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Shiny Cowbird parasitism of a low quality host: effect of host traits on a parasite's reproductive success

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ABSTRACT. The reproductive success of parasitic cowbirds (*Molothrus* spp.) varies among host species and is influenced by the degree of synchronization in timing of egg laying, the duration of parasite and host incubation periods, and the ability of hosts to incubate and rear parasite young. We studied the reproductive success of Shiny Cowbirds (*Molothrus bonariensis*) that parasitized the nests of Creamy-bellied Thrushes (*Turdus amaurochalinus*) in the Monte desert region of Argentina. Shiny Cowbirds frequently parasitized Creamy-bellied Thrush nests (60%), and most cowbirds synchronized egg laying with that of thrushes (79%). Most parasitic eggs (80%) hatched within 1 d of the hatching of the first host egg, and more than 91% of the eggs survived until the end of the incubation. However, only 60% of the cowbird eggs hatched and 52% of young survived. The proportion of Shiny Cowbirds eggs laid in Creamy-bellied Thrush nests that resulted in fledged young was 0.03, including eggs and young lost due to predation or desertion. Despite this low reproductive success, Creamy-bellied Thrushes were heavily parasitized by Shiny Cowbirds in our study area. Shiny Cowbirds may continue to parasitize these thrushes because of diffuse selection or because Shiny Cowbird chicks are more likely to fledge from Creamy-bellied Thrush nests in years or areas with greater food availability when brood reduction does not occur.

SINOPSIS. **Parasitismo del Tordo Renegrido en un hospedador de baja calidad: efecto de las características del hospedador sobre el éxito reproductivo del parásito.**
El éxito reproductivo del los tordos parásitos (*Molothrus spp.*) varía entre sus especies hospedadoras y está afectado por el grado de sincronización en el momento de la puesta de huevos, la duración de los períodos de incubación del hospedador y el parásito y la habilidad del hospedador para incubar y criar a los pichones parásitos. Nosotros estudiamos el éxito reproductivo del Tordo Renegrido (*Molothrus bonariensis*) en nidos del Zorzal Chalchalero (*Turdus amaurochalinus*) en la región del desierto del Monte de Argentina. El Tordo Renegrido parasita frecuentemente los nidos del Zorzal Chalchalero (60%) y la mayoría de los tordos sincroniza su puesta con la de los zorzales (79%). La mayoría de los huevos parásitos (80%) eclosionan entre 1 día antes y un día después del primer huevo del hospedador y más del 91% de los huevos sobreviven hasta el final de la incubación. Sin embargo, solo el 60% de los huevos de tordo eclosionan y el 52% de los pichones sobreviven. La proporción de huevos de Tordo Renegrido puestos en nidos de Zorzal Chalchalero que resultan en volantones fue 0.03, incluyendo los huevos y los pichones perdidos por depredación o abandono. A pesar de este bajo éxito reproductivo, el Zorzal Chalchalero es intensamente parasitado por el Tordo Renegrido en nuestra área de estudio. Es posible que el Tordo Renegrido continúe parasitando a estos zorzales debido a un proceso de selección difusa o porque los pichones de tordo tienen mayores posibilidades de llegar a volantones en nidos de Zorzal Chalchalero en años o en áreas con mayor disponibilidad de alimento, donde no ocurra reducción de nidada.

Key words: brood parasitism, Creamy-bellied Thrush, life history, *Molothrus bonariensis*, reproductive success, Shiny Cowbird, *Turdus amaurochalinus*

For brood parasites, host quality depends primarily on how easily nests can be parasitized and the quality of host parental care. Success at locating and parasitizing nests is affected by host nest abundance and conspicuousness (Friedmann 1963, Friedmann et al. 1977), and host nest defenses, such as nest attentiveness, agonistic behavior toward brood parasites (Neudorf and Sealy 1994, Mermoz and Fernandez 1999, Fernandez and Mermoz 2000), and egg rejection behavior of the host (Rothstein 1975, 1990, Mason 1986, Rohwer and Spaw 1988, Sealy 1995, Peer et al. 2000). Host parental care depends on the incubation efficiency of the parasitic egg (McMaster and Sealy 1998, Peer and Bollinger 2000) and how effectively parasite

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chicks are reared. Synchronization with host laying (Massoni and Reboreda 1999, Mermoz and Reboreda 1999) and similarity in the size of host and parasite eggs (Petit 1991, Peer and Bollinger 1997) are important in ensuring hatching success. After hatching, parasite chicks are more likely to succeed if the food delivered by hosts is appropriate (Kozlovic et al. 1996, Peer and Bollinger 1997, 2000) and if competition with host chicks for food is low (Friedmann 1963, Fraga 1985, Lichtenstein 1998, but see Kilner 2003, Kilner et al. 2004).

Many studies of brood parasites have focused on examining the survival of young parasites in the nests of different hosts that vary in body size or egg mass (Mason 1980, 1986, Strausberger 1998, Kilpatrick 2002), habitat or nest type (Strausberger and Ashley 1997), or nest desertion behavior (Burhans et al. 2000). Few studies have focused on the factors affecting cowbird success with a single host species (Fraga 1978, Lichtenstein 2001, Mermoz and Reboreda 2003).

Friedmann (1929) reported that Creamy-bellied Thrushes (*Turdus amaurochalinus*) were effective hosts for Shiny Cowbirds (*Molothrus bonariensis*), but interactions between these two species have been studied only recently (Astié and Reboreda 2005, 2006). At our study site in Mendoza, Argentina, Creamy-bellied Thrushes are slightly heavier than Shiny Cowbirds (56.5 g vs. 50.0 g, respectively) and are frequently parasitized (frequency = 60%, intensity = 1.6; Astié and Reboreda 2006). Thrushes lay three eggs, but brood reduction affects 69% of the nests where two or more chicks hatch (Astié and Reboreda 2006). The weight of thrush chicks when they leave the nest is typically 45–50 g (Astié and Reboreda 2006). Daily mortality rates are higher in thrush nests where at least one egg has been punctured by Shiny Cowbirds, suggesting a possible positive interaction between parasitism and nest predation (Astié and Reboreda 2006).

Our objective was to examine factors that affect the reproductive success of Shiny Cowbirds in Creamy-bellied Thrush nests. In general, cowbirds are assumed to parasitize high quality hosts, and species greater in the body mass than the parasite are better hosts than smaller ones (Mason 1986). Here we describe a case where a host slightly larger than the parasite is heavily parasitized, but appears to be a low-quality host (Astie and Reboreda 2005, 2006). Our objectives were to determine: (1) how well Shiny Cowbirds synchronize parasitism of nests with egg laying by the host species, (2) the quality of parental care provided by Creamy-bellied Thrushes, and (3) the factors that affect Shiny Cowbird success with this host species. We also propose hypotheses to explain why these cowbirds parasitize such a low-quality host so frequently.

METHODS

Our study was conducted at Guaymallén, about 10 km east of Mendoza City, in the province of Mendoza, Argentina (68° 43′ W, 32° 55′ S). Our study site lies in the Monte desert region of Argentina and consists of large areas of land irrigated for agricultural use. Shiny Cowbirds and Creamy-bellied Thrushes are only found in irrigated areas (Astié 2004). Creamy-bellied Thrushes build open nests at heights of 1.5–3 m, and most nest in vineyards and olive and poplar groves.

Field work was conducted during the Creamy-bellied Thrush breeding season (October–December) from 2000 to 2002. We looked for thrush nests systematically and found most by noting the location of thrushes giving alarm calls. We visited nests every 1–2 d until young fledged or the nest failed. For each visit, we recorded the number of host and parasite eggs and noted whether any eggs had been punctured or hatched. Eggs were marked and numbered with waterproof ink in the order of appearance, and chicks were marked with waterproof ink on their tarsus until they were 8-d old when they were marked with a unique combination of color bands. Chicks were weighed daily with spring scales (10 ± 0.1 g and 50 ± 0.5 g) until they fledged, were predated, or starved.

Synchronization of laying and hatching. We estimated the length of the incubation period for Creamy-bellied Thrushes as the time between the laying of the last egg and the hatching of the last egg (Nice 1954). When nests were parasitized before the start of incubation, the duration of the incubation period of Shiny Cowbirds eggs was estimated as the time from the beginning of incubation until hatching. When nests were parasitized after the start of incubation, the incubation period was calculated as the time from the appearance of eggs in the nest until hatching (Briskie and Sealy 1990). To compare the timing of egg laying by Creamy-bellied Thrushes and Shiny Cowbirds, we considered those nests found during the building and laying periods where we recorded the day when cowbird eggs were laid ($N = 47$ nests). To compare the timing of egg hatching for Creamy-bellied Thrushes and Shiny Cowbirds, we considered those nests found during the building, laying, and incubation periods where eggs hatched ($N = 28$ nests).

The day the first thrush egg was laid in the nest was called Day 0 of the incubation period. We calculated the time from Day 0 and the laying of Shiny Cowbird eggs either by direct observation or indirectly when we knew the hatching date ($N = 106$ eggs). Similarly, we called Day 0 of the nestling period the day the first thrush egg hatched and calculated the time from Day 0 to the day when Shiny Cowbird eggs hatched ($N = 33$ eggs).

Cowbird success in thrush nests. We estimated the quality of Creamy-bellied Thrushes as hosts using the proportion of Shiny Cowbird eggs that produced fledglings. We used data from all parasitized nests found before the eggs hatched ($N = 136$ nests). This estimation included losses by nest predation and desertion as well as egg losses, hatching failures, and chick losses in nests that fledged chicks.

For the rest of the analysis, we excluded nests that were predated or deserted to estimate the quality of the host in successful nests. We estimated egg survival as the proportion of eggs laid by Shiny Cowbirds present at hatching. This proportion was estimated from a subset of nests found during the building and laying stages that survived through the end of the incubation stage ($N = 26$ nests). Similarly, we estimated hatching success as the number of hatchlings divided by the number of eggs present in the nest at the time of hatching. Hatching success was estimated from a subset of nests found during the building, laying, or incubation stages that hatched eggs ($N = 70$). To determine the factors that could have affected hatching success, we examined the relationship between hatching success and the number of eggs present in the nest at the time of hatching, and the day of the nestling period when the parasite egg was laid. For the first analysis, we compared Shiny Cowbird hatching success in nests with two, three, four, or five eggs using the Kruskal–Wallis test. For the second analysis, we performed a logistic regression and included nests where we knew when incubation started, the day the parasite egg was laid, and the number of host and parasite eggs in the nest at the time of hatching ($N = 66$). We used the day of the incubation cycle when the Shiny Cowbird egg was laid as an independent variable and the outcome (hatching or not) as a dependent variable.

We estimated survival of Shiny Cowbird chicks as the number of chicks surviving until the fifth day after hatching over the number of eggs that hatched ($N = 42$). We assumed that a cowbird chick that survived until the fifth day would have fledged if the nest had not been predated. This assumption was based on our observation that most cowbird chicks that died due to brood reduction (24 of 25 nests, or 96%) died before the fifth day. We used this criterion because more than 50% of the nests that reached the nestling stage were predated and, therefore, we had a relatively small sample size of nests that fledged cowbird chicks.

To determine if the survival of Shiny Cowbird chicks was associated with the number of host chicks in the nest or with the time elapsed between the hatching of the first host and parasite chicks, we used nests with only one Shiny Cowbird chick to avoid the possible effect of conspecific competition ($N = 26$). We performed a logistic regression using the number of host chicks as an independent variable and outcome (survival or not) as a dependent variable. Similarly, we performed a logistic regression using the day the parasite egg hatch as an independent variable and outcome (survival or not) as a dependent variable.

Statistical analyses. We used nonparametric statistics due to lack of normality of the data and relatively small sample sizes (Siegel and Castellan 1988). Statistical tests were performed using StatView 5.0 (SAS Institute 1998) with $\alpha < 0.05$ (two-tailed) and GenStat (2007) for logistic regression with a 95% confidence interval. Values reported are means ± SE.

RESULTS

Egg laying and egg hatching synchronization. Creamy-bellied Thrushes laid either three or four eggs (mean clutch size = 3.11 ± 0.07, $N = 35$ nests), and incubation started with the laying of the penultimate egg. The mean

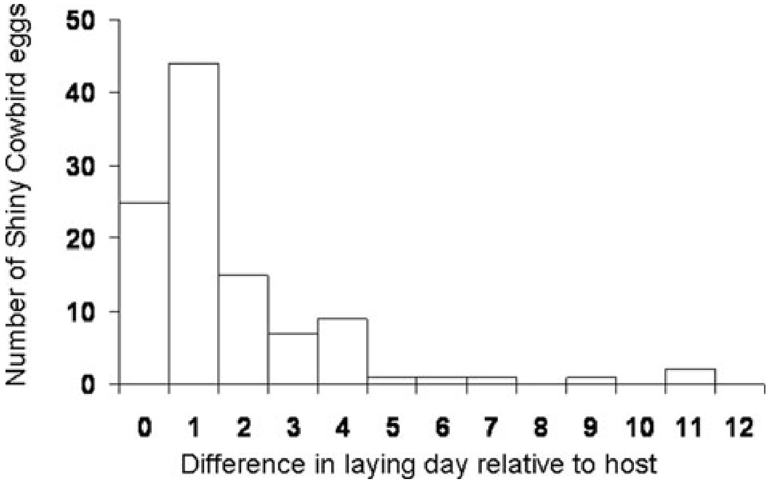

Fig. 1. Frequency distribution of the days when Shiny Cowbirds laid their eggs relative to when Creamy-bellied Thrushes laid eggs. Day 0 corresponds to the laying of the first host egg. The laying stage generally lasts 3 d and incubation starts on Day 1.

duration of the incubation period was 11.5 ± 0.3 days (range = 11–14 days, N = 12 nests). Most Shiny Cowbird eggs (84/106 or 79.2%) were laid during the egg-laying period of hosts (Days 0–2; Fig. 1) and the mean incubation period of Shiny Cowbirds was 12.0 ± 0.6 days (range 11–13 days, N = 3 eggs). As a result, 26 of 33 (78.8%) of Shiny Cowbird eggs hatched 1 d before, the same day, or 1 d after hatching of the first Creamy-bellied Thrush egg (Fig. 2).

Shiny Cowbird success in Creamy-bellied Thrush nests. We found 250 Shiny Cowbird eggs in 146 Creamy-bellied Thrush nests. Only eight cowbird chicks fledged. Thus, the proportion of Shiny Cowbird eggs that reached the fledging stage, including nests that failed due to either predation or abandonment, was 0.03.

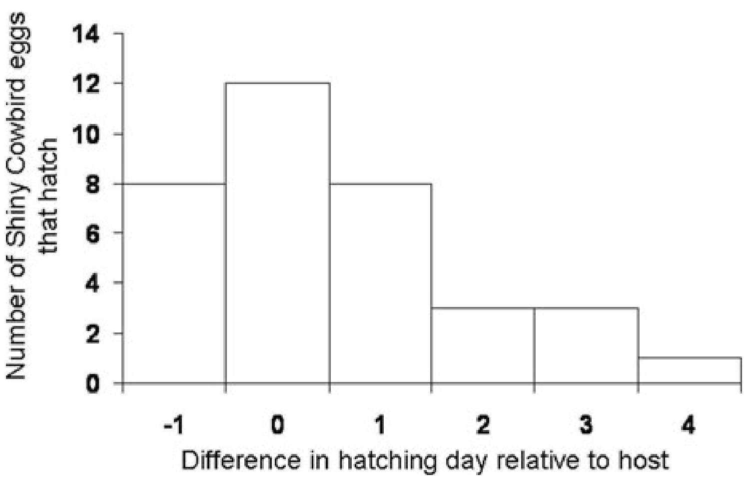

Fig. 2. Frequency distribution of the days when Shiny Cowbirds hatched relative to when Creamy-bellied Thrushes hatched. Day 0 is the day the first Creamy-bellied Thrush egg hatches.

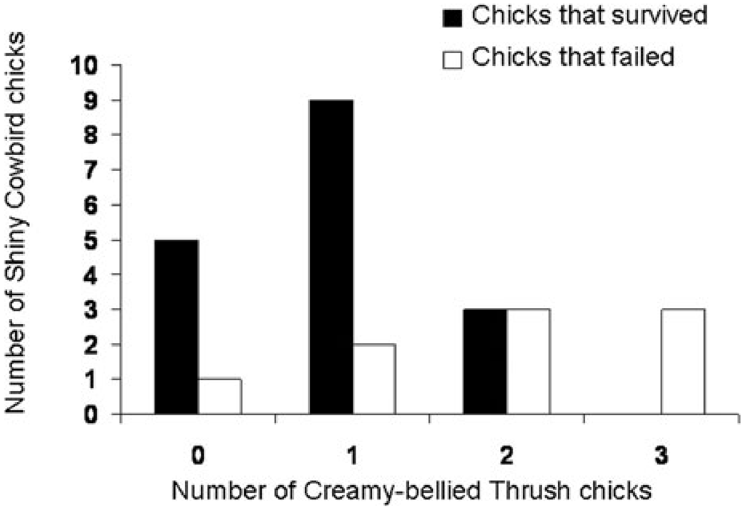

Fig. 3. Number of Shiny Cowbird chicks that survived or failed to survive in nests with different numbers of Creamy-bellied Thrush chicks.

Creamy-bellied Thrush chicks were significantly heavier than Shiny Cowbird chicks at hatching (4.6 ± 0.07 g, $N = 58$ and 3.7 ± 0.13 g, $N = 23$, respectively; Mann–Whitney U-test = 4.9, $P < 0.001$) and before fledging on Day 11 (43.18 ± 1.21 g, $N = 11$, and 29.33 ± 3.68 g, $N = 3$, respectively; Mann–Whitney U-test = 2.6, $P = 0.01$).

The mean survival rate of Shiny Cowbird eggs in successful nests was 0.9 ± 0.05 ($N = 26$ nests), whereas the mean hatching success was 0.6 ± 0.05 ($N = 70$ nests). Hatching success was not related to the number of host and parasite eggs present in the nest at the time of hatching (Kruskal–Wallis, $H = 0.33$, $P = 0.95$), but was partly affected by the timing of cowbird laying relative to that of the host (logistic regression with the time of occurrence of parasitic event as independent variable and occurrence or not of hatching as a dependent variable ($\chi^2 = 3.4$, $P = 0.003$, deviance = 20.2, deviance total = 74.7, $N = 66$).

Survival rates of Shiny Cowbird young in thrush nests were relatively low (mean = 0.52 ± 0.07, $N = 42$ nests). The mean number of Shiny Cowbird eggs hatched per nest was 1.4 ± 0.08, but the mean number of chicks surviving until the fifth day was only 0.8 ± 0.09 ($N = 42$ nests). The presence of another Shiny Cowbird chick in a nest did not affect cowbird survival because the probability of survival was similar when they shared the nest with a host young only and when they shared the nest with another cowbird chick (Mann–Whitney U-test = 1.0, $P = 0.3$, $N = 61$ nests). To determine if the survival of cowbird chicks was associated with the number of nest mates, we performed a logistic regression with survival of the parasite chick (0–1) as a dependent variable and the number of host chicks as an independent variable. For this analysis, we only considered nests where the number of cowbird chicks was 1 ($N = 26$). We found a negative association between the number of host chicks and the survival of parasite chicks (logistic regression: $\chi^2 = 7.4$, $P = 0.006$, $\chi^2 = 3.8$, $P = 0.05$, deviance = 66.7, deviance total = 76.9, $N = 26$ nests, Fig. 3). In contrast, we found no significant association between cowbird chick survival (0–1) and day of hatching relative to the host (logistic regression: $\chi^2 = 1.5$, $P = 0.22$, $N = 18$ nests).

Based on our assumption that a cowbird chick that survived until the fifth day would have fledged if the nest had not been predated, the proportion of Shiny Cowbird eggs that fledged in successful nests, calculated as the product of egg survival (0.91), hatching success (0.60), and chick survival (0.52), was 0.28. Relative to success with other host species in Argentina, Shiny Cowbirds had the lowest hatching success and chick survival in the nests of Creamy-bellied Thrushes (Table 1). Clutch sizes of

Table 1. The reproductive success of Shiny Cowbirds in the nests of different host species.

Species[a]	Mass (g)	Intensity of parasitism (% parasitized nests)	Incubation period (days)	Clutch size	Host quality[b]	Egg success	Hatching success	Fledging success
Bay-winged Cowbird[1]	–	–	–	–	0.07 ($N = 257$ eggs)	–	–	–
Brown-and-yellow Marshbird[2]	80	1.8 (52.8%)	13–15	4–5	0.13 ($N = 352$ eggs)	0.76 ($N = 41$ nests)	0.82 ($N = 72$ nests)	0.93 ($N = 38$ nests)
Chalk-browed Mockingbird[3]	75	(78.1%)	13–15	–	0.07 ($N = 102$ eggs)	–	–	–
Chalk-browed Mockingbird[4]	75	2 (50%)	13–15	–	0.15 ($N = 25$ eggs)	0.88 ($N = 24$ nests)	0.7 ($N = 12$ nests)	0.6 ($N = 9$ nests)
Creamy-bellied Thrush[5]	55	1.5 (60%)	11–14	3	0.03 ($N = 9$ nests)	0.91 ($N = 26$ nests)	0.60 ($N = 70$ nests)	0.51 ($N = 42$ nests)
House Wren[6]	13	1.9 (59%)	14	5–6	0.28 ($N = 93$ eggs)	0.97 ($N = 30$ nests)	0.77 ($N = 30$ nests)	0.87 ($N = 12$ nests)
Rufous-bellied Thrush[7]	70–80	1.7 (66%)	13	3	0.17 ($N = 25$ eggs)	0.95 ($N = 24$ nests)	0.77 ($N = 9$ nests)	0.77 ($N = 5$ nests)
Rufous-collared Sparrow[8]	–	2 (72.5%)	13	3–4	0.07 ($N = 59$ eggs)	–	–	–
Scarlet-headed Blackbird[9]	–	(15.4%)	13–14	–	0.20 ($N = 39$ eggs)	–	–	–
Yellow-winged Blackbird[10]	32	(26.5%)	12–13	–	0.03 ($N = 37$ eggs)	–	–	–

[a]Scientific names and references: [1]*Molothrus badius,* Fraga (1998); [2]*Pseudoleistes virescens*, Mermoz and Reboreda (1994, 1999, 2003); [3]*Mimus saturninus*, Fraga (1985), [4] Sackmann and Reboreda (2003); [5]*Turdus amaurochalinus*, this study; [6]*Troglodytes aedon*, Tuero et al. (2007) and Tuero (2004); [7]*Turdus rufiventris*, Sackmann and Reboreda (2003); [8]*Zonotrichia capensis*, Fraga (1978); [9]*Amblyramphus holocericeus*, Fernandez and Mermoz (2000); and [10]*Agelaius thilius*, Massoni and Reboreda (1998).

[b]Host quality was calculated as the number of chicks that left the nest successfully divided by the total number of eggs founded in nests of that host (including nests that were predated or deserted). Egg success was calculated as the number of eggs present in nest at the time of hatch divided by the number of eggs present at the beginning of incubation. Hatching success was calculated as the number of eggs that hatched divided by the number of eggs in the nest at the end of incubation. Fledging success was calculated as the number of chicks that successfully left the nest divided by the number of eggs that hatched. Shiny Cowbird weight: female 45.6 g, males 55.5 g. Shiny Cowbird incubation period: 12 d.

Creamy-bellied Thrushes were not larger than that of other hosts, but the duration of the incubation period was shorter.

DISCUSSION

Our results indicate that Creamy-bellied Thrushes are low quality hosts for Shiny Cowbirds in our study area, but these thrushes are still heavily parasitized. Shiny Cowbird reproductive success has been reported for at least four other host species. Both hatching and fledging success were higher in the nests of House Wrens (*Troglodytes aedon*; Tuero et al. 2007), Brown-and-Yellow Marshbirds (*Pseudoleistes virescens*; Mermoz and Reboreda 2003), Chalk-browed Mockingbirds (*Mimus saturninus*; Sackmann and Reboreda 2003), and Rufous-bellied Thrushes (*Turdus rufiventris*; Sackmann and Reboreda 2003) than in the nests of Creamy-bellied Thrushes (Table 1). The low success of Shiny Cowbirds in Creamy-bellied Thrush nests was not the result of low reproductive success of this host because more than 80% of their eggs hatched and more than 80% of their young fledged in nests that were not parasitized and that did not suffer egg punctures (Astié and Reboreda 2006).

This host–parasite system has features that suggest that Creamy-bellied Thrushes should be good hosts, including that Creamy-bellied Thrushes and Shiny Cowbirds are similar in size, host clutch size is small (three eggs) and so competition with nest mates should be low, and host nests are easily found and parasitized by Shiny Cowbirds. In addition, we found that, in most cases, parasitism was synchronized with host laying. However, contrary to expectations, only 60% of Shiny Cowbird eggs hatched and 50% of the hatched chicks fledged. We found no association between the number of eggs in the nest and hatching success of the parasite egg. Some hatching failures were the result of late laid eggs, but logistic regression analysis indicated that this variable explained only 27% of the total variation (20.21/74.70 deviance) and, therefore, we cannot conclude that this was a major cause of hatching failures. One possible explanation for the remaining failures is that Shiny Cowbird eggs are smaller than Creamy-bellied Thrush eggs (Astié and Reboreda 2005). This could reduce the incubation efficiency of the parasite egg (Peer and Bollinger 2000), but additional study is needed to determine if that is the case.

We found that the survival of parasite chicks was affected by the number of host chicks in a nest, with this variable explaining 86.7% of the observed variation (66.67/76.92 deviance). One possible explanation for this is that larger host chicks out-compete Shiny Cowbird chicks for food and, therefore, most young cowbirds starve (Astié 2004). In addition, most Creamy-bellied Thrush nests suffered brood reduction at our study site (Astié and Reboreda 2006), resulting in the death of the smallest chick that, in parasitized nests, is always a Shiny Cowbird.

Rufous-bellied Thrushes exhibit similar levels of parasitism (more than 60%) and have been described in two different studies as low- (Lichtenstein 1998) and high- (Sackmann and Reboreda 2003) quality hosts. Lichtenstein (1998) reported that 68% of Shiny Cowbird chicks starved in the nests of Rufous-bellied Thrushes. However, Lichtenstein (1998) manipulated the number of chicks to create broods with one thrush and one Shiny Cowbird chick of the same age. In contrast, Sackmann and Reboreda (2003) found that 60% cowbird chicks survived in nonmanipulated nests. Lichtenstein (1998) also showed that at least 30% of Shiny Cowbird eggs hatched before the first host egg in nonmanipulated nests. This age difference between parasite and host chicks probably compensates for differences in the body mass of hosts and parasites and may explain differences between studies.

Brown-and-yellow Marshbirds, on the other hand, possess characteristics that suggest they may be a poor quality host. These marshbirds are much larger than Shiny Cowbirds and have large broods (four or five chicks per nest; Mermoz and Reboreda 2003). Contrary to expectations, Shiny Cowbirds do well in nests of this host because the incubation period of the brood parasite is shorter than that of the host. Thus, Shiny Cowbird chicks are always heavier than host chicks because they usually hatch 1 or 2 d earlier (Mermoz and Reboreda 2003).

Our results, and those of previous studies, suggest that a combination of all host and parasite characteristics is important in determining parasite success. Synchronization of egg laying by parasites and hosts as well as similar sizes at the time of hatching are important, but some characteristics related to host life history are also important, including clutch size, length of the incubation period, hatching success, number of chick competitors in the nest, and chick survival rates. The Shiny Cowbird–Creamy-bellied Thrush system in Mendoza is not favorable for Shiny Cowbirds because incubation periods of both species are similar, cowbirds chicks are smaller than thrush chicks when they hatch, and Creamy-bellied Thrushes suffer brood reduction.

Despite the low reproductive success of Shiny Cowbirds in Creamy-bellied Thrush nests in our study, this host species is still heavily parasitized. Continued parasitism of nests of low quality hosts may be due to (1) low availability of alternative hosts in the study site (Barber and Martin 1997), (2) a shotgun strategy where egg production is so cheap that it is more profitable to lay eggs in any nest found rather than spending time looking for the nests of better hosts (Rothstein 1990, Kattan 1995, 1997, Davies 2000), or (3) diffuse selection as a consequence of being such a generalist (Rothstein et al. 1986). Low availability of alternative host nests is not a plausible explanation in our study area because at least two other species, House Wrens and Rufous-collared Sparrows (*Zonotrichia capensis*), are better quality hosts than Creamy-bellied Thrushes (Fraga 1978, Tuero et al. 2007) and are also more abundant (Astié, unpubl. data). Similarly, the shotgun hypothesis does not fit the behavior of Shiny Cowbirds because they synchronize egg laying with that of hosts (Lichtenstein 1998, Massoni and Reboreda 1998, Mermoz and Reboreda 1999, our study). However, diffuse selection of hosts (Rothstein et al. 1986) seems to be a plausible explanation. Given that Shiny Cowbirds are such generalists, they may not have evolved specific strategies for choosing particular hosts. More likely, Shiny Cowbirds have evolved the ability to recognize some general characteristics for choosing potentially good hosts. A cost associated with this strategy is that they can make mistakes and parasitize low quality hosts that share some characteristics with high quality hosts.

Another possible explanation is related to brood reduction as a host life-history trait. Among species that exhibit brood reduction, entire clutches might be expected to survive in good years with more or better-quality food. Given that one of the main causes of failure of the Shiny Cowbird in Creamy-bellied Thrush nests was brood reduction, it is possible that Creamy-bellied Thrushes would be better quality hosts in years or locations with more or better-quality food. Because we found no difference in the reproductive success between years (Astié 2004), data concerning the success of Shiny Cowbirds in nests of Creamy-bellied Thrushes at locations that vary in food availability are needed to test our hypothesis.

In conclusion, Creamy-bellied Thrushes are poor quality hosts for Shiny Cowbirds because both species hatch simultaneously, cowbirds chicks are smaller than thrush chicks at the time of hatch, and most cowbird chicks starve because host chicks out-compete cowbird chicks for food. However, despite this low reproductive success, Creamy-bellied Thrushes were heavily parasitized by Shiny Cowbirds. Shiny Cowbirds may continue to parasitize these thrushes because they are host generalists and because their chicks are more likely to survive in Creamy-bellied Thrush nests in years or areas with greater food availability when brood reduction does not occur.

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