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Effects of Shiny Cowbird *Molothrus bonariensis* parasitism on different components of House Wren *Troglodytes aedon* reproductive success

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Avian brood parasites, including cuckoos and cowbirds, have multiple negative effects on their hosts. We analysed the effects of Shiny Cowbird *Molothrus bonariensis* parasitism on different components (e.g. egg losses, hatching success, chick survival and nest abandonment) of House Wren *Troglodytes aedon* reproductive success. We also conducted an experiment to discriminate between two mechanisms that may reduce hatching success in parasitized clutches: lower efficiency of incubation due to the increase in clutch volume and disruption of host incubation by the early hatching of Cowbirds. Egg puncturing by Shiny Cowbirds reduced host clutch size at hatching by 10–20%, and parasitized nests had a decrease in hatching success of 40–80%. Egg losses and hatching failures were positively associated with the intensity of parasitism. Brood reduction was greater in parasitized nests, but the growth rate of the chicks that fledged was similar to that in unparasitized nests. The combined effects of egg losses, hatching failures and brood reduction decreased the number of fledged chicks by 80%. In addition, egg puncturing increased the likelihood of nest abandonment by Wrens. Experimental data showed that hatching failures occurred when there was a combination of: (1) an increase in the volume of the clutch by the addition of the Cowbird egg without removal of host eggs, and (2) the addition of the Cowbird egg before the onset of incubation. This was relatively common in House Wren nests, as Cowbirds generally parasitize before the onset of incubation. Our results indicate that Shiny Cowbird parasitism imposes a major impact on House Wrens, as it affects all components of the Wren's reproductive success.

Avian brood parasites, including cuckoos and cowbirds, usually have multiple negative effects on the reproductive success of their hosts (Ortega 1998, Rothstein & Robinson 1998). In cowbirds (*Molothrus* spp.) these negative effects include: (1) reduction of host clutch size by removal (Petit 1991, Payne & Payne 1998, Clotfelter & Yasukawa 1999, Hoover 2003) or puncturing (Hoy & Ottow 1964, Post & Wiley 1977, Nakamura & Cruz 2000) of eggs when female cowbirds visit their nests; (2) decrease in hatching success (Petit 1991, Kattan 1998, Hoover 2003) by the inability of the host to incubate an enlarged clutch efficiently (Petit 1991, Trine 2000), or because the early hatching by cowbirds may disrupt female incubation behaviour (Walkinshaw 1961, Petit 1991, but see McMaster & Sealy 1999); (3) lower survival of host nestlings (Marvil & Cruz 1989, Hoover 2003) or host fledglings after they leave the nest (Payne & Payne 1998, Hoover 2003) due to competition for food with cowbird chicks; and (4) higher nesting failure during the egg stage due to egg destruction (Petit 1991, Clotfelter & Yasukawa 1999, Smith *et al.* 2003), or during the chick stage because cowbird vocalizations may increase the risk of nest predation (Massoni & Reboreda 1998, Dearborn 1999). In addition to these immediate reproductive costs, cowbird parasitism may reduce the future reproductive value of the host if survival of the parents is affected by raising a brood with cowbirds (Rothstein & Robinson 1998). These negative effects associated with parasitism may increase with the number of cowbird eggs in parasitized nests (i.e. intensity of parasitism; Trine 2000, Hoover 2003, Astié & Reboreda 2006).

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The Shiny Cowbird *Molothrus bonariensis* is a South American obligate brood parasite of more than 240 hosts (Friedmann & Kiff 1985, Ortega 1998, Lowther & Post 1999). The majority of the studies that have investigated the impact of Shiny Cowbird parasitism on host reproductive success have been conducted in hosts similar or greater in mass than the parasite (i.e. Fraga 1985, Mermoz & Reboreda 1994, Lichtenstein 1998, Massoni & Reboreda 1998, Sackmann & Reboreda 2003, Astié & Reboreda 2006). These studies indicate that the main cost of parasitism in large hosts is the puncturing of eggs. There have also been some studies that analysed the impact of Shiny Cowbird parasitism in hosts lower in mass than the parasite (King 1973, Fraga 1978, Cruz & Andrews 1997, Kattan 1998). Although these studies showed that parasitism produced considerable costs, they did not analyse in detail the effects of parasitism on the different components of the reproductive success of the host (i.e. egg losses, hatching success, chick survival and nest abandonment). Studies conducted in hosts of the Brown-headed Cowbird *M. ater*, a North American generalist parasite, showed that lower host mass and greater incubation length (surrogate measures of the mass difference and hatching asynchrony between host and parasite) were positively associated with the extent of hatching failures and brood reduction in the presence of Brown-headed Cowbird parasitism (Lorenzana & Sealy 1999, Hauber 2003a).

Measurement of the costs of brood parasitism on hosts is important for understanding the evolution of the virulence in avian brood parasites (Kilner 2005) as well as the coevolution of host anti-parasitic defences (Rothstein & Robinson 1998, Hosoi & Rothstein 2000). In this study we analysed the effects of Shiny Cowbird parasitism on different components of the reproductive success of House Wrens *Troglodytes aedon*. The House Wren is a common host of Shiny Cowbirds (Friedmann & Kiff 1985, Kattan 1998) and has a considerably lower mass than the parasite (approximately 15 vs. 45–50 g) and a greater incubation length (approximately 15 vs. 12 days). Therefore, we would expect that, in addition to the reduction of clutch size by egg puncturing, parasitized clutches of House Wrens should have substantially decreased hatching success and chick survival, and that these effects should be positively associated with intensity of parasitism.

We also conducted a field experiment to discriminate between two different mechanisms that have been proposed as the cause of hatching failures in parasitized clutches: (1) lower incubation efficiency due to the increase in the volume of the clutch, and (2) disruption to incubation behaviour due to the early hatching of the Cowbird chick. We manipulated the volume of the clutch by creating clutches of one Cowbird egg and three or five host eggs, and the hatching date of the Cowbird chick by parasitizing nests 1 day before or 3 days after the onset of incubation. If the decrease in hatching success is caused by a lower incubation efficiency, we would expect a lower hatching success in clutches with an enlarged volume, whereas if it is caused by disruption to incubation behaviour, we would expect a lower hatching success in clutches with early hatching of the Cowbird chick.

METHODS

Study site

The study was carried out in 'Reserva El Destino' (35°08′S, 57°23′W), near the town of Magdalena, in the Province of Buenos Aires, Argentina, from October 2003 to January 2004, October 2004 to January 2005, and October 2005 to January 2006. Our study site is an almost flat, marshy grassland with old and second growth stands dominated by Tala *Celtis tala* and Coronillo *Scutia buxifolia*. This site is included within the Biosphere Reserve (MAB-UNESCO) 'Parque Costero del Sur', an area of approximately 30 000 ha.

Data collection

House Wrens nest in natural as well as in artificial cavities (Johnson 1998, Kattan 1998). To facilitate data collection, during August and September 2003 we placed 100 nestboxes within an area of approximately 650 ha. Nestboxes were located in Tala trees at a height of 1.5–1.8 m and they were separated by at least 30 m. The external measurements of the boxes were 25 × 17 × 13 cm (height, width, depth), while the internal ones were 23 × 14 × 10 cm. The box had an entrance hole 4.5 cm in diameter and a roof opening that allowed us to monitor the progress of the nest.

We followed 90, 59 and 54 House Wren nesting attempts during the 2003–04, 2004–05 and 2005–06 breeding seasons, respectively. In the three breeding seasons, first nesting attempts started in early October and the last attempts in mid January. We used nests from the 2003–04 breeding season to describe the breeding biology of host and parasite and to analyse the impact of brood parasitism on host reproductive success, while nests of the 2004–05 and 2005–06 breeding seasons were used mainly to conduct the experiment (see below).

We visited nestboxes daily or every other day until the chicks fledged or the nest failed. At each visit we recorded the number of parasite and host eggs and the occurrence of punctures in them. We also recorded the laying and hatching date of each egg, and the fate of each chick. Eggs were marked with waterproof ink and measured with callipers (length and width) to the nearest 0.1 mm. Chicks were marked with waterproof ink on the tarsus and weighed with a digital portable balance (Ohaus LS 200) to the nearest 0.1 g.

Punctures made by Shiny Cowbirds result in one big, usually triangular, hole through the eggshell. Shiny Cowbird punctures are very different from those made by House Wrens to eggs of neighbouring conspecifics (small punctures usually traversing the eggshell; Belles-Isles & Picman 1986). In our study site we did not observe the latter type of puncture in House Wren or Shiny Cowbird eggs. In addition, in the nest-boxes where we reduced the entrance hole to avoid the access of Shiny Cowbirds (see below) we never observed punctured eggs. Therefore, we are confident that punctures in House Wren eggs were produced by Shiny Cowbirds. House Wrens generally remove punctured eggs within 24–48 h after the puncture event.

In the grassland regions of Argentina and Uruguay, Shiny Cowbirds have an egg polymorphism with three different patterns: white immaculate (unspotted), intermediate (white with a few fine spots) or spotted (Hudson 1874; Friedmann 1929). Some hosts accept all egg morphs, whereas others accept spotted but reject white and intermediate eggs (Mason 1986). In these cases, some nests observed as unparasitized may have been parasitized with white eggs, which were subsequently rejected by the host prior to their detection by observers. Because House Wrens do not reject Shiny Cowbird eggs (Mason 1986), in this study we were able to discriminate unambiguously between parasitized and unparasitized nests.

We assumed that a nest was depredated if all the eggs or chicks disappeared between two consecutive visits, and deserted if the eggs were cold to the touch for two consecutive days and the parents did not defend the nest.

Data analysis

We estimated clutch size of House Wrens only from unparasitized nests found during construction and visited daily until the clutch was complete. We assumed that the clutch was complete when the number of host eggs remained constant for at least two consecutive days. The incubation period was estimated as the time elapsed since the laying of the last egg until the hatching of the last nestling in clutches where all eggs hatched (Nice 1954). For this estimation we considered unparasitized nests only, as the presence of parasite eggs affects the hatching of House Wrens' eggs (see below). Incubation period for Shiny Cowbirds was estimated as the time elapsed from the beginning of full incubation (just after laying the penultimate Wren egg) until hatching (Briskie & Sealy 1990). For this analysis we considered only nests where parasitism occurred before the onset of incubation.

To estimate the frequency and intensity (Cowbird eggs per parasitized nest) of parasitism we considered only nests found in construction and laying and where the host completed laying. We used this criterion because most parasitism by Shiny Cowbirds in House Wrens occurred during laying and nest failure during this stage was associated with punctures produced by Cowbirds (see Results). Therefore, the inclusion of nests found during later stages could underestimate the frequency of parasitism.

We analysed the effect of parasitism on: (1) number of host eggs lost, (2) hatching success, and (3) host chick survival and growth rate. We calculated hatching success as the number of hatchlings divided by the number of eggs present in the nest at the time of hatching, and chick survival as the number of fledglings divided by the number of hatchlings. We determined the effect of parasitism on host chick growth by comparing the growth rates of chicks in unparasitized and parasitized nests. We estimated growth rate from the slope of a linear regression of weight vs. chick age for chicks 1–9 days old (hatching day = day 0). During this period growth rate was almost linear ($F_{1,320} = 2775.6$, $P < 0.001$, $r^2 = 0.88$). To avoid pseudoreplication we used the means for whole broods. To calculate the mean growth rate of the brood we did not consider data from chicks that starved during the nestling period.

To analyse the effect of parasitism during the egg stage we considered as parasitized those clutches that received Cowbird eggs during laying or incubation, while to analyse the effect of parasitism during the nestling stage we considered as parasitized only those nests where Cowbirds hatched.

For each nest we calculated the volume of the clutch as the sum of the volumes of the host and parasite eggs present in the nest during incubation (i.e. we excluded punctured eggs). Egg volume was calculated as $l \times w^2 \times x$ where l and w were the length and width of the eggs (mm), and x is a species-specific constant. The value used for this constant was 4.91×10^{-4} for House Wren eggs (Johnson 1998), and 5.15×10^{-4} for Shiny Cowbird eggs (Nolan & Thompson 1978).

Experimental procedures

We conducted a field experiment to test the effects on host hatching success of: (1) an enlarged volume of the clutch by the addition of one Cowbird egg, and/or (2) an early hatching Cowbird. Because Shiny Cowbirds puncture host eggs and this results in a reduction of host clutch, we also created experimental groups where host clutch was reduced from five (modal clutch size in our study area) to three eggs.

We manipulated the volume of the clutch by creating clutches with three host eggs plus one Cowbird egg (hereafter small clutch volume) or five host eggs plus one Cowbird egg (hereafter large clutch volume). To create the small clutch volume group we removed the fourth and the fifth host eggs immediately after they were laid. This procedure allowed us to maintain a clutch volume approximately equal to that in unparasitized nests, as the volume of one Shiny Cowbird egg is approximately 2.5–3 times larger than the volume of a House Wren egg (see Results). To create the large clutch volume group we did not remove host eggs except in the few cases where House Wrens laid six eggs (in these cases we removed the sixth egg on the day it was laid). We manipulated the hatching date of the Cowbird chick by parasitizing nests with natural Cowbird eggs during day 2 or day 6 (day 0 corresponds to the laying of the first host egg). House Wrens start incubation with the laying of the penultimate egg (day 3) and its incubation period is approximately 15 days, while for Shiny Cowbird eggs in House Wren nests it is 12–13 days (see Results). Therefore, we had a group of nests where the Cowbird chick hatched 2 or 3 days before the first host chick hatched (hereafter early hatching Cowbird), and a group of nests where the Cowbird chick hatched the same or the following day after the first host chick hatched (hereafter simultaneously hatching Cowbird). In short, we created four experimental groups of nests: (1) small clutch volume and early hatching Cowbird ($n = 7$ nests), (2) small clutch volume and simultaneously hatching Cowbird ($n = 10$ nests), (3) large clutch volume and early hatching Cowbird ($n = 8$ nests), and (4) large clutch volume and simultaneously hatching Cowbird ($n = 10$ nests). House Wrens abandoned none of these nests, but Shiny Cowbird chicks did not hatch in two nests of the small clutch volume/early hatching Cowbird group, five nests of the small clutch volume/simultaneously hatching Cowbird group, two nests of the large clutch volume/early hatching Cowbird group, and four nests of the large clutch volume/simultaneously hatching Cowbird group. These nests were excluded from the analysis.

To avoid host egg punctures and natural parasitism by Shiny Cowbirds in the experimental nests we reduced the nestbox opening to a diameter of approximately 3 cm (Pribil & Picman 1997). This opening size allowed House Wrens but not Shiny Cowbirds to access to the nestbox (none of our experimental nests was parasitized or had punctured eggs). After hatching, we enlarged the nestbox opening to a diameter of approximately 4.5 cm to allow Cowbird chicks to fledge.

Shiny Cowbird eggs used in these experiments were collected from House Wren nestboxes that did not have a reduced opening, or from Chalk-browed Mockingbird *Mimus saturninus* nests present in the same area. The eggs were collected the same day they were laid and in all cases they were collected during host laying (i.e. they were not incubated by the host previously to the experiment). Each egg was kept in a fresh environment for 24–48 h prior to its translocation to an experimental nest. All the experiments were conducted during the 2004–05 and 2005–06 breeding seasons. Nests were assigned randomly to each experimental group.

Statistical analysis

Data are presented as mean ± se. Probability of hatching success and probability of nest abandonment were analysed with logistic regression, the former using the ratio of the number of eggs hatched to the total clutch size as the analysis variable, and the latter expressing abandonment as 1 (abandoned) or 0 (not abandoned). For variables that were distributed approximately normally, we used parametric statistical tests. Otherwise, non-parametric statistical tests

Table 1. Values of the main reproductive parameters of House Wrens and Shiny Cowbirds.

	House Wren		Shiny Cowbird	
Variable	Mean ± se	Sample size (nests)	Mean ± se	Sample size (eggs or chicks)
Clutch size	5.2 ± 0.1	22		
Egg length (mm)	17.5 ± 0.08	74	23.8 ± 0.1	78
Egg width (mm)	13.1 ± 0.4	74	19.1 ± 0.1	78
Incubation period (days)	14.8 ± 0.3	11	12.7 ± 0.5	13
Weight at hatching (g)	1.6 ± 0.07	29	4.2 ± 0.1	29
Asymptotic weight (g)	11.5 ± 0.3	13	40.3 ± 1.4	15

were used. All significance levels are for two-tailed tests. Statistical tests were performed by using StatView 5.0 (SAS Institute Inc. 1998).

RESULTS

Breeding biology of House Wrens and Shiny Cowbirds

The main reproductive parameters of House Wrens and Shiny Cowbirds are presented in Table 1. The frequency of Shiny Cowbird parasitism was 60% (46/76 nests) and its intensity was 1.7 ± 0.1 eggs per parasitized nest ($n = 76$ nests). Fifty-nine per cent of parasitized nests received more than one Shiny Cowbird egg (up to four). Of 93 Shiny Cowbird eggs observed, 42% were spotted, 33% were intermediate and 25% were white immaculate. We did not detect significant differences in size between egg morphs (ANOVA, length: $F_{2.51} = 0.95$, $P = 0.4$; width: $F_{2,51} = 0.95$, $P = 0.4$).

Most Shiny Cowbird eggs (53/93) were laid during the laying period of the host (days 0–4), and we only had one case where the Cowbird eggs were laid before the start of host laying. No Wren's egg hatched in 42% of the nests where Shiny Cowbird chicks hatched ($n = 33$), and in 68% of the nests where eggs of both species hatched ($n = 19$), the Cowbird egg hatched before or on the same day as the first Wren's egg. On average, Shiny Cowbird eggs hatched 1.6 ± 0.6 days ($n = 19$ nests) before Wren eggs in the same nest.

Impact of Shiny Cowbird parasitism on House Wren reproductive success

As a result of Shiny Cowbird pecking behaviour, there were losses of House Wren eggs during laying and incubation. There was a tendency for the number of Wren's eggs present before hatching to decrease with the number of Shiny Cowbird eggs laid (Kruskal–Wallis test, $H_3 = 7.1$, $n = 52$ nests, $P = 0.07$, Fig. 1A). In unparasitized nests, the number of Wren's eggs at the time of hatching was significantly lower than the number of Wren's eggs laid (Mann–Whitney U-test, $U = 447.5$, $Z = -1.93$, $P < 0.05$), indicating that egg punctures were also present in these nests.

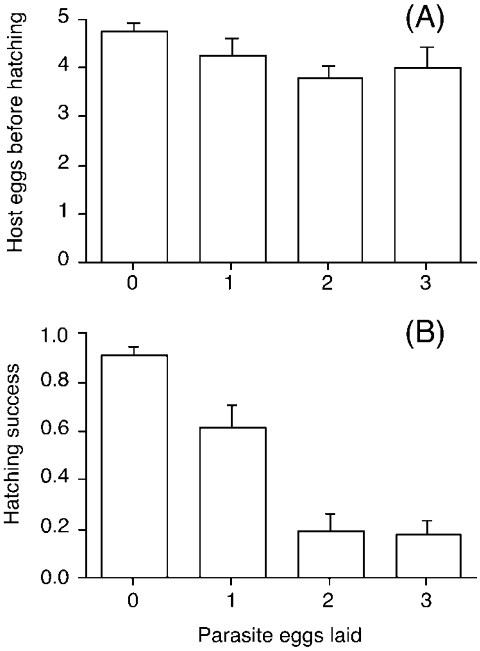

Figure 1. (A) Number of House Wren eggs at the time of hatching and (B) proportion of House Wren eggs that hatched (mean ± se) in unparasitized nests ($n = 22$) or parasitized with one ($n = 12$), two ($n = 14$) or three ($n = 4$) Shiny Cowbird eggs.

We found a negative association between Wrens' hatching success and number of Cowbird eggs (logistic regression, $\chi^2_{10} = 72.2$, $n = 52$ nests, $P < 0.001$, Fig. 1B). Hatching success decreased by approximately 40% in nests with one Cowbird egg and 80%

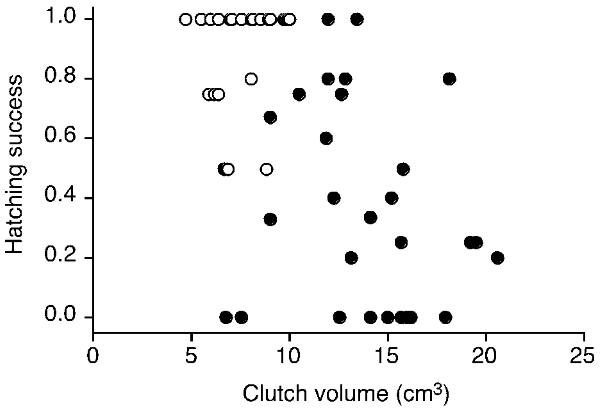

Figure 2. Proportion of House Wren eggs that hatched as a function of the volume of the clutch. Unfilled and filled circles correspond to unparasitized and parasitized clutches, respectively.

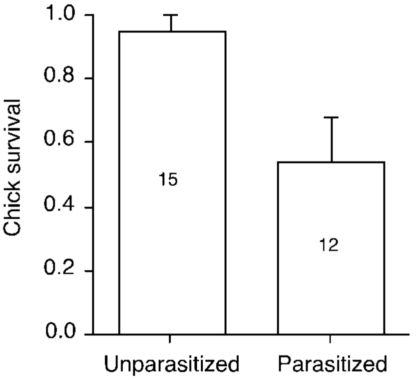

Figure 3. Proportion of hatched chicks (± se) that fledged in unparasitized nests and nests that hatched one Cowbird chick. Numbers on columns represent the number of nests in each category.

in nests with more than one Cowbird egg. We also analysed the association between hatching success and clutch volume during incubation. Because the number of host eggs punctured increased with the number of Cowbird eggs laid, there were several combinations of host and parasite eggs (2–6 host eggs, and 0–3 parasite eggs), and therefore a wide range of clutch volumes (5–20 cm^3, Fig. 2). House Wren hatching success was negatively associated with the volume of the clutch (logistic regression, $\chi^2_{10} = 42.3$, $n = 52$ nests, $P < 0.001$, Fig. 2).

The survival of host chicks was lower in parasitized than in unparasitized nests (logistic regression, $\chi^2_3 = 12.7$, $n = 27$, $P < 0.01$, Fig. 3), but the growth rate of Wren's chicks that fledged did not differ between parasitized and unparasitized nests (parasitized: 1.27 ± 0.06 g/day, $n = 15$ nests; unparasitized: 1.24 ± 0.03 g/day, $n = 26$ nests; Mann–Whitney *U*-test, $U = 210$, $Z = -0.41$, $P = 0.68$). On average, the number of House Wren chicks that fledged in unparasitized nests was 4.3 ± 0.4 ($n = 15$ nests), whereas in parasitized nests it was 0.85 ± 0.3 chicks ($n = 20$ nests). For this analysis we only considered nests that fledged at least one host or parasite chick.

We also analysed the nesting success of House Wren nests during the 2003–04 breeding season ($n = 87$ nests). Forty-two per cent of these nests were successful (i.e. they fledged at least one host or parasite chick), 28% were depredated and 30% were abandoned. There was no association between depredation and parasitism (chi-squared test, $\chi^2_1 = 0.28$, $P = 0.6$). Similarly, nest abandonment was not associated with the number of Cowbird eggs present in the nest (logistic regression, $\chi^2_1 = 1.9$, $n = 87$, $P = 0.58$, Fig. 4A), but there was a positive association between nest abandonment and the number of host eggs punctured (logistic regression, $\chi^2_1 = 8.44$, $n = 87$, $P < 0.01$, Fig. 4B).

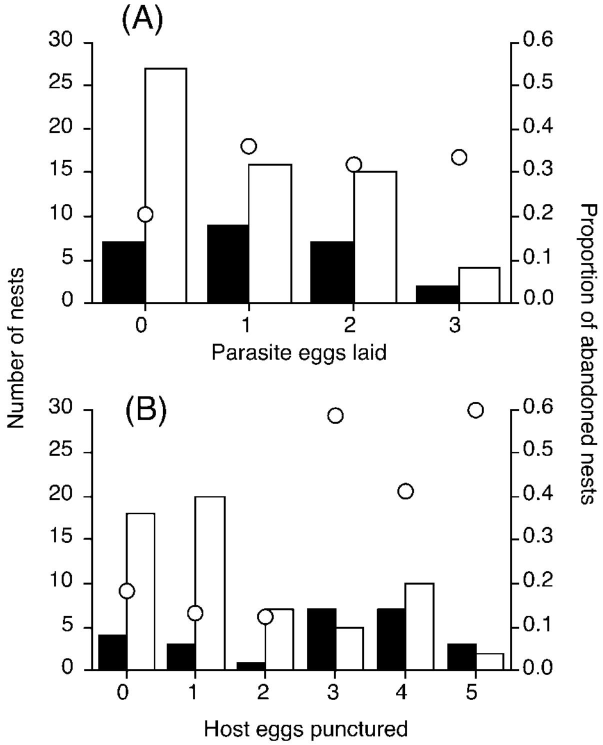

Figure 4. Association between nest abandonment and (A) number of parasite eggs laid, and (B) number of host eggs punctured. Black and white bars show the number of abandoned and non-abandoned nests, respectively. Empty circles show the proportion of abandoned nests.

Table 2. Effects of the manipulation of clutch volume and the timing of Shiny Cowbird hatching on length of incubation, hatching asynchrony and hatching success of House Wren eggs. Fledging success was estimated from nests that survived the whole nestling period (sample sizes indicated in parenthesis). Data are means ± se.

Clutch size Hatching *n*	Small Early 5	Small Simultaneous 5	Large Early 6	Large Simultaneous 6
Clutch volume (cm^3)	8.53 ± 0.32	8.98 ± 0.09	12.2 ± 0.29	12.46 ± 0.28
Incubation period of first host egg (days)	15.6 ± 0.51	15 ± 0.32	15.17 ± 0.17	15.5 ± 0.85
Incubation period of parasite egg (days)	13.2 ± 0.58	13.0 ± 0.0	12.5 ± 0.22	12.67 ± 0.33
Hatching interval (days)	–2.4 ± 0.25	1 ± 0.32	–2.67 ± 0.21	0 ± 0.36
Hatching success	1 ± 0	1 ± 0	0.73 ± 0.11	0.97 ± 0.03
Fledging success	1 ± 0	1 ± 0	0.42 ± 0.3	0.8 ± 0
	(2)	(2)	(3)	(2)

Causes of hatching failure

The volume of the clutch in the large clutch volume groups was approximately 35% greater than in the small clutch volume groups (Table 2). The length of the incubation period of the first House Wren egg that hatched did not differ between groups (Kruskal–Wallis test, $H_3 = 1.01$, $P = 0.75$, Table 2). Similarly, the length of the incubation period of Shiny Cowbird eggs did not differ between groups (Kruskal–Wallis test, $H_3 = 1.96$, $P = 0.5$, Table 2). Therefore, in the early hatching groups, Shiny Cowbird chicks hatched on average 2–3 days before the first host chick, while in the simultaneous hatching groups they hatched the same day, or 1 day after the hatching of the first host chick (Table 2).

Hatching success differed significantly between groups (Kruskal–Wallis test, $H_3 = 12.1$, $P < 0.05$, Table 2). *A posteriori* contrasts indicated that the only significant differences were between the group with early hatching Cowbird and large clutch volume and the other three groups ($P < 0.05$).

DISCUSSION

Our results show that Shiny Cowbird parasitism reduced several components of the reproductive success of House Wrens. First, parasitized nests had a lower clutch size at hatching as a result of punctures. This reduction was also present in unparasitized nests. Secondly, parasitism reduced the hatching success and this reduction was positively associated with intensity of parasitism and with the volume of the clutch. Thirdly, nests with Cowbird chicks had a lower proportion of Wren chicks fledged, though the growth rate of the chicks that survived was similar to that of chicks in unparasitized nests. These three additive effects resulted in a severe reduction in the number of chicks that fledged from parasitized nests (20% of those that fledged in unparasitized nests). Furthermore, egg puncturing by Shiny Cowbirds increased the likelihood of nest abandonment by Wrens.

There has been one previous study on the interactions between Shiny Cowbirds and House Wrens, in the Cauca Valley, Colombia (Kattan 1996, 1997, 1998). Our results agree qualitatively with those of Kattan in that Shiny Cowbird parasitism produces a significant decrease in reproductive success of House Wrens as a consequence of egg destruction, hatching failure and lower chick survival. However, the studies differ in two aspects. First, the extent of synchronization between parasitism and host laying that we observed was greater than that observed by Kattan (1997). This discrepancy could be due to latitudinal differences in Wren clutch size (modal clutch size was three eggs in Kattan's study, five eggs in our study), giving Cowbirds a larger time window for synchronizing parasitism. However, Kattan found that 35% of the eggs were laid before the start of host laying, whereas in our study early laying by Cowbirds was negligible (one of 94 eggs). Secondly, in our study the proportion of Wren's eggs destroyed during laying and incubation was lower (10–20%) than in Kattan's (1998) study (67%). This discrepancy could be attributed to differences in frequency and intensity of parasitism between study sites. In Kattan's study site, the frequency and intensity of parasitism in nestboxes was 94% and 5.65 eggs per nest (Kattan 1998), whereas in our study the respective figures were 60% and 1.7 eggs per nest.

Our results indicate that in successful House Wren nests, egg puncturing was a relatively minor cost of parasitism, even in nests where there was multiple parasitism. The lower number of punctured eggs per parasitic event in a small (this study) compared with a large host with a similar frequency and intensity of parasitism (i.e. Astié & Reboreda 2006) is consistent with the hypothesis of the reduction of competition (Friedmann 1929, Hoy & Ottow 1964, Blankespoor *et al.* 1982, Sealy 1992). This hypothesis proposes that cowbirds remove or peck host eggs in order to reduce the number of competitors of the cowbird chick. Therefore, it would be expected that egg puncturing would be more frequent when host chicks are of similar competitive ability to parasite chicks for food, as normally happens in large hosts (Fraga 1985, Lichtenstein 1998, Astié & Reboreda 2006).

The main cost of parasitism for House Wrens was the reduction in hatching success (40% in single parasitized nests and 80% in multiple parasitized nests). Hatching failures were not associated with egg-capping (i.e. the slipping of a hatched Cowbird eggshell fragment over an intact Wren shell; Hauber 2003b) as we never observed this phenomenon in House Wren nests.

Although our sample sizes were relatively small, experimental data indicate that the early hatching of the Cowbird chick did not affect hatching success, as we did not observe hatching failures in the group with small clutch volume and early hatching Cowbirds. This indicates that early hatching of the Cowbird chick alone does not disrupt the incubation behaviour of the host, or that if incubation behaviour is disrupted, this does not affect the Wren's hatching success. Hauber (2003a) found that the proportion of hatching failures in Eastern Phoebes *Sayornis phoebe* tended to be greater as the asynchrony between the earlier Brown-headed Cowbird hatching and the hatching of the host increased. One possible explanation for this difference is that in our experiment hatching asynchrony was 2–3 days, whereas in Hauber's experiments it was up to 10 days.

Similarly, the increase in the volume of the clutch alone did not affect hatching success, as we did not observe hatching failures in the group with large clutch volume and simultaneously hatching Cowbirds. This result indicates that Wrens are capable of efficiently incubating an enlarged clutch. We only observed hatching failures in Wren eggs when there was a combination of an early hatching Cowbird chick (addition of the Cowbird egg before the onset of incubation) and an increase in the volume of the clutch. This result was similar to that observed by McMaster and Sealy (1999) in a study of the effect of Brown-headed Cowbird early hatching on Yellow Warbler *Dendroica petechia* incubation behaviour.

One interpretation for the previous results is that in hosts lower in mass than the parasite, the increase in the volume of the clutch by the addition of the Cowbird egg before the onset of incubation affects the development of host eggs, but once incubation starts host eggs are less sensitive to changes in clutch volume. Our observational data indicate that this situation was relatively common in House Wren nests, as Cowbirds generally parasitize before the onset of incubation and they did not puncture many Wren eggs. If our interpretation is correct, we would expect unhatched Wren eggs to show no embryo development, whereas if the hatching failure was the result of changes in host incubation behaviour, eggs should have a well-developed embryo. Unfortunately, we did not dissect all the Wren eggs that did not hatch, but in the four cases where we did, there was no development of the embryo.

In summary, our results indicate that Shiny Cowbird parasitism has a major impact on House Wrens, as it affects all components of the Wren's reproductive success (egg survival, hatching success, chick survival and nest abandonment). Because our study was conducted in nestboxes and not in natural cavities, we cannot be sure that natural populations of House Wrens face a similar frequency and intensity of parasitism. However, even if the frequency of parasitism in natural cavities was much lower than that observed, we would expect a significant effect of Shiny Cowbird parasitism on House Wren reproductive success.

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