks beg louder and more intensively (Gotchfeld 1979; Lichtenstein 1997) and therefore increase the detectability of the nest by predators, as it is true for other species (Redondo and Castro 1992). Alternatively, the presence of the parasite chick could increase the parent's rate of visits to the nest, which in turn could increase nest detectability by predators (Skutch 1949).

3. Parasitized nests that were neither deserted nor predated had fewer host eggs and therefore hatched and fledged fewer chicks. This cost was the consequence of the puncture of host eggs and, although it was more severe in parasitized nests, it also occurred in non-parasitized nests. There was no detectable effect of the presence of a parasitic egg during incubation on the hatching success of the host. Similarly, on the nests that escaped predation, the presence of a parasitic chick did not affect the fledgling success of the host's chicks.

Lack of antiparasite defenses on the yellow-winged blackbirds

One of the more frequent antiparasitic defense used by other host species is the rejection of parasite eggs (Rothstein 1982, 1990). That defense can be ruled out for this host. Our observations in naturally parasitized nests and artificial parasitism experiments show that yellow-winged blackbirds do not reject either white or spotted shiny cowbird eggs, contrary to the prediction made by Friedmann et al. (1977). Nest desertion is another potential defense against parasitism (Graham 1988; Rothstein 1990). However, yellow-winged blackbirds desert their nests in response to high egg loss, whether parasitic eggs are present or not, and therefore desertion appears to be a generalized response to partial clutch reduction, and not an antiparasite defense on this species (Hill and Sealy 1994).

Because shiny cowbird parasitism markedly reduces yellow-winged blackbird reproductive success, and parasitic spotted eggs are readily distinguishable from the eggs of the host, the acceptance of cowbird eggs at the nest is puzzling. There are two prevailing hypotheses to explain the failure of hosts to evolve antiparasitic defenses. The "evolutionary lag" hypothesis (Rothstein 1982) states that defenses would be adaptive but have not yet become common because it takes time for new genetic variants to appear and to spread by natural selection. Alternatively, the "evolutionary equilibrium" hypothesis (Rohwer and Spaw 1988) states that defense behaviors (i.e., egg rejection or desertion) have costs greater than non-defense ones and are therefore less adaptive.

Neither hypothesis can be definitively dismissed with the available data.

The evolutionary equilibrium hypothesis suggests that the costs of developing defenses, such as egg ejection or nest desertion, should outweigh the benefits. Nest desertion as a response to the presence of parasitic eggs at the nest could be a risky choice because yellow-winged blackbird nesting success decreases markedly during the breeding season, as a consequence of increased rates of parasitism and nest predation (V. Massoni and J.C. Reboreda, unpublished work).

Costs associated with a rejection defense are the likelihood of recognition errors (falsely rejecting their own brood) (Davies et al. 1996) or the damage inflicted to own eggs when trying to eject the parasitic one (Røskaft et al. 1993). For this host, however, the advantages of egg rejection seem substantial; ejection of the parasitic egg would significantly lower the high nestling predation rates caused by the presence of cowbird chicks at the nests. In addition, egg ejection could potentially be achieved with little cost by this species (see Sealy 1996 for costs of egg rejection in a much smaller host).

In spite of the seemingly big advantages for the evolution of egg rejection, this host does not reject cowbird eggs, thus suggesting that a time lag between the host and the parasite might better explain the lack of defenses. It should be noted, though, that our study was conducted in an area at the center of the distribution of both species (Ridgely and Tudor 1989), presumably a region where both species have coexisted for a long time. Nevertheless, it is still possible that the genetic variants for the defensive behaviors have not yet appeared.

Alternatively, those advantages might not constitute enough selection pressure for antiparasitic defenses to evolve because, if not predated, there are no effects of cowbird parasitism on host hatching and fledgling success. Also, yellow-winged blackbirds that deserted in response to clutch reduction may have escaped real parasitism and its related costs, thus possibly weakening the selection pressure for truly antiparasitic defenses to evolve (Hill and Sealy 1994).

What is the functional significance of shiny cowbird white eggs?

Friedmann et al. (1977) predicted that yellow-winged blackbirds would accept shiny cowbird eggs of the white morph and reject eggs of the spotted morph. Our results indicate that this host accepts both morphs and, consequently, all shiny cowbird hosts studied until now are either dual acceptors or rejectors of the white morph (Mason 1986; Mermoz and Reboreda 1994; Lyon 1997). This observation raises again the question of the possible adaptive value of the white morph. The hypothesis that egg polymorphism in shiny cowbird could be a case of mimicry (females that lay white eggs parasitize hosts with white eggs while the ones with spotted eggs do it with hosts with spotted eggs) does not have any empirical support (Mason 1987). In addition, in a study conducted in our study site, the frequency of the white morph laid in parasitized nests of a white-morph egg rejector, the brown-and-yellow marshbird, *Pseudoleistes virescens*, was 20% (Mermoz 1996). This value does not differ from the frequency of white morph eggs observed on this study. These results indicate that shiny cowbird females that lay white eggs do not avoid parasitize hosts that reject their eggs and, therefore, the selective pressures that maintain the frequencies of the white morph still remain unknown.

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