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REPRODUCTIVE SUCCESS OF SHINY COWBIRD (*MOLOTHRUS BONARIENSIS*) PARASITIZING THE LARGER BROWN-AND-YELLOW MARSHBIRD (*PSEUDOLEISTES VIRESCENS*) IN ARGENTINA

Myriam E. Mermoz[1,2,3] and Juan C. Reboreda[1]

[1]*Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II, Ciudad Universitaria, C1428EHA Buenos Aires, Argentina;*
[2]*Departamento de Ecología y Comportamiento Animal, Instituto de Ecología A.C., Xalapa, Veracruz 91070, México*

Abstract.—Shiny Cowbirds (*Molothrus bonariensis*) often parasitize larger hosts. It has been proposed that larger hosts are preferred by that parasite because they provide higher reproductive success, but available data are quite variable. We studied the reproductive success of Shiny Cowbirds in nests of Brown-and-yellow Marshbirds (*Pseudoleistes virescens*), a larger and often multiply parasitized host. To estimate the extent of interspecific competition, we compared the hatching success of parasite eggs in nests with and without reduction of the clutch size of the host as a result of egg punctures inflicted by the parasite, and the survival and growth of parasite chicks reared with and without host chicks. To estimate the extent of intraspecific competition, we compared Shiny Cowbird egg losses, hatching success, and chick survival in singly versus multiply parasitized nests. Reproductive success of Shiny Cowbirds was 8% with depredation causing 80% of losses. Clutch reduction due to egg punctures were higher in multiply than in singly parasitized nests, but it did not improve hatching success of parasite eggs. Neither survival nor growth of parasite chicks was affected by the presence of host chicks. Shiny Cowbird hatching success and chick survival did not differ between singly and multiply parasitized nests. Parasite chicks were smaller than same-age Brown-and-yellow Marshbird chicks. However, because parasite chicks hatched one or two days before host chicks and had a higher growth rate, they were the larger chicks in the nest. Overall Shiny Cowbird reproductive success in Brown-and-yellow Marshbird nests was apparently higher than that reported in other smaller or similar-sized hosts. We think that host life-history traits like large clutch size, a longer incubation period, and slower growth rate of chicks are responsible for the high reproductive success of Shiny Cowbirds with Brown-and-yellow Marshbirds.
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Resumen.—*Molothrus bonariensis* frecuentemente parasita hospedadores de mayor tamaño. Se ha propuesto que este parásito de cría preferiría hospedadores más grandes porque con ellos obtiene un mayor éxito reproductivo, pero los datos existentes son variables. Estudiamos el éxito reproductivo de *Molothrus bonariensis* en nidos de *Pseudoleistes virescens*, un hospedador de mayor tamaño con alto parasitismo múltiple. Para estimar la intensidad de la competencia interespecífica, determinamos el éxito de eclosión de huevos parásitos en nidos donde hubo remoción de huevos del hospedador debido a picaduras realizadas por el parásito, y la supervivencia y crecimiento de pichones parásitos en nidos con o sin pichones del hospedador. Para estimar la intensidad de la competencia intraespecífica, comparamos las pérdidas y el éxito de eclosión de huevos y la supervivencia de pichones entre nidos con parasitismo simple y múltiple. El éxito reproductivo de *Molothrus bonariensis* fue del 8% siendo la depredación responsable del 80% de las pérdidas. La pérdida de huevos del hospedador por picaduras fue mayor en nidos con parasitismo múltiple que simple pero esta pérdida no aumentó el éxito de eclosión de los huevos parásitos. La supervivencia y el crecimiento de los pichones parásitos no fueron afectados por la presencia de pichones del hospedador. El éxito de eclosión de *Molothrus bonariensis* y la supervivencia de sus pichones no difirieron entre nidos con parasitismo simple o múltiple. Los pichones parásitos fueron más pequeños que los del hospedador. Sin embargo, debido a que los pichones parásitos eclosionaron uno o dos días antes que los del hospedador, fueron casi siempre los pichones de mayor tamaño dentro del nido. El éxito reproductivo de *Molothrus bonariensis* en nidos de *Pseudoleistes virescens* fue aparentemente mayor que el descripto para otros hospedadores de tamaño similar o más pequeños. Pensamos que características de historia de vida de *Pseudoleistes virescens* tales como el tamaño de puesta grande, el

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[3] E-mail: mermoz@bg.fcen.uba.ar

mayor período de incubación de sus huevos y la tasa de crecimiento menor de sus pichones, son responsables del alto éxito reproductivo de *Molothrus bonariensis* en nidos de *Pseudoleistes virescens*.

Obligate avian brood parasites lay their eggs in nests of other species, the hosts, which incubate the eggs and perform all parental care that parasite chicks need for their normal development. Some brood parasites use only one or very few hosts, whereas others are generalists and use a large number of hosts (Rothstein 1990).

Within the parasitic cowbirds (Icteridae), Shiny Cowbirds (*Molothrus bonariensis*) and Brown-headed Cowbirds (*M. ater*) are generalists, each having been recorded parasitizing >200 host species (Friedmann and Kiff 1985, Ortega 1998). Shiny and Brown-headed cowbirds do not have some specializations found in other brood parasites, including defense of a territory for avoiding intraspecific competition (Dufty 1982, Fleischer 1985, Fraga 1985, Davies and Brooke 1988), selection of hosts that do not discriminate against parasitic eggs (Rothstein 1976; Scott 1977; Davies and Brooke 1989a, b; Neudorf and Sealy 1994; Mermoz and Reboreda 1999), and egg or chick mimicry (Nicolai 1974, Brooke and Davies 1988, Fraga 1998). However, they usually puncture or remove eggs from nests they parasitize (Hudson 1874, Sealy 1992, Massoni and Reboreda 1998, Mermoz and Reboreda 1999) and synchronize parasitism with host egg-laying (Massoni and Reboreda 1998, Strausberger 1998, Mermoz and Reboreda 1999; but see Kattan 1997).

For a generalist cowbird, parasitizing a host larger than itself does not appear to be the best alternative for a number of reasons. Access to nests can be dangerous, especially with hosts that behave aggressively toward the parasitic female when she approaches the nest (Robertson and Norman 1976, Peer and Bollinger 1997, Strausberger and Horning 1998, Mermoz and Fernández 1999). Poor contact of the smaller parasite egg with host brood patch may prevent effective incubation (Peer and Bollinger 1997). Prey size can be too large to be handled by the smaller cowbirds (Peer and Bollinger 1997). Finally, larger host chicks may outcompete parasitic chicks for food (Fraga 1985, Scott and Lemon 1996, Peer and Bollinger 1997, Lichtenstein 1998).

Most Brown-headed Cowbird hosts are smaller in size than the parasite (Lowther 1993, Strausberger and Ashley 1997). On the contrary, available data for Shiny Cowbirds indicate that they frequently parasitize hosts similar or larger in size (Mason 1986, Wiley 1988). Mason (1986) proposed that larger hosts would be preferred because they would provide higher reproductive success for the parasite. However, data on the reproductive success of Shiny Cowbirds in larger hosts are quite variable and show that in some cases that parasite has similar or higher reproductive success than in smaller hosts (Wiley 1985, 1986), whereas in other cases its success is lower (Gochfeld 1979, Fraga 1985, Lichtenstein 1998).

Here, we studied the reproductive success of Shiny Cowbirds parasitizing a larger and common host, the Brown-and-yellow Marshbird (*Pseudoleistes virescens*; Hudson 1874, Orians 1980, Mermoz and Reboreda 1999). Brown-and-yellow Marshbird adults are ~50% heavier than Shiny Cowbirds, whereas parasite eggs are 30% smaller in volume than host eggs (Hoyt 1979, Mermoz and Reboreda 1994). We measured the effect of nest failure, interspecific competition, and intraspecific competition on Shiny Cowbird reproductive success. To estimate the extent of competition between the parasite and its host, we determined: (1) hatching success of parasite eggs in nests without and with host-clutch reduction produced by egg punctures inflicted by the parasite, and (2) survival and growth of parasite chicks reared with and without host chicks. To estimate the extent of intraspecific competition, we compared Shiny Cowbird egg survival, hatching success, and chick survival in singly versus multiply parasitized nests.

METHODS

Study area and general methodology.—The study was carried out near the town of General Lavalle (36°26'S, 56°25'W), Buenos Aires province, Argentina during the 1992–1994 breeding seasons (October to December). The study area is part of the "flooding Pampas," a flat and low region with little land >4 m above sea level. It includes marshes and humid grasslands with scattered patches of native woodland trees (*Celtis tala* and *Jodina rhombifolia*) at higher elevations. The climate is temperate subhumid with mean monthly temperatures of 23°C in January (summer) and 13°C in July (winter), and ~1,500 mm of annual rainfall (Soriano 1991).

The Brown-and-yellow Marshbird (hereafter "marshbird") builds a cuplike nest at height of 0.5–1.5 m. Most nests in our study (89%) were built on exotic thistles (*Cynara cardunculus*, *Carduus* spp.) in upland areas (Mermoz and Reboreda 1998). Nests were tagged inconspicuously with a numbered tag placed in the plant, and its location was flagged with a color mark placed 10 m from the nest. At each nest an initiation date was determined corresponding to the day when the first marshbird egg was laid. When the nest was found during incubation, the number of marshbird eggs and their incubation stage were used to estimate the initiation date (Hays and LeCroy 1971). Nests were checked daily or every other day until either the chicks fledged or the nest failed. Each egg was marked with waterproof ink and checked for cracks or punctures in every visit. Chicks were marked with waterproof ink or color banded on the tarsus and weighed with Pesola scales until they fledged, 11–14 days after hatching.

Effect of nest failure on Shiny Cowbird reproductive success.—To estimate the effect of nest predation and nest desertion on Shiny Cowbird (hereafter referred to as "cowbird") reproductive success, only nests found during construction or egg-laying were considered. In those nests the proportion of cowbird chicks that fledged was determined. Losses of parasite eggs or chicks were assigned to nest failure, partial predation, egg ejection (see below), hatching failures, or nestling mortality. Those cases in which the nest was depredated or deserted (mainly as a result of bad weather condition) were considereds as nest failures.

Egg-survival, hatching, and fledging success.—In our study area, cowbird eggs have two distinct morphs: white-immaculate (~20% of eggs; Massoni and Reboreda 1998) and spotted. Marshbirds eject 94% of white eggs by grasping them with their beak (Mermoz 1996). It was assumed that the disappearance of undamaged white eggs between our visits was the result of ejection behavior of the host. In some cases it was observed that white or spotted cowbird eggs with punctures disappeared between our visits. In those cases it was assumed that the loss of eggs was the result of egg puncture by cowbirds followed by host-nest sanitation (marshbirds usually remove eggs with broken shells in <24 h). In other cases it was observed that undamaged spotted eggs had disappeared between consecutive visits. In those cases, it could not be determined whether egg losses were the result of host-nest sanitation of undetected egg-puncture events or partial depredation. We calculated egg survival as the proportion of eggs laid that survived to hatching. Egg survival was estimated from only nests found during nest construction or egg-laying that hatched chicks. Similarly, hatching success was calculated as number of hatched chicks divided by number of eggs present in the nest at the time of hatching (Koenig 1982), and fledging success as number of chicks fledged over number of chicks hatched. Hatching and fledging success were estimated from nests found during construction, egg-laying, or incubation that hatched and fledged chicks, respectively. Overall, cowbird reproductive success (including egg-survival, hatching, and fledging success) was estimated from nests found during construction, egg-laying, or incubation that fledged chicks. To control for cowbird egg-losses that could have occurred before the nests were found, values of reproductive success were recalculated using only nests found during construction or egg-laying. Finally, chick mortality was estimated by intra- or interspecific competition from nests that had hatched one cowbird and at least other chick of either species.

Incubation periods of host and parasite eggs.—Incubation period for marshbird eggs was estimated as the time elapsed from laying of last egg and hatching of last marshbird chick in clutches where all eggs hatched (Nice 1954). Because hatching of host chicks usually occurs over two days, it was concluded that marshbirds begin full incubation after laying their penultimate egg (Clark and Wilson 1981, Briskie and Sealy 1990). Therefore, when the parasite egg was laid before the host penultimate egg, the incubation period of the parasite was estimated as the time elapsed from the laying of the penultimate host egg and hatching of the parasite nestlings (Briskie and Sealy 1990). When the parasite egg was laid after the host had laid its penultimate egg, incubation period was estimated as the time elapsed between laying and hatching of the parasite egg. The hatching interval between host and parasite nestlings was estimated as the number of days elapsed between the hatching of the cowbird chick and the first marshbird chick in singly parasitized nests.

Growth curves.—To estimate growth curves of host and parasite chicks, mean daily weight of same-age nestlings was used. Data were excluded from chicks that died in the nest because we inferred that in those cases the growth curves were atypical. Growth curves were adjusted to a logistic curve using Ricklefs' (1967) methodology. The asymptote of the growth curve (A), the mean growth rate (K) and the inflection point or age of maximum growth (t_0) was estimated. With that methodology, logistic curves were transformed into straight lines. The slope magnitude of that line is one-fourth of the mean growth rate. The estimated adjusted weight reached at time t is:

$$\text{Estimated weight} = \frac{A}{1 + e^{-K(t-t_0)}}$$

Also estimated were the parameters of Ricklefs' adjusted weight for every chick. To do that, a nonlinear model and least-squares estimation minimized with the Quasi-Newton option in the SYSTAT program (Wilkinson et al. 1992) were used. To guarantee a good fit with the Quasi-Newton option, only data from chicks weighed at least five times were used. To determine the effect of the presence of host chicks on the growth of cowbird chicks, the growth parameters of the parasite chicks were estimated from nests where host chicks did and did not hatch. For those two categories, the weight reached just before the chicks fledged (days 11–14 after hatching) and the values of the parameters A, K, and t_0 were compared. The composition and number of chicks in a brood varied between one to four cowbirds and one to four marshbirds with all possible combinations up to six chicks. Although differences in number of host and parasite chicks could affect the weight gain of individual cowbird chicks, there were not enough nests in each category to analyze its effect. Therefore, to control for differences in brood composition, for each weight parameter (A, K, and t_0) of parasite chicks a multiple-regression analysis was performed with number of cowbird and marshbird chicks as independent variables (Zar 1996).

Weights of adult cowbirds were obtained from birds netted between August and November 1991 at the campus of Universidad Nacional de Luján (34°40'S, 59°10'W), whereas weights of adult marshbirds were obtained from birds netted between September and December 2001 at General Lavalle.

Statistical analysis.—Parametric tests were used only for normally distributed data. Normally distributed data included all growth parameters. Otherwise, nonparametric tests with corrections for ties were used. For independent comparisons, Mann-Whitney U or Kruskal-Wallis tests were used; and for paired comparisons, Wilcoxon signed-rank test was used. When sample sizes were ≥20 the asymptotic test procedure was used, whereas when sample sizes were smaller, Fischer's exact tests (Zar 1996, Mundry and Fischer 1998) were used. For the analysis of contingency tables, the Fisher's exact test (two categories) or the chi-square test (more than two categories; Zar 1996) was used. Statistical power of our tests was estimated when results were nonsignificant with $P > 0.20$ and sample sizes relatively small (Johnsson 1996). Power estimation was performed for multiple regressions (Borenstein et al. 1997) and for some Mann-Whitney U or Kruskal-Wallis tests. Specific algorithms for power estimation of nonparametric tests are not available. Therefore, the arc sine of the square root of the proportion was calculated to achieve a better adjustment of the data to a normal distribution and then the power of the corresponding t-tests for unequal variances or analysis of variance (ANOVA) (Erdfelder et al. 1996) was estimated. All our power estimations were retrospective; therefore, their results have to be considered with caution (Gerard et al. 1998). Results are presented as mean ± SE. All statistics are two-tailed.

RESULTS

Effect of host-nest failure on cowbird reproductive success.—We found 418 marshbird nests, 69.2% (289) during construction or egg-laying, 27.5% (115) during incubation, and 3.3% (14) after the chicks had hatched. Sixty-six percent of nests ($n = 276$) were parasitized, with half the nests multiply parasitized with between two and eight cowbird eggs. Mean number of parasitic eggs per parasitized nest was 1.89 ± 0.09 ($n = 187$ parasitized nests found during construction or egg-laying). In those 187 parasitized nests, cowbirds laid 352 eggs (36 of the white morph) that resulted in 47 nestlings and 28 fledglings. Cowbird reproductive success estimated from those 187 nests was 8% (28 of 352 eggs). Most cowbird-egg losses were the consequence of predation. Two hundred forty-five eggs were lost as a result of whole-nest predation and 35 eggs due to partial nest predation or egg punctures. Losses of cowbird eggs not preyed upon encompass egg ejection by marshbirds (15 eggs, all of the white morph) and hatching failures (10 eggs). Of the 47 cowbird nestlings that hatched, 16 were lost because of whole-nest predation, one due to partial nest predation, and two because of unknown causes.

Survival and hatching success of cowbird eggs.—Proportion of cowbird eggs laid that remained in the nest at the time of hatching was 0.76 ± 0.06 ($n = 41$ nests). Majority of eggs lost had been previously punctured by cowbirds. Multiply parasitized nests lost more parasite eggs than singly parasitized ones (Mann-Whitney U-test: $Z = -2.12$, $P = 0.027$; Table 1). Hatching success of parasite eggs averaged 0.82 ± 0.04 ($n = 72$ nests) and did not differ between singly and multiply parasitized nests (Kruskal-Wallis test, $H = 2.41$, $P > 0.50$, power = 0.78; Table 1).

Marshbirds lay between four and five eggs (Mermoz and Reboreda 1998), and parasitized clutches have approximately two cowbird eggs. Cowbird females often puncture eggs in parasitized nests and marshbirds usually remove the eggs with punctures within 24 h. In those nests in which cowbird females do not puncture any egg, combined clutches (i.e. host plus parasite eggs) will have more than five eggs. To estimate the effect of cowbird egg-puncture behavior on the hatching success of parasite eggs, we compared hatching success in nests where total number of eggs (host plus parasite) was

Table 1. Estimates of Shiny Cowbird reproductive success in singly and multiply parasitized nests. Values are mean ± SE with number of nests in parenthesis. Only the proportion of parasitic eggs that remained in the nest at the end of the incubation stage (egg survival rate) differed between single and multiply parasitized nests ($P = 0.027$).

	Single	Multiple
Egg survival rate	0.83 ± 0.08 (23)	0.67 ± 0.08 (18)
Hatching success	0.81 ± 0.07 (23)	0.73 ± 0.1 (11)[c]
		0.82 ± 0.05 (28)[d]
Fledging success	0.91 ± 0.07 (20)	0.87 ± 0.01 (8)[c]
		0.86 ± 0.08 (10)[d]
Reproductive success[a]	0.62 ± 0.1 (24)	0.50 ± 13 (10)[c]
		0.61 ± 0.08 (17)[d]
Reproductive success[b]	0.57 ± 0.14(14)	0.51 ± 0.11 (12)

[a] Fledgling and egg considering all nests that were found before the first nestling hatched.

[b] Fledgling and egg considering only nests that were found during construction or egg-laying.

[c] Nests parasitized with two eggs (hatching success) or nestlings (fledging success).

[d] Nests parasitized with 3–5 eggs (hatching success) or nestlings (fledging success).

up to 5 eggs and nests in which clutch size was 6–10. There was no difference in cowbird hatching success between clutches with up to 5 eggs and clutches with 6–10 eggs (Mann-Whitney U-test, $Z = 0.58$, $P = 0.66$; Table 2).

Fledging success of cowbirds.—Proportion of parasite chicks that fledged in successful nests (i.e. nests that fledged at least one chick of either species) was 0.89 ± 0.04 ($n = 38$ nests). The effect of interspecific competition for food, measured as the proportion of nestlings that died, differed between species. Survival of cowbird chicks in mixed broods not depredated was higher than survival of host chicks (Wilcoxon signed-rank test, $T = 32$, df = 17, $P < 0.05$; Table 2). Starvation of parasite chicks in nests with mixed broods was extremely rare. The parasite chick died in only 1 of 28 singly parasitized nests with mixed broods. In that nest, the parasite egg was laid after incubation had started and the parasite chick hatched two days after the first host chick.

Mortality of cowbird chicks did not differ between nests with one versus more than one parasite chicks. We detected starvation of the parasite chick in 1 of 28 nests that had one parasite chick, and in 3 of 19 nests that had 2 to 4 parasites chicks (Fisher's exact test, $P = 0.29$). In two of the three multiply parasitized nests that loss chicks, four of the parasite egg but none of the host eggs hatched. Therefore, in those cases, mortality was the consequence of intraspecific competition. In the other nest, three cowbird and two marshbird nestlings hatched, but only one parasite and one host chick fledged.

Intraspecific competition between cowbirds.—We did not detect a decrease in cowbird reproductive success with increased intensity of parasitism. Cowbird reproductive success, measured as the proportion of fledglings per parasite egg laid, did not differ between singly and multiply parasitized nests (Kruskal-Wallis test, $H = 93$, $P > 0.7$, power = 0.76; Table 1). We obtained the same result when we controlled for possible

Table 2. Reproductive parameters of Shiny Cowbird and Brown-and-yellow Marshbird. Values are mean ± SE with number of nests in parenthesis and ranges in brackets.

	Shiny Cowbird	Brown-and-yellow Marshbird	P
Incubation period (days)	11.95 ± 0.18 (20) [10–13]	14.09 ± 0.17 (10) [13–15]	<0.001
Hatching success (nests with <6 eggs)[a]	0.80 ± 0.06 (34)	0.65 ± 0.05 (34)	NS
Hatching success (nests with ≥6 eggs)[a]	0.85 ± 0.05 (23)	0.60 ± 0.07 (23)	<0.01
Chick survival[a]	0.95 ± 0.03 (36)	0.73 ± 0.06 (36)	<0.05

[a] Mixed clutches and broods.

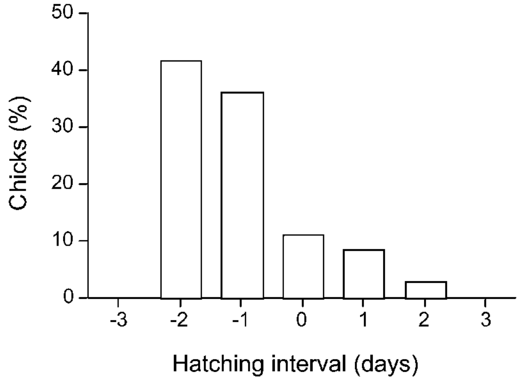

Fig. 1. Frequency distribution of intervals (days) between time of hatching of Shiny Cowbird and first Brown-and-yellow Marshbird chicks. Data are from single parasitized broods ($n = 36$). A zero day interval corresponds to cases where chicks of both species hatched the same day. Negative values correspond to cases where parasite chick hatched before first host chick, whereas positive values indicate the opposite.

parasite egg losses that could have occurred before we found the nest (Mann-Whitney *U*-test; $U' = 103.5$, $P > 0.2$, power = 0.65; Table 1). The presence of another parasite chick did not affect the fledging success of Shiny Cowbirds either. Survivorship of Shiny Cowbird chicks, measured as the proportion of nestlings that fledged, did not vary among nests with 1–4 parasite nestlings (Kruskal-Wallis test, $H = 1.41$, $P > 0.5$, power = 0.78; Table 1).

Incubation period, timing of hatching, and weight increase.—Incubation period of parasite eggs was on average two days shorter than that of host eggs (Mann-Whitney *U*-test; $U' = 215$, $P < 0.001$; Table 2). As a consequence, in 78% of the nests, parasite chicks hatched one or two days earlier than the first host chick (Fig. 1).

The growth curves of parasite and host chicks (Fig. 2) show that parasite chicks reached a weight between 74.4 and 89.8% of the weight of adult males and females, respectively (Table 3). Parasite and host chicks differed in all growth parameters. Growth of host chicks adjusted for a greater asymptotic weight A (ANOVA, $F = 33.05$, df = 1 and 114, $P < 0.0001$; Table 3), but parasite chicks had a greater mean growth rate K and reached their age of maximum growth (t_0) one day earlier (K: ANOVA, $F = 20.74$, df = 1 and 114, $P < 0.001$; and t_0: ANOVA, $F = 19.34$, df = 1 and 114, $P < 0.001$; Table 3). Mean weight at the time chicks fledged (days 11–14) was greater for host chicks than for parasite chicks (ANOVA, $F = 83.5$, df = 1 and 94, $P < 0.0001$; Table 3).

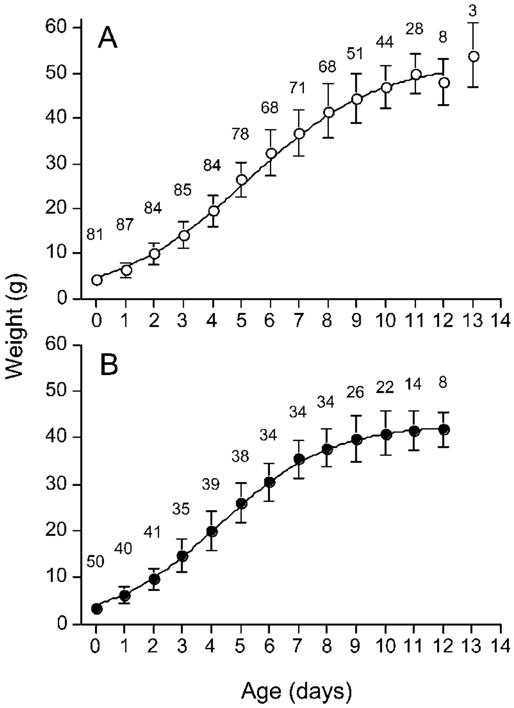

Fig. 2. Growth curves of Brown-and-yellow Marshbird (A) and Shiny Cowbird (B) chicks. Dots indicate the weight in grams (mean ± SD with sample sizes over them). Day 0 corresponds to day of hatching. Interpolation lines were plotted using the parameters of Ricklefs (1967) approximation to a logistic function. Parameters were $A = 52.74$, $K = 0.44$, $t_0 = 5.23$ with a fit of $r^2 = 0.98$ for Brown-and-yellow Marshbirds; and $A = 42.85$, $K = 0.52$, $t_0 = 4.29$ with a fit of $r^2 = 1$ for Shiny Cowbirds.

Survival of cowbird chicks was not affected by the presence of marshbird chicks (Kruskal-Wallis test; $H = 0.31$, $P = 0.85$; Table 4). Weight of cowbirds at the time they fledged was not affected by the presence of host nestmates (ANOVA, $F = 0.007$, df = 1 and 36, $P = 0.93$, Table 4). In addition, presence of host chicks did not affect the magnitude of any parameter of Ricklefs' estimation (A: ANOVA, $F = 0.73$, df = 1 and 36, $P = 0.73$; K: ANOVA, $F = 0.33$, df = 1 and 36, $P = 0.57$; t_0: $F = 0.43$, df = 1 and 36, $P = 0.51$; Table 4). Growth of cowbirds was not affected by the composition of the brood. We did not find a significant effect of number of cowbird or marshbird chicks in the nest (independent variables) on Ricklefs' growth parameters (A: ANOVA, $F = 0.38$, df = 2

TABLE 3. Weight parameters of Shiny Cowbird and Brown-and-yellow Marshbird. Values are mean ± SE with number of individuals in parenthesis and ranges in brackets.

	Shiny Cowbird	Brown-and-yellow Marshbird	P
Male adult weight (g)	55.5 ± 0.15 (21)	81.3 ± 0.90 (22)	–
Female adult weight (g)	46 ± 0.12 (31)	78.6 ± 1.87 (21)	–
Weight of fledglings (g)	41.3 ± 0.62 (39) [34.5–48]	49.0 ± 0.62 (57) [40–58]	<0.0001
Ricklefs' A (g)	43.5 ± 0.86 (38)	54.5 ± 1.2 (78)	<0.0001
Ricklefs' K (day^{-1})	0.581 ± 0.15 (38)	0.50 ± 0.1 (78)	<0.001
Ricklefs' t_0 (days)	4.27 ± 0.14 (38)	5.15 ± 0.13 (78)	<0.001

Ricklefs' parameters: A = asymptote of the growth curve, K = average growth rate, t_0 = age of maximum growth.

and 35, $P = 0.68$; K: ANOVA, $F = 0.48$, df = 2 and 35, $P = 0.62$; t_0 : $F = 1.88$, df = 2 and 35, $P = 0.16$; power for all tests > 0.7).

Although marshbird chicks were 20% heavier than cowbird chicks at hatching (Fig. 2), in 78% of the instances cowbirds hatched one or two days earlier than the first host chick (Fig. 1). Therefore, in most cases the cowbird chicks were the oldest and heaviest throughout all nestling period except when they were close to reaching their asymptotic weight (Fig. 3).

DISCUSSION

Reproductive success of cowbirds in successful nests.—Cowbirds successfully parasitized marshbirds and, in spite of the smaller size, parasite eggs were properly incubated and parasite chicks were not outcompeted for food by host chicks. Host-clutch reduction due to egg punctures inflicted by cowbirds did not improve hatching success of parasite eggs. That result contrasts with the one observed in Great-spotted Cuckoo (*Clamator glandarius*), a brood parasite that uses larger hosts like the Eurasian Magpie (*Pica pica*). In that system, damage of host eggs by the parasite improves the hatching success of late-laid parasitic eggs (Soler et al. 1997). Similarly, Brown-headed Cowbird eggs experimentally added to nests of Common Grackle (*Quiscalus quiscula*) had better hatchability or a shorter incubation period when host eggs were removed (Peer and Bollinger 1997).

Competition with host nestlings did not affect survival or growth of cowbird chicks. Those results also differ from other brood parasites reared together with larger host chicks. Great-spotted Cuckoo chicks reared with magpie chicks reach a lower asymptotic weight than those reared alone, and the weight at the time they leave the nest affects their probability of survival (Soler et al. 1994a, b). Our findings are probably the result of the shorter incubation period of cowbird eggs and synchronization of parasitism with host egg-laying (Mermoz and Reboreda 1999). As a consequence, Shiny Cowbird chicks hatched 1–2 days in advance to host chicks (Fig. 2: 78% of instances), which guarantees that they were the oldest and heaviest chicks in the nest throughout most of the nesting cycle (Fig. 3). Differences in growth patterns between cowbird and marshbird chicks could also explain why parasitic chicks were not outcompeted for food by host chicks. Cowbird chicks had a greater mean growth rate than marshbirds. That difference in growth rates is

TABLE 4. Effect of the presence of Brown-and-yellow Marshbird chicks on Shiny Cowbird nestling survival and growth rate. Values are mean ± SE with sample size (number of nests or individuals) in parenthesis. There were no significant differences between groups for all variables considered.

	Without host chicks	With host chicks
Chick survival	0.95 ± 0.05 (10)	0.94 ± 0.05 (14)
Weight of fledgling (g)	41.5 ± 1.84 (4)	41.7 ± 0.66 (35)
Ricklefs' A (g)	43.1 ± 1.77 (11)	43.7 ± 0.99 (27)
Ricklefs' K (day^{-1})	0.60 ± 0.03 (11)	0.58 ± 0.02 (27)
Ricklefs' t_0 (days)	4.41 ± 0.24 (11)	4.21 ± 0.17 (27)

Ricklefs' parameters: A = asymptote of the growth curve, K = average growth rate, t_0 = age of maximum growth.

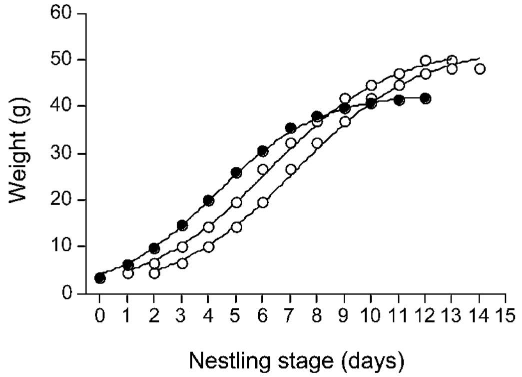

FIG. 3. Growth curves of Shiny Cowbirds (black dots) and Brown-and-yellow Marshbirds (white dots) chicks as a function of nestling stage. Day 0 corresponds to the time of first chick hatching. Because parasite chicks hatch one or two days before host chicks, growth curves of host chicks start one or two days after the parasite one. As the figure shows, if parasite chicks hatch one or two days before the first host chick, they will be the heaviest chick in the nest until they are close to reaching the asymptotic weight.

consistent with the results of allometric comparative studies done by Ricklefs (1968, 1969, 1973, 1979, 1982), which show that larger species tend to grow slower than smaller ones. Marshbirds and cowbirds had mean growth rates greater than those predicted by the general equation $K = 1.11\ A^{-0.278}$ (Ricklefs 1968) as it was described for other icterids (Teather and Weatherhead 1994). Although cowbird and marshbird chicks fledge at a weight lower than their respective adult masses, the percentage of the adult weight was considerably smaller for the host than for the parasite (60.3–62.3 vs. 74.4–89.8%, Table 3). Other characteristics associated with chick maturity, such as feather growth and mobility skills, were more developed in parasite than in host nestlings. Cowbird fledglings were covered with feathers and had relatively good walking and flying abilities. In contrast, feather development of marshbird fledglings was incomplete and they left the nest with bare heads and good walking but less developed flying skills (M. E. Mermoz pers. obs.). Previous work with other hosts of *M. b. bonariensis* (the subspecies present in our study area) reported that parasite chicks reached asymptotic weights of 32–36 g (J. R. King 1973; Fraga 1978, 1985; Lichtenstein 1998) and did not grow after day 8 (J. R. King 1973; Fraga 1978, 1985). In our study, parasite chicks grew until days 10–11 and reached a weight of 35–48 g. Only cowbird chicks reared in other marsh-nesting Icterids like Yellow-winged (*Agelaius thilius*) and Scarlet-headed (*Amblyramphus holosericeus*) blackbirds reached similar asymptotic weights (Massoni and Reboreda 1998, Mermoz and Fernández 1999).

The reproductive success of cowbirds in marshbird nests was as high in multiply parasitized nests as in singly-parasitized ones. Proportion of chicks fledged per egg hatched or the proportion of chicks fledged per egg laid did not differ between singly and multiply parasitized nests.

Reproductive success of cowbirds considering nest failures.—Eight percent of cowbird eggs fledged taking into account nest failures. That rate is similar to those reported for other hosts, either smaller or larger, than nests in our study area. Reproductive success of cowbirds in smaller hosts varies between 5.8% in Rufous-collared Sparrow (*Zonotrichia capensis*; Fraga 1978) and 9.6%, in Yellow-winged Blackbird (V. Massoni and J. C. Reboreda unpubl. data). Values for larger hosts vary between 5.9–8.3% in Chalk-browed Mockingbird (*Mimus saturninus*; Fraga 1985, P. Sackman and J. C. Reboreda unpubl. data, F. Rabuffetti and J. C. Reboreda unpubl. data), 0–13% in Rufous-bellied Thrushes (*Turdus rufiventris*; P. Llambías and J. C. Reboreda unpubl. data, P. Sackman and J. C. Reboreda unpubl. data), and 20% in the Scarlet-headed Blackbird (Fernández and Mermoz 2000). However, if we consider only data gathered from nests found early in the nesting cycle as we did here, to avoid underestimating the effect of nest predation (Mayfield 1975), estimates of cowbird reproductive success are considerably reduced. Under those conditions, cowbird reproductive success decreased to 0% in Scarlet-headed Blackbird (G. J. Fernández and M. E. Mermoz unpubl. data), 2.7% in Yellow-winged Blackbird (Massoni and Reboreda 1998) and 4.8% in Chalk-browed Mockingbird (F. Rabuffetti and J. C. Reboreda unpubl. data).

Reproductive success of brood parasites is closely tied to host-nesting success. Some authors have used the Mayfield estimate (Mayfield 1975) of host-nesting success as a potential estimate of the reproductive success of their brood parasites (Mason 1986, Strausberger and Ashley 1997). Nesting success of marshbirds estimated with Mayfield method varies between 13 and 30%, depending on whether nests are built in uplands or flood-prone areas (Mermoz and Reboreda 1998). Differences between that potential (13–30%) and actual values of cowbird reproductive success (8%) in marshbird nests were the consequence of egg and chick losses not attributable to nest predation. Specifically, other causes of cowbirds' losses included marshbird ejection of parasitic eggs, egg punctures by other cowbirds, hatching failures due to bad synchronization between parasitism and host egg-laying, and chick mortality due to nestling–nestling competition. Because estimates of reproductive success of brood parasites based on Mayfield estimates of host-nesting success do not include such kind of losses, they would always result in an overestimation.

Larger versus smaller hosts: Which is the best alternative for a cowbird?—Mason (1986) proposed that larger hosts are preferred by cowbirds because they provide higher reproductive success to the parasite as a result of the lower depredation rates of their nests. That interpretation did not consider other confounding variables that could affect cowbird reproductive success. Nest predation rates may be more influenced by the structure and site of the nest than by the size of the host (Martin 1993, 1995). Closed nests have a lower depredation rate than open nests (Martin 1995), and most "good quality" hosts mentioned by Mason (1986) have closed nests. In addition, a low depredation rate does not ensure high reproductive success for the parasite, as closed nests may be more difficult for monitoring, and therefore could preclude a good synchronization of parasitism with host laying. In agreement with that interpretation, closed nests have a high proportion of parasitic events not synchronized with host egg-laying, and high rate of multiple parasitism on already deserted nests (Friedmann 1929, Kattan 1997).

Chalk-browed Mockingbird and Rufous-bellied Thrush provide examples of how host size per se does not explain the reproductive success of the parasite. Those species are similar in size to marshbirds (Chalk-browed Mockingbird: 75.3 g; F. Rabuffetti and J. C. Reboreda unpubl. data; Rufous-bellied Thrush: 79.6 g, P. Llambías, V. Ferretti and J. C. Reboreda, unpubl. data). However, as a result of the similar incubation period of the parasite and host eggs and the larger size of host chicks, cowbird chicks have a lower survival rate when reared with host chicks (Fraga 1985, Lichtenstein 1998). Thus, the reproductive success of cowbirds in those hosts depends more on the incubation period of host eggs and differences in size of chicks at hatching. Similarly, differences in size between parasite and host chicks could explain the higher survival of Brown-headed Cowbirds in nests of Common Grackles without host nestmates (Peer and Bollinger 1997). The reproductive success of cowbirds is not guaranteed even when differences in size are slight, as it happens with Brown-headed Cowbirds parasitizing Northern Cardinals (*Cardinals cardinalis*; Eckerle and Breitwisch 1997). Brown-headed Cowbird females can synchronize parasitism with that host (Scott and Lemon 1996, Strausberger and Ashley 1997). However, survivorship in mixed broods is lower for the parasite than for host chicks, and no cowbird young survive in broods with three or more cardinal chicks. Also, Brown-headed Cowbirds reared in mixed broods reach a lower asymptotic weight than those in broods that have only cowbirds (Scott and Lemon 1996).

To avoid those potential costs, cowbirds could follow simple rules such as only parasitize in hosts with smaller eggs (as occurs with captive Brown-headed Cowbirds which tend to parasitize nests with small eggs; A. P. King 1973). However, a negative aspect of that decision is that smaller hosts seldom can rear more than one parasite chick per nest (Fraga 1978, Wiley 1985, Massoni and Reboreda 1998). Selection of small hosts could generate costs for females laying in multiply parasitized nests. That small host effect could be important for cowbirds, because multiple parasitism is relatively common (Fraga 1978, 1985; Kattan 1997; Lyon 1997; Mermoz and Reboreda 1999). In addition, the majority of parasite eggs laid in multiply parasitized nests belong to different females (Lyon 1997, Mermoz and Reboreda 1999). In consequence, selection for larger hosts would be particularly important for second and subsequent laying cowbird females.

In conclusion, the reproductive success of a parasitic cowbird in a particular host species is more related to life-history traits of the host than to body size. In particular, life-history traits of marshbirds that influence reproductive success of cowbirds include open nests, low nest attentiveness during egg-laying (Mermoz 1996), a modal clutch size of 4–5 eggs, and longer incubation (Mermoz and Reboreda 1998). Those traits facilitate synchronization of parasitism with host egg-laying that would be the first requirement for successful parasitism. The longer incubation period of that host guarantees that parasite eggs laid during host egg-laying will hatch one or two days ahead of host chicks, giving them a head start. In addition, parasite chicks have a higher growth rate and reach the day of maximum growth one day earlier than host chicks. Given those factors, Shiny Cowbird females have a time window of 6–7 days to successfully parasitize Brown-and-yellow Marshbird nests.

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