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Impacts of brood parasitism by shiny cowbird *Molothrus bonariensis* on the breeding success of a small host, the black-backed water tyrant *Fluvicola albiventer*

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Abstract

The shiny cowbird *Molothrus bonariensis* parasitizes many species with different life-history traits and has a detrimental effect on the survival of the progeny of the hosts. In response, hosts have developed numerous antiparasitic defenses. Here, we examined the effects of brood parasitism by shiny cowbird on the clutch and brood sizes (83 nests) in a small host, the black-backed water tyrant *Fluvicola albiventer*. We also studied whether the death of parasite nestlings was related to the care of the foster parents and whether the host had any antiparasitic defense against the shiny cowbird. Our results indicate that brood parasitism significantly decreased the host hatching and fledging successes. The majority of nest failures (57%) were caused by brood parasitism. Shiny cowbird parasitism occurred in 52% of nests and the intensity of parasitism was 1.23 ± 0.53 eggs per parasitized nest. Of the total host eggs, 54% were damaged. During the incubation stage, 20 nests (47%) were abandoned because of egg punctures by shiny cowbirds females. Only two parasitic fledglings were recorded, while the remaining nestlings either died from starvation (*n* = 12) or predation (*n* = 3). Foster parents abandoned parasitic nestlings between 5 and 10 days old. Our findings demonstrate that the shiny cowbird has very low rates of fledging success when parasitizing black-backed water tyrant. Also, parasitism had a high reproductive cost in the black-backed water tyrant because a very low proportion (7%) of the parasitized nests (*n* = 43) were successful.

Key words: brood parasitism, host defenses, nest desertion, shiny cowbird, small host.

Obligate avian brood parasites rely upon host species to care for their offspring (Davies 2000), lay their eggs in the host's clutch, and leave the foster parents to take all care of them. Because a host quality depends primarily on how easily nests can be parasitized and on the quality of host parental care (Astié and Reboreda 2009), there is a wide variation in the success of parasitism and its impact on host species (Reboreda et al. 2003; Walsh et al. 2015; Jones et al. 2022). Thus, to understand the impact of brood parasitism, it is necessary to study different host species with different natural history characteristics. Understanding this impact is currently important because many parasitic species negatively affect the reproductive success of host populations, eventually increasing their extinction risk (Ducatez 2014). In addition, the study of the breeding success and the costs of brood parasitism on different hosts is relevant for understanding the coevolution of antiparasitic defenses as well as the behavior of the parasite species (Rothstein and Robinson 1998; Hosoi and Rothstein 2000; Tuero et al. 2007; Yang et al. 2022).

Brood parasites can reduce hosts breeding success in multiple ways. For instance, parasites can reduce the clutch size by removing and destroying the host eggs, which sometimes causes the host to abandon its nest (Sealy 1992; Massoni and Reboreda 1998; Hosoi and Rothstein 2000). In other cases, host nestling survival can be impacted by parasites because the host's breeding success is evicted or killed by parasitic nestlings (Davies 2000; Hoover 2003; Payne 2005) or is outperformed by parasitic nestlings (Hoover 2003; Scharf et al. 2022). The interactions between parasites and their hosts often lead to a coevolutionary arms race, which may result in hosts evolving defenses against parasitism. For instance, the hosts may respond aggressively to brood parasites that come close to the nest (Welbergen and Davies 2009; Gloag et al. 2013; Šulc et al. 2020), reject parasitic eggs (Davies 2000; Soler et al. 2015) or abandon parasitized nests and re-nested (Hosoi and Rothstein 2000). These defense mechanisms act as a selective pressure on parasites, driving them to develop counter-defenses. For example, the cuckoos lay eggs

that closely resemble those of their hosts (Brooke and Davies 1991; Soler et al. 2003).

The shiny cowbird *Molothrus bonariensis* is a nonmimetic, generalist brood parasite with more than 275 hosts (Lowther 2023). This species has a broad distribution in South America, with growing expansion in North America and the Caribbean. Shiny cowbirds usually have multiple negative effects on the breeding success of their hosts (Ortega 1998; Tuero et al. 2007). Several authors reported that egg-puncture behavior by females is one of the most important costs of brood parasitism (Massoni and Reboreda 1998; Astié and Reboreda, 2006, 2009; Fiorini et al. 2014) since it reduces the host clutch (Fiorini et al. 2009; Gloag et al. 2012). Furthermore, brood parasitism can reduce the hatching success and the survival of nestlings (Tuero et al. 2007; Scharf et al. 2021, 2022).

Several hypotheses have been proposed to explain egg-destruction and the potential benefits of this behavior (Sealy 1992; Peer 2006; Reboreda et al. 2017). For example, Shiny cowbird females may puncture host eggs 1) to assess the degree of incubation and determine whether it is appropriate to parasitize the nest (Massoni and Reboreda 1998), 2) to reduce the clutch size and thus to reduce the competition for food with nest mates (e.g. Fiorini et al. 2009; Cossa et al. 2017; Reboreda et al. 2017), 3) and/or to induce hosts to abandon their nests and renest (i.e. "nest farming") (Arcese et al. 1996; Swan et al. 2015). A lower impact of egg punctures can be expected on hosts smaller than the parasite if the purpose is to reduce competition for food with nestmates because large parasitic nestlings competitively outperform small host nestmates (Spottiswoode and Colebrook-Robjent 2007; Fiorini et al. 2009, 2019). Nest farming occurs when the parasite finds a nest that has a complete clutch and that incubation already started (Rothstein 1982). For instance, the females of Brown-headed Cowbird *M. ater* manipulate their hosts by destroying their nests completely, forcing them to initiate a new breeding cycle, thus creating future opportunities for parasitism (Sealy 1992).

Hosts can employ defense mechanisms to discriminate and reject parasitic eggs ("rejecters") (Peer et al. 2005; Grim et al. 2011; Segura et al. 2016). These mechanisms include nest abandonment, burial of parasitic eggs with nest material, and egg ejection (Davies 2000; Peer et al. 2005; Tuero et al. 2012). Although many species abandon their parasitized nests, nest desertion can be attributed to partial or complete clutch loss, which may or may not be a specific antiparasitic response (Rothstein 1982; Hill and Sealy 1994; Kosciuch et al. 2006). In contrast, other host species accept parasitic eggs ("accepters") (Peer et al. 2005). Accepting parasitic eggs allows them to mitigate some costs of parasitism (e.g. investing less energy in defending the nest or by avoiding nest abandonment) and produce successful nestlings (Peer et al. 2005; Tuero et al. 2007; Gloag et al. 2012).

Hosts can also discriminate and reject parasitic nestlings, though these behaviors that have been poorly documented. Nestling "recognition" is defined as the internal process that can lead to both "nestling rejection," which always results in death (e.g. nest desertion), and "nestling discrimination," which does not necessarily result in death (e.g. differential parental allocation of food within a parasitized brood) (Grim 2007). Evidence for parasitic nestling rejection includes nest desertion during the nestling stage (Grim et al. 2003; Langmore et al. 2003; Grim 2007) and ejection of brood parasitic nestlings (Sato et al. 2010; Tokue and Ueda 2010).

Some authors have studied the discrimination of parasitic nestlings as a defense strategy that has developed in hosts with larger nestlings (Lichtenstein 2001) or mixed-species broods (consisting of both their own offspring and parasite nestlings) (Payne et al. 2001; Grim et al. 2009; Moskát et al. 2017). For example, Lichtenstein (2001) reported that Shiny cowbird nestlings (50 g) have a low success rate in nests of larger hosts because the parents choose their own nestlings over the smaller parasitic nestlings. Conversely, smaller host nestlings are often outcompeted by larger parasitic nestlings (Marvil and Cruz 1989; Gloag et al. 2012; Bortolato et al. 2019), and, in general, there is no difference in parental care between parasite and host nestlings when they are similar in size (Lichtenstein and Sealy 1998). Alternative antiparasitic strategies based on "discrimination without recognition" suggest that: *i*-parents can abandon a parasitic nestling when the energy investment (i.e. the "parental fatigue" hypothesis) or the duration of the parental care period, regardless of the level of energetic investment (i.e. the "time limit" hypothesis), is significantly higher than that required for raising a host brood (Grim 2007). Furthermore, the "single nestling" hypothesis suggests that parents could abandon the parasitic nestling because it is alone in the nest (Langmore et al. 2003).

In this study, we examined how breeding parameters of black-backed water tyrant *Fluvicola albiventer* are affected by the brood parasitism of the Shiny Cowbird. The black-backed water tyrant is a wetland-dependent tyrannid with a broad distribution over much of the eastern part of South America (Farnsworth and Langham 2020). Although species of the genus *Fluvicola* sp. have been mentioned as occasional cowbird hosts that accept parasite eggs and successfully rear parasite nestlings, little information exists regarding their breeding success and the effects of cowbird parasitism (Cruz and Andrews 1997; de la Peña 2015; Farnsworth and Langham 2020). The black-backed water tyrant (11 g) has a considerably lower mass than Shiny cowbird (45–50 g) but has a similar reproductive cycle duration (27 days approximately, Lichtenstein 2001; Di Giacomo 2005). Therefore, we expect that parasitized clutches to have lower nestling survival and breeding success due to the combined effects of the intensity parasitism and egg losses. Additionally, we predict that Shiny cowbird nestlings will succeed in the nests of this smaller host, as the larger parasitic nestlings outcompete the smaller host nestlings.

Materials and Methods

Study area

This study was realized in an area of fluvial wetlands of the Parana River in Santa Fe province, Argentina (31°38'10"N, 60°40'31"W). The area corresponds to an Ecological Reserve managed by the National University of Littoral (UNL, Spanish acronyms) of Argentina and the Foundation for Habitat and Development. The mean temperatures range between 25 °C in January and 12.5 °C in July. This floodplain wetland presents the spatial and temporal environmental heterogeneity that characterizes this type of ecosystems and that is the basis for sustaining a rich biodiversity (Morrone 2001).

Data collection

We searched active nests during six breeding seasons (September–January 2012–2019). Once discovered, nests were monitored every 1–2 days from the start of

the egg-laying stage until either failure or fledging to the young. Eggs were numbered in indelible ink according to their order of appearance. During each visit, we recorded the number of host and parasite eggs and nestlings. Host eggs were examined to determine the number of eggs that had been punctured by shiny cowbirds females. Punctured eggs were identified by the presence of a relatively large, usually triangular hole in the eggshell (Tuero et al. 2007; Astié and Reboreda 2009). We observed that punctured host eggs were not removed between consecutive visits and that the remaining eggs were united with the punctured egg due to the leakage of its contents into the nest. We measured the maximum length (*A*) and the breadth (*B*) of eggs with a caliper (to the nearest 1 mm) and mass for each egg with a weighing precision scale (weighing scale with a precision of 0.1 g). The volume of eggs (*V*) was calculated using the formula provided by Hoyt (1979): $V = 0.541AB^2$. Parasite eggs were classified into one of two morphs based on their coloration: immaculate white and spotted (brown spots on a variable color background, with spotting ranging from nearly absent to very intense). Weight (weighing ± 0.1 g) and total body length of host and parasitic nestlings at different ages were measured using a weighing precision scale and a caliper (to the nearest 1 mm), respectively. Nests were classified according to the type of failure as 1) predated nests, when eggs and/or nestlings disappeared between consecutive visits, and there was no more parental activity near the nest; 2) deserted nests without recognizable causes, when eggs were cold, or nestlings were dead, and no further parental activity was observed; 3) weather-affected nests when cold eggs or dead nestlings were found following weather events such as rain or storms, and 4) deserted nests due to brood parasitism, when all eggs in parasitized nests were damaged or nestlings were found dead, and no further parental activity was observed. We recorded the parental care behavior during the nestling stage at one of the parasitized nests using a video camera (Full HD, resolution: 1920 × 1080, 30 fps). The camera was placed in front of the nest at a distance of 0.5 at 1 m. The parents were videotaped for the first 6 h after sunrise, as this protocol standardized the time of day and sampling duration, providing data on nest attentiveness averaged over the first 6 h of each day (Martin and Ghalambor 1999; Martin et al. 2000). Lastly, we estimated nestling-feeding frequency as the number of parental visits per hour to the nest for feeding the nestlings.

Data analysis
For the host species, we calculated 1) the average and range of clutch size (number of eggs per nest when the clutch is complete); 2) the average and range of brood size (number of nestlings hatched); 3) the average and range of brood size at fledging (number of nestlings fledged that were alive at the time of fledging). Four metrics of breeding performance were assessed 1) egg survival, as the proportion of eggs that survive to hatch date from the number of eggs laid; 2) hatching success, as the proportion of eggs that hatched from egg those that survived to the end of incubation; 3) fledging success, as the proportion of nestlings present in the nest on the last check before fledging; and 4) breeding success, as the proportion of nesting attempts in which at least one young fledged, that is, a nesting attempt was classified as successful in which at least one host young fledged. We estimated the frequency of parasitism (proportion of parasitized nests) and intensity of parasitism at the incubation stage (number of parasitic eggs per nest) and nestling stage (number of parasitic nestlings per nest). We used Fisher's Exact Test to compare to assess whether variation in failure probability between incubation and nestling stage depended on whether nests were parasitized or not. Spearman rank correlation coefficient was used to test the association between the number of parasitic eggs and the number of eggs with punctures. In order to test whether the clutch size, brood size, and brood size at fledging varied between parasitized and nonparasitized nests, we performed an ordinal regression by *Ordinal* package (CLM, Christensen 2022). The four metrics of breeding performance (egg survival, hatching success, fledging success, and breeding success) and the frequency of egg punctures between parasitized and nonparasitized nests were compared using Binomial-based generalized linear models in R (*glm* in package *stats*, R Core Team 2022). Values reported are means ± SD.

Results
General results
During the six breeding seasons, a total of 83 nests of black-backed water tyrant were monitored (Table 1). Among these nests, 40 (48%) were nonparasitized, while 43 (52%) were parasitized by shiny cowbird. The frequency of Shiny cowbird parasitism was 52% (43/83 nests) (Table 1) and the intensity of parasitism was 1.23 ± 0.53 eggs per nest (range 1–3) (Table 1). Multiple parasitism was observed in 8 nests (19%, 2 or 3 eggs).

The breeding cycle of black-backed water tyrant lasted 26.5 ± 2.03 days, while shiny cowbirds had a breeding cycle of 26 ± 0.30 days.

Out of the total of 83 nests, 16 (19%) were successful and 67 (81%) were unsuccessful because of different causes. The

Table 1. Number of nests studied of black-backed water tyrant *Fluvicola albiventer* and frequency of parasitism, intensity of parasitism and frequency of nests desert because of brood parasitism by shiny cowbird *Molothrus bonariensis* parasitism during six breeding seasons

Breeding season	Number of nests	Frequency of parasitism (%)	Intensity of parasitism (Mean ± SD)	Nests deserted because of brood parasitism (%)
2012–2013	10	50	0.50 ± 0.53	40
2013–2014	11	45	0.45 ± 0.52	45
2014–2015	20	25	0.25 ± 0.44	30
2016–2017	22	55	0.75 ± 0.91	41
2017–2018	14	79	0.93 ± 0.62	64
2018–2019	6	83	1.13 ± 0.64	83

most frequent cause of nest failures was deserted for brood parasitism (*n* = 38, 57%) (Table 1), followed by predation (*n* = 18, 27%), desertion for other causes (*n* = 9, 13%), and adverse weather conditions (*n* =2, 2%).

Of the total of nest failures, 57 (85%) were recorded during the incubation stage and 10 (15%) during the nestling stage. Nest failure during the incubation and nestling stages did not depend on whether the nests parasitized or not (Fisher's Exact Test: *P* = 0.75). In nonparasitized nests, 55% (22 nests) of nests failed during the incubation stage and 13% (5 nests) failed during the nestling stage. In parasitized nests, 79% (34 nests) of nests failed during the incubation period and 14% (6 nests) failed during the nestling stage. A higher number of abandoned nests was observed in parasitized (57%) compared to nonparasitized (13%).

Effects of brood parasitism

Parasitized nests had smaller clutch size, brood size, and the number of fledging's than nonparasitized nests (Table 2). The frequency of eggs punctures was higher in parasitized nests than in nonparasitized nests (Table 2). In addition, there was a positive association between the number of parasitic and punctured host eggs (Spearman: r_s = 0.71, *P* < 0.001).

Of the total number of parasitized nests (*n* = 43), 27 (63%) nests lost all their host eggs because of punctures made by female shiny cowbirds. Among these nests, 7 continued with incubation only with parasitic eggs (1.71 ± 0.76 eggs per nest), while 20 nests were abandoned. In the remaining parasitized nests (*n* = 16 nests, 37%), 6 continued with the incubation with a reduced host clutch size (1.33 ± 0.52 eggs per nest) due to punctures made by female shiny cowbirds, 4 nests continued incubating with a reduced clutch size due to causes other than parasitism (infertility or embryonic death), and only 6 nests did not show a reduction in clutch size.

The proportion of host eggs that survived to hatch did not vary between nonparasitized and parasitized nests (Table 2 and Figure 1). On the other hand, hatching, fledging, and breeding success were higher in nonparasitized nests than in parasitized (Figure 1).

We recorded 57 host nestlings (*n* = 27 nests), with 2.11 ± 0.75 nestlings per nest (range 1–3). A total of 17 nestlings hatched in parasitized nests (*n* = 9) and 40 in nonparasitized nests (*n* = 18), indicating that 70% of black-backed water tyrant nestlings hatched in nonparasitized nests.

We recorded 34 fledglings of black-backed water tyrant (*n* = 16 nests), 5 fledglings in parasitized nests (*n* = 3), and 29 in nonparasitized nests (*n* = 13), that is, 85% of nestlings reached a fledging stage in nonparasitized nests. In the parasitized nests, the nestlings of black-backed water tyrant were successful only when the parasitic eggs did not hatch because these were laid during incubation (*n* = 2 nests) or when the host's eggs had already started hatching (*n* = 1 nest) and thus, parasitic eggs did not complete incubation stage. In nests with parasitic nestlings, 12 black-backed water tyrant nestlings were found dead due to crushing and starvation.

Brood parasitism

We found 52 eggs of shiny cowbirds (*n* = 43 nests). The eggs were 22.71 ± 1.98 mm in length, 18.24 ± 2.22 mm in width, weighed 4.48 ± 0.90 g, and had a volume of 39.20 ± 10.68 cm³ (*n* = 40 eggs measures). All cowbird eggs belonged to the spotted morph, with varying spotting densities ranging from weak to very intense. Among the 52 parasite eggs, 17 (33%) were laid in coincidence with the laying of the host. Six of these eggs (12%) hatched together with host eggs and 11 eggs (21%) hatched alone in the nest without host nestling. Three shiny cowbird eggs (6%) were laid after the host started incubation or when host nestlings had just hatched. As a result, these later-laid parasite eggs did not receive complete incubation and did not hatch. Finally, 32 eggs with unknown laying dates (62%) did not hatch because the nests were deserted (29 nests) or predated (3 nests).

A total of 17 parasite nestlings hatched in 13 nests. The average number of parasitic nestlings per nest was 1.13 ± 0.35 (range 1–2). In nine nests, only parasitic nestlings hatched (*n* = 11 nestlings). We observed that three nests experienced deformation from a closed/globular shape to an open/cup shape probably due to the large size of the parasite nestlings and thus the parasite nestlings were exposed.

Only two parasitic fledglings (*n* = 2 nests) were recorded. Out of the 17 parasite nestlings, 12 were found dead in the nest (*n* = 13 nests), and 3 were predated (*n* = 3 nests). In six nests where both host and parasitic nestlings hatched, the host nestlings died due to crushing or starvation. After that, the parasite nestlings were abandoned at 5–10 days old, showing signs of starvation. We collected three nestlings for laboratory analysis, which revealed empty stomachs and poor body conditions, indicating death by starvation.

We filmed a nest three times, totaling 6.37 h of filming. Initially, the nest contained two host nestlings (6 g and 7

Table 2. Comparison of host clutch size, brood size, number of fledglings, frequency of egg punctures, hatching success, fledging success, and breeding success between nonparasitized and parasitized nests of black-backed water tyrant *Fluvicola albiventer*

	Nonparasitized nests	Parasitized nests	β	LRT	*P*
Clutch size	2.35 ± 1.03 (18)	1.74 ± 1.24 (12)	–1.12 ± 0.43	9.95	0.01
Brood size	2.22 ± 0.81 (18)	1.89 ± 0.60 (9)	–1.19 ± 0.48	6.45	0.01
Brood size at fledging	2.23 ± 0.83 (13)	1.67 ± 0.58 (3)	–1.91 ± 0.69	9.73	0.002
Frequency of eggs punctures	0.10 ± 0.30 (40)	0.75 ± 0.44 (43)	2.47 ± 0.57	23.77	< 0.01
Egg survival	0.40 ± 0.46 (40)	0.25 ± 0.38 (43)	–0.75 ± 0.47	2.64	0.10
Hatching success	0.38 ± 0.45 (40)	0.19 ± 0.38 (43)	–1.13 ± 0.53	4.86	0.03
Fledging success	0.28 ± 0.43 (40)	0.06 ± 0.22 (43)	–1.35 ± 0.71	4.18	0.04
Breeding success	0.33 ± 0.47(40)	0.07 ± 0.26 (43)	–1.85 ± 0.69	9.17	0.002
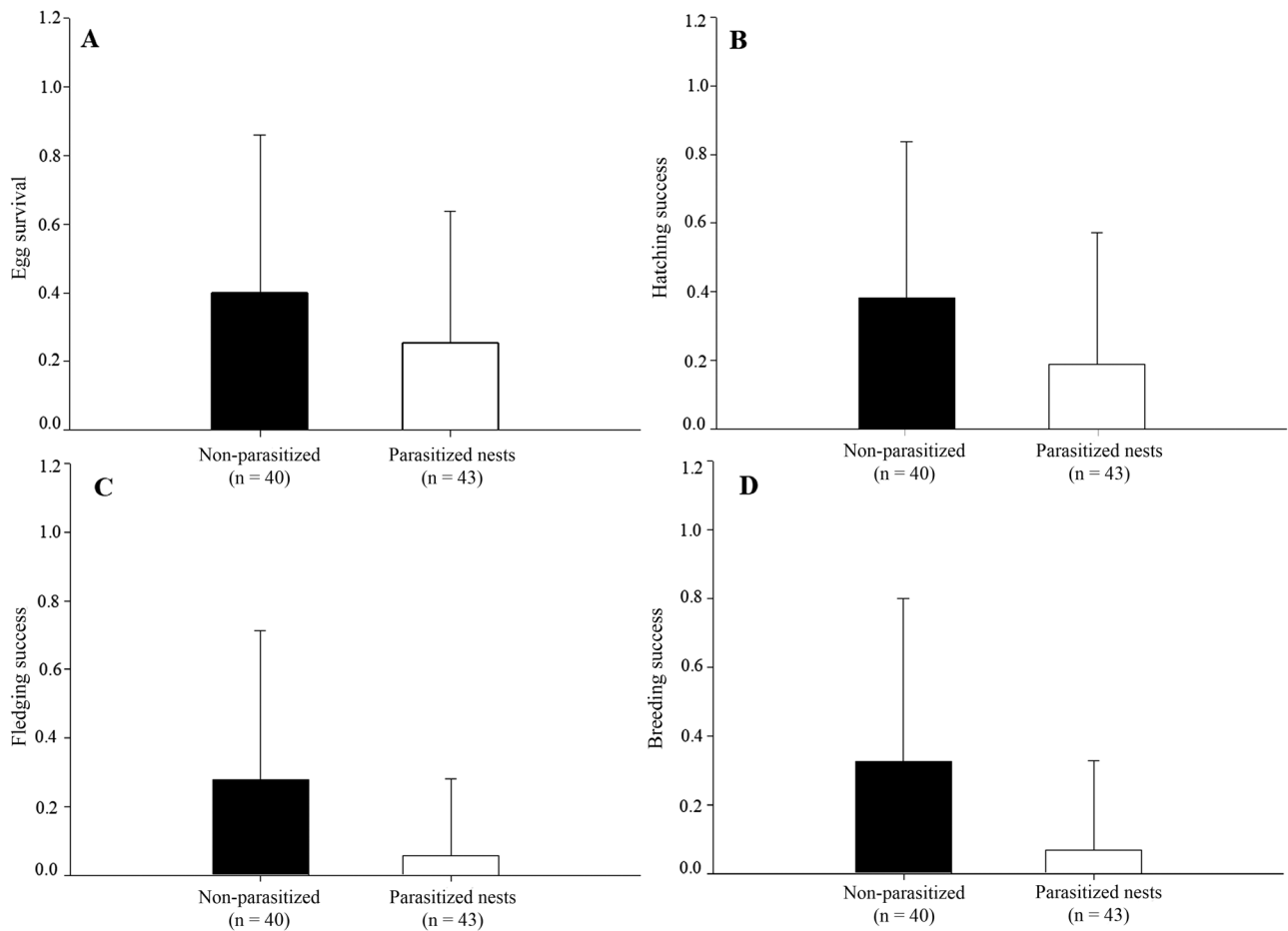
Figure 1. Host's egg survival (A), hatching success (B), fledging success (C), and breeding success (D) in nonparasitized and parasitized nests of black-backed water-tyrant *Fluvicola albiventer*.

g) along with a parasite nestling (12 g). The parents made 18.2 visits per hour to feed these three nestlings. In the next nest monitoring, we found the two host nestlings dead in the nest. On that day (the second filming), we filmed the nest with a parasite nestling (32 g). We observed that the parasite nestling spent 80% of its time requesting food through vocalizations (cheeping) and with its beak open. The host parents performed 2.34 visits per hour. After 2 days (the third filming), the 10-day-old parasitic nestling was not fed, and its body mass remained the same as the previous visit (32 g). The parasite nestling was not found during the following monitoring. We observed that shiny cowbird begged relatively more intensively than host nestlings. However, we register a decrease in parental response as the parasite nestling grew older and was raised in the absence of host nestlings.

Discussion

Results showed that brood parasitism by shiny cowbird in nests of black-backed water tyrant, a parasitism relationship in which the host (11 g) is smaller than the parasite (45 g), significantly decreases the chances of hatching from the eggs or that the nestlings can become independent (Figure 1). Our findings support the prediction that shiny cowbird parasitism negatively affects the breeding success of black-backed water tyrant, as it was negatively related to

hatching success and nestling survival. Thus, these results support that egg-puncture behavior by females is an important cost of brood parasitism by shiny cowbirds (Astié and Reboreda 2006, 2009; Fiorini et al. 2014) due to it reduces the host clutch size and sometimes causes the host to abandon its nest (Sealy 1992; Fiorini et al. 2009; Gloag et al. 2012). However, contrary to our prediction, shiny cowbird had very low breeding success parasitizing nests of black-backed water tyrant. Over six breeding seasons, only two parasitic fledglings were recorded.

The majority of parasite eggs were laid while the black-backed water tyrant was also laying her eggs. This is consistent with the high level of synchronization between shiny cowbird parasitism and the host's egg-laying observed in other species in Argentine (e.g. Massoni and Reboreda 1998; Fiorini et al. 2009; Ellison et al. 2019; Mermoz et al. 2021). In all cases when parasitism occurred asynchronously in this study (i.e. after the onset of incubation), the parasitic eggs failed to hatch. In these cases, the laying of parasitic females occurred when black-backed water tyrant had already started the incubation. As a result, the parasite eggs did not hatch because they had not received complete incubation. Thus, these findings support the hypothesis that, for parasitic females, the timing of parasite egg-laying relative to the host's egg-laying is crucial for ensuring the successful hatching of the nestlings (Soler et al. 2015, 2020; Ruiz-Raya and Soler 2020). In these nests where the parasitism attempts failed, the

breeding attempts of black-backed water tyrant were successful since they produced host fledglings.

We expected a relatively low impact of parasitism on host eggs since reducing the competition with host nestmates through egg punctures is not critical for the success of shiny cowbird parasitizing black-backed water tyrant. However, in the black-backed water tyrant, the most significant negative impact of parasitism was observed on the eggs due to punctures by the shiny cowbird female (Table 2). Similar findings have been reported in other studies, where shiny cowbirds have been observed damaging the eggs of several bird species, including the Brown-and-yellow-marsh bird *Pseudoleistes virescens* (Mermoz 1996), the Yellow-winged Blackbird *Agelasticus thilius* (Massoni and Reboreda 1998), the Rufous-bellied Thrush, and the Chalk-browed Mockingbird *Mimus saturninus* (Astié and Reboreda 2006; Fiorini et al. 2009). On the other hand, since most nests with egg punctures received parasitic eggs regardless of whether the nests were in the laying or incubation stages, our results do not support the hypothesis that egg punctures are used by the parasite to assess the degree of incubation and decide if it is appropriate to parasitize the nest. In addition, because most of the parasitism events were synchronized with those of the host, it seems unlikely that parasitic females were using puncture behavior to induce renesting (i.e. the hypothesis of nest farming, Swan et al. 2015).

The punctures of eggs and laying of parasitic eggs were followed by a high percentage of nest desertion (50% of failures, Table 1). Most of the nests had a total (27 nests) or partial (6 nests) loss of the brood. The damaged eggs were not removed during nest sanitation. In addition, the punctures made by female shiny cowbirds caused the contents of the egg to leak into the nest, which caused more damage to the clutch and made the removal of the damaged eggs even more difficult. According to our results, numerous studies have found a high rate of nest desertion after parasitism attempts in small-sized host species (Rothstein 1982; Hosoi and Rothstein 2000; Kosciuch et al. 2006). This could mean that desertion is the only viable antiparasitic defense for small host species that are unable to remove the parasitic eggs (Hosoi and Rothstein 2000; Soler et al. 2015; Zhang et al. 2021). However, desertion is costlier than egg ejection in terms of energy and time investment (Hoover 2003; Guigueno and Sealy 2010; Soler et al. 2015). Numerous cases of nest desertion have been observed in various host species, including Leaf warbler *Phylloscopus warblers* (Martín-Vivaldi et al. 2013), Yellow warblers *Dendroica petechia* (Guigueno and Sealy 2010); Hooded Warbler *Setophaga citrina* (Lignac and Mumme 2023). On the other hand, although there are many report cases of nest abandonment, the cues that trigger parents to abandon their nests remain unclear (Hosoi and Rothstein 2000; Avilés 2018). In our study, the parents of black-backed water tyrant deserted their nests in response to the loss of eggs. It remains to be determined whether the parent's abandonment of the nests can be a specific response to brood parasitism or whether it also occurs due to other factors such as predation and nest disturbances (Hosoi and Rothstein 2000; Guigueno and Sealy 2010).

Nests that contained both host nestlings and one or two parasitic nestlings experienced a complete loss of host brood. This is consistent with the expected impact on hosts that are smaller than the parasite due to the host's nestlings being competitively outmatched by the parasitic nestlings (Spottiswoode and Colebrook-Robjent 2007; Fiorini et al. 2009, 2019). Similarly, Marvil and Cruz (1989) and Woodworth (1997) observed that dead small vireos (*Vireo latimeri*, *V. solitarius*) were buried beneath larger cowbird nestlings and that vireos had died of starvation in parasitized nests. Therefore, nestlings of the small host can die from starvation if they do not receive adequate food, and they may also be crushed by larger parasitic nestlings. The black-backed water tyrant (11 g) is a small host of the shiny cowbird (45 g). It is evident from our findings that the difference in size of the shiny cowbirds nestlings impacts the survival of these small host nestlings (Figure 1). As a result, the large body size of parasitic nestlings probably caused the death of the host nestlings by crushing and starvation.

Despite the high number of recorded parasitism attempts ($n = 43$), the black-backed water tyrant successfully raised only two parasitic nestlings during the six breeding seasons (Table 2). In general, we observed that the parasitic nestlings did not survive in the nests of black-backed water tyrant. We found that all shiny cowbird nestlings were deserted in the absence of host nest mates, even in nests with only one parasitic nestling. Many hypotheses have been proposed to explain why parasitic nestlings do not survive in host nests (e.g. lower-quality food items, discrimination with and without recognition; Grim et al. 2003; Grim 2007; Soler 2017). In this study, we found that the parasitic nestlings died due to starvation when they were abandoned by the foster parents during the advanced stages of brooding (i.e. 5- to 10-day-old nestlings). Because black-backed water tyrant has an invertebrate-based diet (Beltzer 1985), this protein-based diet would be a suitable diet for nestlings of shiny cowbirds (Mason 1986; Kozlovic et al. 1996). We observed that the parents were near the abandoned nests, but they did not feed the nestlings in the advanced stages of brooding. In addition, video recordings in a nest of the black-backed water tyrant that contained host and parasite nestlings and later contained only parasite nestlings showed that, although parasitic nestlings actively begged for food, these were not fed in the advanced stages of brooding (i.e. 5- to 10-day-old nestlings). If the host parents perceive a higher cost of rearing, that is, a higher physiological exhaustion (the parental-fatigue hypothesis), they may decide to abandon parasite nestlings (Grim 2007). The physiological exhaustion could work as a proximate cue triggering desertion (Grim 2007). This decision may have benefits for parents who have already lost their offspring, such as reducing the current reproductive effort and increasing survival and future reproduction (Grim et al. 2003; Anderson and Hauber 2007). For the hosts, every single day the host avoids such care adds to the host's fitness (Soler 2017). Thus, the parental-fatigue hypothesis could explain the abandonment of nests that contained only parasitic nestlings. However, further experimental work is required to test a valid explanation of the abandonment for parasitic nestlings in the advanced stages of brooding.

Black-backed water tyrant was heavily parasitized by shiny cowbirds at the study site (Table 1). However, shiny cowbirds had low breeding success in nests of the black-backed water tyrant. Similar findings were reported by Cruz and Andrews (1997) for the Pied Water-Tyrant *F. pica*, which is a closely related species to the black-backed

water tyrant and is the primary host of shiny cowbirds in the llanos of Venezuela. Shiny cowbirds had low breeding success when parasitizing Pied Water-Tyrants, with only 3 out of 47 parasitized nests producing at least one parasitic fledgling. Astié and Reboreda (2009) proposed several possible explanations for the parasitism of nests in low-quality hosts. These include: "I) the low availability of alternative hosts in the study site (Barber and Martin 1997), II) a shotgun strategy, where egg production is so cheap that it is profitable to lay eggs in any nest found rather than spending time looking for the nests of better hosts (Rothstein 1990; Kattan 1996; Davies 2000), or III) diffuse selection as a consequence of being such a generalist (Rothstein et al. 1986)." In the case of black-backed water tyrant, the availability of alternative hosts was high in the study area, including chestnut-capped blackbird *Chrysomus ruficapillus*, house wrens and rufous-collared sparrows (Mermoz and Reboreda 1998; Tuero et al. 2007). Indeed, finding appropriate host nests for laying is crucial for the reproductive success of brood parasitism (Soler et al. 2020). Thus, as a result of the heavy parasitism by shiny cowbirds in the nests of black-backed water tyrant despite the availability of other hosts, this explanation may be excluded. Another possible explanation is that shiny cowbirds are generalists and do not selectively the best host in the study area (Astié and Reboreda 2009). This suggests that diffuse selection, where the parasitic behavior is not specifically adapted to a particular host, may be the most suitable explanation for our results.

Our results revealed that the black-backed water tyrant is highly parasitized by shiny cowbirds, with a parasitism rate ranging from 25% to 83%. The high intensity of cowbird parasitism caused low production in this host. However, the black-backed water tyrant is a low-quality host for shiny cowbirds because the host parents abandoned parasitized nests with reduced host clutches or with only parasitic nestlings in the brood. Desertion of parasitized nests could be an antiparasitic defense or a general response of black-backed water tyrant to clutch and brood losses (Kosciuch et al. 2006; Grim et al. 2011; Soler et al. 2014). Further studies are needed to differentiate between these alternatives. Specifically, the abandonment of shiny cowbird nestlings by the host parents requires further investigation. Clearly, the black-backed water tyrant is a lower-quality host species for the shiny cowbird, yet it continues to be heavily parasitized, resulting in a significant reduction in its breeding success.

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Conflicts of interest

The authors declare no competing interests.

Author contributions

Lorena Sovrano: Conceptualization (equal); Formal analysis (equal); Resources (equal); Supervision (equal); Writing–original draft (lead). **Evelina Jésica León:** Investigation (equal); Methodology (equal); Writing—review and editing (equal). **Rodrigo Lorenzón:** Investigation (equal); Methodology (equal); Writing—review and editing (equal). **Pamela Olguín:** Methodology (equal); Resources (equal); Writing–review & and editing (equal). **Adolfo Beltzer:** Conceptualization (equal); Formal analysis (equal); Supervision (equal); Writing—review and editing (equal). **Alejandro Giraudo:** Supervision (equal); Writing—review and editing (equal).

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