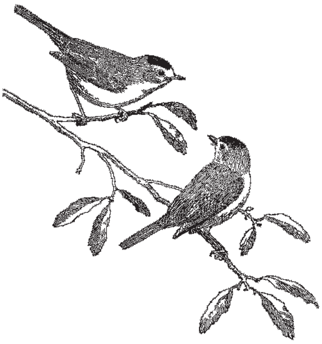

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REPRODUCTIVE SUCCESS AND NESTLING GROWTH OF THE BAYWING PARASITIZED BY SCREAMING AND SHINY COWBIRDS

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ABSTRACT.—We studied the breeding biology of the Baywing (*Agelaioides badius*), a shared host of Screaming (*Molothrus rufoaxillaris*) and Shiny (*M. bonariensis*) cowbirds. We monitored 193 nests from December 2002 to March 2007 in the Province of Buenos Aires, Argentina. Baywings used a wide variety of nesting sites, mainly old nests of furnarids. Their breeding season lasted from late November to February and was closely matched by that of Screaming Cowbirds. The breeding season for Shiny Cowbirds started in late September but overlapped that of Baywings. Frequency and intensity of Screaming Cowbird parasitism were 93% and 5 eggs per parasitized nest, while for Shiny Cowbirds they were 16% and 1.4 eggs. Host clutch size was 4.0 ± 0.1 eggs and did not vary with time of breeding. Weight at hatching and age of maximum growth were similar for host and Screaming Cowbird nestlings. Shiny Cowbird nestlings had higher weight at hatching and lower age of maximum growth than the other two species. Screaming and Shiny cowbird nestlings had higher growth rates and asymptotic weights than host nestlings. Sex-specific growth curves of Screaming Cowbirds indicated males had higher growth rate and asymptotic weight than females. Only 19% of the nests produced fledglings. Host egg survival, hatching success, and nestling survival were 0.92, 0.88, and 0.94, respectively. Excluding nest failures, hosts fledged 0.78 chicks per egg laid. Baywings were smaller than Screaming and Shiny cowbirds, and experienced a high frequency and intensity of parasitism. However, the effect of parasitism on host hatching success and chick survival was low and comparable to that observed in larger hosts. *Received 1 September 2009. Accepted 8 March 2010.*

Obligate brood parasites lay their eggs in nests of individuals of other species (hosts), which provide all parental care for eggs and young. Brood parasitism in birds has evolved independently at least seven times, one of them in the genus *Molothrus*, within the New World icterine blackbirds (Lanyon 1992, Davies 2000, Sorenson and Payne 2002). This genus encompasses five parasitic species that show great variation in number of hosts they use (Ortega 1998). The basal species of the clade, the Screaming Cowbird (*M. rufoaxillaris*), is an extremely specialist parasite with only three known host species: Baywing (*Agelaioides badius*) (Hudson 1874, Friedmann 1929), Chopi Blackbird (*Gnorimpsar chopi*) (Sick 1985, Fraga 1996, Mahler et al. 2009), and the Brown-and-yellow Marshbird (*Pseudoleistes virescens*) (Mermoz and Reboreda 1996, Mermoz and Fernández 2003). The Baywing is largely the primary host among these species with frequencies of parasitism often exceeding 80% of the

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nests (Mason 1980, Fraga 1998). In contrast, the Shiny Cowbird (*M. bonariensis*) is one of the most derived species (Lanyon 1992) and an extremely generalist parasite with more than 230 known hosts (Ortega 1998, Lowther and Post 1999). Shiny Cowbirds also parasitize Baywing nests but at a relatively low frequency (16–20% of the nests; Mason 1980, Fraga 1998). Screaming and Shiny cowbirds occasionally converge in Baywing nests resulting in an unusual three-sided host-parasite system (Fraga 1998).

There are several reports of Screaming and Shiny cowbird parasitism in nests of Baywings (Hudson 1874, Friedmann 1929, Mason 1980, Fraga 1998), but there are relatively few quantitative data on the breeding biology of this host and its interactions with both parasites. Previous studies indicate Baywings seldom build their nests, but exploit a wide variety of covered nesting sites, including old nests built by other species and holes in trees (Hoy and Ottow 1964, Fraga 1988). This nesting behavior has been proposed as an explanation for the late breeding of this species in Argentina (Friedmann 1929), where nesting attempts of Baywings typically occur from November to March (Fraga 1998). Baywings lay clutches of three to five eggs, but host eggs are often outnumbered by eggs of parasites (Hoy and Ottow 1964, Mason 1980, Fraga 1998, De Mársico and Reboreda 2008). The intensity of Screaming Cowbird parasitism in nests of Baywings is among the highest reported for a cowbird host (Mason 1986, Fraga 1998, Reboreda et al. 2003, Ellison et al. 2006, but see Kattan 1997, Trine 2000).

Multiple parasitism is likely to be costly for Baywings because Screaming and Shiny cowbirds often puncture host eggs during nest visits, which may reduce host clutch size even in unparasitized nests (Hoy and Ottow 1964, Fraga 1998, Massoni and Reboreda 2002, Astié and Reboreda 2006). Screaming and Shiny cowbirds, in addition, have a shorter incubation period than Baywings (Fraga 1998), which provides parasite nestlings a head start when parasitism is properly synchronized with host laying (Fraga 1998, Duré Ruiz et al. 2008, Fiorini et al. 2009). This increases the risk of host nestlings being outcompeted by larger cowbird nestlings (Payne and Payne 1998, Hoover 2003, Duré Ruiz et al. 2008).

Fraga (1986) estimated the effect of Screaming Cowbird parasitism on egg and nestling survival of Baywings. His estimates, however, may have overestimated the costs of parasitism because other sources of breeding failure such as nest predation were rare during his study (Fraga 1986). In addition, data of host and parasite nestling growth in Baywing nests are scarce. Fraga (1998) estimated growth parameters for Baywing and Screaming Cowbird nestlings, but his results did not account for non-independence among host nestlings from the same brood. Screaming and Shiny cowbirds also have a marked sexual size dimorphism (Mason 1987), but sex-specific growth curves of Screaming and Shiny cowbirds are lacking. Male and female parasite nestlings may have different growth patterns, and may differentially compete for food with host nestlings and experience different costs of competition (Weatherhead 1989, Tonra et al. 2008). Growth patterns of nestlings of both parasite species in Baywing nests have not been compared. Screaming and Shiny cowbird nestlings in nests of the Brown-and-yellow Marshbird, another shared host, did not differ in growth constant, asymptotic weight, and age of maximum growth (Mermoz and Fernández 2003); it remains unknown if the same is true for the primary host of the Screaming Cowbird.

Our objective was to use a large data set of 193 nests from five consecutive breeding seasons to examine: (1) quantitative data on several aspects of the nesting biology of the Baywing, (2) baseline estimates of host reproductive success and nest productivity, and (3) novel data on nestling growth in Baywing nests, providing the first report of sex-specific growth curves of Screaming and Shiny cowbirds.

METHODS

Study Area.—Our study was conducted from December 2002 to March 2007 at the private reserve El Destino near Magdalena (35° 08′ S, 57° 23′ W) in Buenos Aires Province, Argentina. The study site is a flat area of 320 ha within the Biosphere Reserve Parque Costero del Sur (MAB-UNESCO). Vegetation comprises woodland patches dominated by *Celtis tala* and *Scutia buxifolia* surrounded by grasslands and marshes (Cagnoni et al. 1996). Baywings are year-round residents in this area.

Potential nesting sites for Baywings within our study area included old nests of other species and cavities in trees. We placed 50 wood nest boxes between 2002 and 2003 to facilitate data collection. Boxes were 30 × 20 × 16 cm (height, width, and depth), and had a 58-mm diameter circular entrance hole and a removable roof to allow nest inspection. All boxes were attached to trees at the edge or in the interior of woodland patches at heights of 1.8–2.5 m. Nest boxes were separated by at least 50 m. Previous observations indicated that Baywings did not use empty boxes, and we partially filled them with artificial nests of wood sticks and plant fibers. One hundred additional nest boxes, similar yet smaller than those for Baywings (25 × 17 × 13 cm in height, width, and depth, entrance hole = 45 mm), were placed in the area (also attached to trees at a height of 1.2–1.8 m) starting in 2003 and were also available to Baywings. Most of these boxes had inactive House Wren (*Troglodytes aedon*) nests by the time Baywings started breeding. All nest boxes were cleaned prior to the beginning of each breeding season, and the large ones were re-filled with new artificial nests.

Data Collection.—We looked for Baywing nests throughout each breeding season (mid Nov–late Feb). Most nests were found along edges of woodland patches or in isolated trees at heights of 1.3–10 m. We limited our study to those nests at heights $<$ 5 m, which could be inspected using a portable ladder. Nest boxes were checked twice each week to detect any new nesting attempt. We recorded whether each nest was in a natural site or a nest box. We classified natural sites by identity of the nest builder when it was known, or the nest architecture.

Active nests (i.e., nests with a defending pair of Baywings) were checked every 1–3 days until they fledged chicks or failed. We assigned each nest an initiation date, corresponding to laying of the first Baywing egg. This date was ascertained directly when the nest was found before or during host laying, or indirectly through backdating from hatching dates (considering an incubation period of 13 days since the laying of the penultimate egg; Fraga 1998), when the nest was found during incubation. We examined the nest contents during each visit taking all eggs and nestlings from the nest. Individual eggs were assigned to the host or each parasite species on the basis of background color, spotting pattern, and shape (Friedmann 1929; Fraga 1983, 1986). Maximum width and length of host and parasite eggs were measured to the nearest 0.1 mm using a vernier caliper. Hatchlings of each species were identified using skin and bill coloration as diagnostic cues (Friedmann 1929; Fraga 1979, 1986). We assigned the laying date of Screaming and Shiny cowbird eggs either directly or through backdating from hatching dates (incubation period: 12 days for both species; Fraga 1998) whenever possible. We assumed that laying in half of the cases occurred the same day the egg was found, and in the other half the eggs were laid the previous day when nests were inspected every other day and the parasite egg appeared between two successive visits. All eggs and nestlings were marked with waterproof ink for identification. Nestlings were weighed daily or every other day to the nearest 0.1 or 0.5 g using Pesola spring scales of 10- and 60-g capacity, respectively. We visited nests at approximately the same hour of the day whenever possible to record weights at regular daily intervals. All nestlings were banded at 10–11 days of age with a unique combination of color leg bands and a numbered aluminum band.

We took a small amount (15–30 μL) of blood from a subsample of parasite nestlings at 8 to 11 days of age through brachial vein puncture with a 31G needle. Blood was collected with an 80 μL heparinized capillary tube, immediately mixed with 0.5 mL of lysis buffer (100mM Tris pH 8, 10 mM NaCl, 100mM EDTA, 2% SDS) and stored at room temperature until analysis. Individuals were identified as male or female genetically following Ellegren (1996). DNA was extracted from blood samples using a standard salting-out protocol (Miller et al. 1988) and diagnostic sex-linked alleles were amplified using the P8/P2 primer set (Griffiths et al. 1998). Amplifications were performed in 10 μL reaction volumes using 50–100 ng of DNA template, 0.5 μM forward and reverse primers, 0.25 μM dNTPs, 2.5 mM $MgCl_2$, and 0.25 u Taq-Polymerase. Annealing temperatures were set at 50° C and repeated for 30 cycles. PCR products were separated in 3% agarose gels stained with ethidium bromide. The presence of one band indicated males (ZZ), whereas two bands indicated females (ZW).

We stopped visiting nests once nestlings were banded and blood-sampled to avoid inducing premature fledging. However, we continued observing the nest daily or every other day from a distance of 5–10 m to identify the date of fledging. Host and parasite fledglings typically remain in the natal territory for at least 3 weeks (Fraga 1991), and we could confidently identify whether young fledged successfully or not.

We artificially parasitized 56 Baywing nests with fresh Shiny Cowbird eggs (n = 51) or newly hatched nestlings ($n = 5$) obtained from parasitized Chalk-browed Mockingbird (*Mimus saturninus*) and House Wren nests. Shiny Cowbird eggs laid in Chalk-browed Mockingbird and House Wren nests did not differ in width from those in Baywing nests (ANOVA: $F_{2,98} = 2.3$, $P = 0.10$; D. T. Tuero, unpubl. data). However, eggs from Chalk-browed Mockingbird nests were longer (ANOVA: $F_{2,98} = 8.7$, $P < 0.001$) and had greater volume (ANOVA: $F_{2,98} = 5.8$, $P < 0.004$) than those in nests of the other two host species (Tukey *post-hoc* test: $P < 0.05$; D. T. Tuero, unpubl. data). Artificially parasitized nests were checked as described above, and data on eggs and nestlings were collected in the same way as in naturally parasitized nests.

Data Analysis.—Frequency of parasitism was calculated as number of nests with parasite eggs or chicks over total number of nests found and intensity of parasitism as number of parasitic eggs per parasitized nest. Overall intensity of parasitism was estimated using a subset of nests found before or during host laying to avoid underestimating the number of cowbird eggs that were laid asynchronously and later removed from the nest cup by Baywings (Hoy and Ottow 1964, Fraga 1998, De Mársico and Reboreda 2008). We compared the intensity of parasitism among years for each cowbird species using the Kruskal-Wallis test. Data from 2002 were excluded for the analysis corresponding to Shiny Cowbirds because only one of the parasitized nests was found early in the nesting cycle. We used the Kolmogorov-Smirnov test for two independent samples (Siegel and Castellan 1989) to compare the frequency distribution of Baywing nesting attempts and frequency of parasitic events of Screaming Cowbirds during the breeding season (divided into weekly intervals). We estimated the extent of overlap between the breeding seasons of Baywings and Shiny Cowbirds using laying dates of parasite eggs in nests of Baywings ($n = 23$) and of two primary hosts in the study area, Chalk-browed Mockingbird ($n = 335$ eggs) and House Wrens ($n = 176$ eggs). Data on laying dates for these species were collected during 2003, 2006, and 2007 (V. D. Fiorini and D. T. Tuero, unpubl. data).

We estimated clutch size of Baywings using a subsample of 32 nests found before laying, visited daily during laying, and which survived at least until laying ended. We used these criteria to avoid missing egg losses because hosts often remove punctured eggs (Massoni and Reboreda 2002, Astié and Reboreda 2006). We estimated total clutch size from nests parasitized after the host began to lay that survived until hatching. We used two estimates: initial clutch size, defined as the number of host and parasite eggs that remained in the nest by the end of host laying, and final clutch size, defined as the number of host and parasite eggs by the end of incubation. Host incubation period was estimated as the number of days elapsed since laying of the last host egg until hatching of the last host chick (Nice 1954). The incubation period of Screaming and Shiny cowbird eggs was estimated as the number of days elapsed since the start of incubation until the day of hatching of the parasite chick (Briskie and Sealy 1990). We calculated the number of parasite chicks at hatching from nests that were parasitized during host laying that survived until the nestling stage.

We calculated egg volume (cm^3) for host, and Screaming and Shiny cowbirds as $0.515\ l\ w^2$, where l and w are egg length and width (in cm); 0.515 is a species specific constant (Nolan and Thompson 1978). Measures of Baywing eggs were averaged over host clutch for statistical analyses. The sample of Shiny Cowbird eggs included those in Baywing nests ($n = 11$) as well as those in nests of Chalk-browed Mockingbird ($n = 61$) and House Wrens ($n = 29$) from the same study area (D. T. Tuero, unpubl. data).

Growth curves were built using data from nestlings that survived at least 10 days and were weighed daily or every other day. Nestlings that were depredated or died in the nest were excluded from the analyses. We used non-linear regressions to adjust daily weights of each nestling following the logistic function for weight: $W = A/(1 + \exp(-K^*(T - T_0)))$, where A is the asymptotic weight, K is the growth constant and T_0 is the age of maximum growth (Ricklefs 1967). Regressions used a non-linear model and least-squares estimation minimized with the Quasi-Newton option in SYSTAT 9.0 (SPSS, Chicago, IL, USA). Parameter estimates and weight at hatching were obtained for each individual nestling from the adjusted curves. Maximum growth rate ($g_{\max}$) was calculated using the expression: $g_{\max} = K * A/4$ (Richner 1991). Host nestlings from the same brood were not independent, and growth parameter estimates of individual nestlings from the same nest were averaged to generate a growth curve for each brood. We used data from 69

Baywing nestlings in 25 nests (5 broods with 1, 4 with 2, 9 with 3, 6 with 4, and 1 with 5 nestlings) to build growth curves. Five broods were unparasitized, 12 were parasitized by Screaming Cowbirds only (9 with 1, and 3 with 2 parasitic chicks), three were parasitized by Shiny Cowbirds only (each with a single parasitic chick), and five had one chick of each parasite species. Mean (± SE) brood size was 4.0 ± 0.3 chicks per brood, including host and parasite chicks. We obtained growth data for 18 Screaming Cowbird nestlings from 13 broods (10 with 1, 3 with 2, and 1 with 5 Screaming Cowbird chicks). These broods had, on average, 2.9 ± 0.4 host chicks (range = 0–4), and three also had one Shiny Cowbird chick. Mean brood size was 4.7 ± 0.4 chicks per brood (range = 1–8). Data from Screaming Cowbird chicks from the same brood were averaged. We also obtained growth data for 10 Shiny Cowbird nestlings from 10 different broods. These broods had, on average, 3.4 ± 0.7 host chicks (range = 2–5), and four were also parasitized by Screaming Cowbirds (3 with 1, and 1 with 2 Screaming Cowbird chicks). Mean brood size was 4.9 ± 0.3 (range = 3–6). We ascertained the gender of 10 Screaming (6 females and 4 males) and seven Shiny (5 females and 2 males) cowbird nestlings. We used this subsample to obtain sex-specific growth parameters of each parasite species, but comparisons of growth parameters among Baywing, and Screaming and Shiny cowbird nestlings used the full data set.

The date of fledging was established directly in a few cases where we observed the fledglings leaving the nest. Chicks in most nests fledged between two successive visits, and we assumed that in half of the cases they did it the same day we observed them out of the nest, and in the other half, that they fledged 1 day earlier.

We estimated nest survival as the proportion of nests that produced at least one host or parasite fledgling. Host and parasite reproductive success was estimated using three parameters: (1) egg survival, calculated as the proportion of host or parasite eggs that survived until the end of incubation in nests that survived until the nestling stage; (2) hatching success, calculated as the proportion of host or parasite eggs that hatched from those that survived; and (3) chick survival, calculated as the proportion of host or parasite chicks that fledged from those that hatched in nests that survived the entire nesting cycle. Survival of parasite eggs was estimated from nests found before or during host laying that survived until hatching. We considered as parasitized those clutches that received cowbird eggs during laying or incubation to analyze the effect of parasitism on egg survival and hatching success. We considered as parasitized those nests with parasite chicks to analyze the effect of parasitism on nestling survival. Counts included parasitic eggs or chicks artificially placed in Baywing nests. Overall host productivity in successful nests was estimated as the number of host chicks fledged divided by host clutch size. Productivity of Screaming and Shiny cowbirds was estimated as the number of parasite chicks fledged divided by the total number of parasite eggs laid in nests that were found before or during host laying and survived until fledging, including those that were laid before the beginning of host laying. Only naturally parasitized nests were considered to estimate productivity.

Statistical tests followed GenStat Discovery Edition 3 (GenStat 2007) and results are presented as $\bar{x}$ ± SE. All tests are two tailed and significance was accepted at $P < 0.05$.

RESULTS

Nest Site Use.—We found 193 Baywing nests. Eighty-nine (46%) were in old, closed nests made of sticks built by species of the Furnariidae (e.g., *Anumbius annumbi*, *Phacellodomus* spp., *Synallaxis* spp.), 40 (21%) in large nest boxes, 16 (8%) in old Rufous Hornero (*Furnarius rufus*) nests, 16 (8%) in old Great Kiskadee (*Pitangus sulphuratus*) nests, 14 (7%) in cavities in trees, 10 (5%) in small nest boxes previously used by House Wrens, five (3%) were open cup-nests built by Baywings, and three (2%) were in unusual nesting sites (an old Chalk-browed Mockingbird nest, a broken tree branch, and an old nest of the paper wasp [*Polybia scutellaris*]). There were no differences among years in frequency of nests found in natural or artificial nesting sites (χ^2_4 = 6.6, P = 0.16).

Considering nests with known clutch initiation date (n = 116), the median date of clutch initiation differed among nest types, indicating that use of nest sites varied during the breeding season (Kruskal-Wallis test: H_5 = 13.9, P = 0.017, n = 12 Great Kiskadee nests, 27 nest boxes, 9 natural cavities, 53 old furnarid nests made of sticks, 7 Rufous Hornero nests, and 8 nests of other types). *Post-hoc* comparisons indicated that old Great Kiskadee nests were

TABLE 1. Clutch and brood composition at Baywing nests in the Reserve El Destino (2002–2006). Bw = unparasitized nests, Bw + Sc = nests parasitized by Screaming Cowbirds only, Bw + Sh = nests parasitized by Shiny Cowbirds only, and Bw + Sc + Sh = nests parasitized by both species. Only naturally parasitized nests with known clutch size were considered for egg and chick counts. Values represent number of eggs or nestlings of each species as $\bar{x} \pm$ SE and the corresponding sample sizes (number of nests).

	Bw	Bw + Sc	Bw + Sh	Bw + Sc + Sh
Eggs laid				
Bw	4.1 ± 0.3 (12)	3.7 ± 0.1 (142)	0 (1)	3.8 ± 0.2 (21)
Sc		4.9 ± 0.3 (142)		4.6 ± 0.5 (21)
Sh			1.0 (1)	1.2 ± 0.1 (21)
Eggs incubated				
Bw	4.6 ± 0.2 (7)	3.5 ± 0.1 (80)		3.6 ± 0.3 (11)
Sc		2.4 ± 0.2 (49)		1.8 ± 0.4 (21)
Sh				0.6 ± 0.2 (21)
Young at hatch				
Bw	4.4 ± 0.2 (5)	3.2 ± 0.2 (49)		2.8 ± 0.5 (6)
Sc		1.0 ± 0.1 (49)		1.0 ± 0.4 (6)
Sh				0.7 ± 0.3 (6)
Young fledged				
Bw	4.7 ± 0.3 (3)	2.9 ± 0.2 (28)		2.7 ± 0.9 (3)
Sc		1.2 ± 0.2 (28)		0.3 ± 0.3 (3)
Sh				0.3 ± 0.3 (3)

occupied significantly later than small nest boxes ($P < 0.05$). Baywings used non-active nests in most cases, but in two cases we observed usurpation of active nests (1 nest of Firewood-gatherer [*Anumbius annumbi*] and 1 nest box occupied by House Wrens). Only five nests in our sample were built by Baywings; all were open cup nests with a lax structure of grasses and a 'roof' provided by surrounding foliage.

Nest reuse occurred both within and among breeding seasons. We observed nest reuse in 51/51 cases within breeding seasons when the nest failed due to clutch ejection by hosts in response to multiple parasitism, but we only observed nest reuse in 1/46 cases when the nest failed due to predation. We observed nest reuse in 11 cases among breeding seasons (nest sites that were used in 2 or more consecutive breeding seasons), although we could not establish if the same breeding pair was involved. Reuse occurred in five of these cases in nests that had been successful in the previous breeding season whereas in the others, the nest failed in the previous breeding season.

Incidence of Cowbird Parasitism.—Ninety-four percent of the nests (181/193) were parasitized, 155 by Screaming Cowbirds only, one by Shiny Cowbirds only, and 25 by Screaming and Shiny cowbirds. Frequency of parasitism did not differ among years (Screaming Cowbird: $\chi^2_4 = 0.38$, $P = 0.98$; Shiny Cowbird: $\chi^2_4 = 7.19$, $P = 0.13$). There were no differences in frequency of parasitism combining data from all years between natural nests ($n = 153$) and nest boxes ($n = 40$) for Screaming ($\chi^2_1 = 1.44$, $P = 0.76$) and Shiny ($\chi^2_1 = 0.52$, $P = 0.47$) cowbirds.

Average intensity of parasitism was 5.0 ± 0.3 eggs for Screaming Cowbirds ($n = 140$ nests) and 1.4 ± 0.1 eggs for Shiny Cowbirds ($n = 19$ nests; Table 1). We did not detect differences among years in intensity of parasitism by Screaming (Kruskal-Wallis test: $H_4 = 5.9$, $P = 0.21$) or Shiny (Kruskal-Wallis test: $H_4 = 3.3$, $P = 0.34$) cowbirds; the later result should be interpreted cautiously given the small sample size. Pooling data from all years indicated the intensity of Screaming Cowbird parasitism did not differ between natural nests ($n = 98$) and nest boxes ($n = 42$; Mann-Whitney *U*-test: $Z = -0.31$, $P = 0.76$). Similarly, the intensity of Shiny Cowbird parasitism did not differ between natural nests ($n = 11$) and nest boxes ($n = 8$; Mann-Whitney *U*-test: $Z = -0.61$, $P = 0.54$).

Screaming Cowbirds parasitized Baywing nests either before, during, and after host laying. On average, a parasitized nest received 1.3 ± 0.3

Screaming Cowbird eggs before host laying, 1.2 ± 0.2 during host laying, 1.1 ± 0.2 eggs during the incubation stage, and 0.4 ± 0.1 eggs after nestlings had hatched (n = 39 parasitized nests found before or during host laying that survived until the nestling stage). Eggs laid before host laying were removed from the nest by Baywings before they started to lay. Eggs laid after the host began laying were accepted and incubated, but only those laid during host laying typically hatched. Shiny Cowbirds also parasitized Baywing nests either before or during host laying. Nests received, on average, 0.8 ± 0.6 and 0.5 ± 0.6 Shiny Cowbird eggs before and during host laying, respectively (n = 18 parasitized nests).

Breeding Seasons.—The earliest and latest clutch initiation dates for Baywings were 27 November and 7 February, respectively. The first Screaming Cowbird parasitism was recorded on 26 November (in a nest at pre-laying stage) and the latest on 11 February (Fig. 1). The frequency of Screaming Cowbird parasitism matched the frequency distribution of Baywing nesting attempts in all breeding seasons (Kolmogorov-Smirnov test: $P > 0.10$ for all comparisons; Fig. 2).

The earliest Shiny Cowbird parasitism event was recorded on 29 September in a Chalk-browed Mockingbird nest and the latest, on 23 January in a Baywing nest. Even though Shiny Cowbirds started laying earlier than Baywings, they overlapped considerably in breeding seasons (Fig. 3). Shiny Cowbird parasitism mostly (44%) occurred in December and January. Nearly 90% of all Baywing clutches were initiated during the same interval. Only 10% of Baywing nesting attempts began too late to be parasitized by Shiny Cowbirds.

Clutch Size, Incubation, and Nestling Periods.—Baywings laid, on average, 4.0 ± 0.1 eggs per nest (range = 2–5, mode = 4, n = 32 nests), and host clutch size did not vary with clutch initiation date (Spearman rank correlation: $r = 0.22$, $Z = 1.23$, $P = 0.23$, n = 32 nests). Initial clutch size in nests parasitized solely by Screaming Cowbirds was 5.3 ± 0.2 eggs, and final clutch size was 6.4 ± 0.2 eggs (n = 49 nests). Only two nests naturally parasitized by Shiny Cowbirds survived until hatching, and they were also parasitized by Screaming Cowbirds. Initial clutch size in these nests was 7.0 ± 1.0 eggs, and final clutch size was 8.0 ± 1.0 eggs (Table 1).

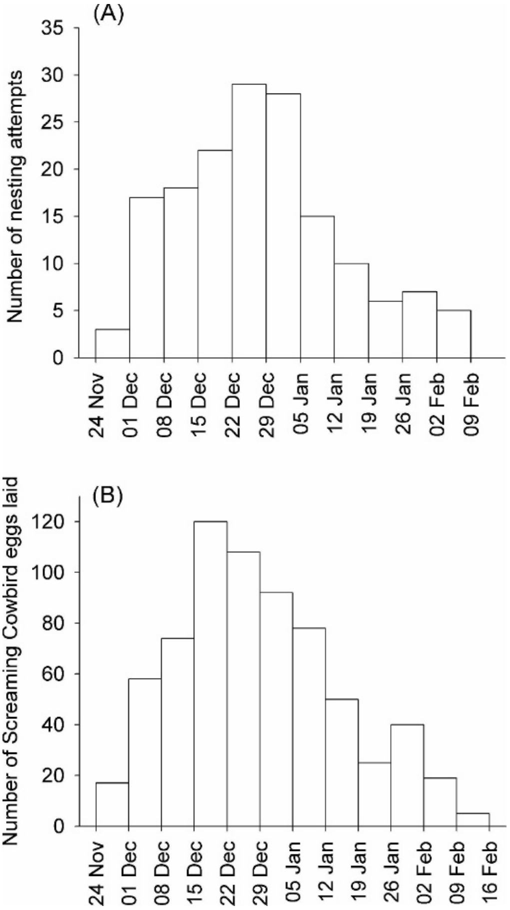

FIG. 1. Breeding season of (A) Baywings and (B) Screaming Cowbirds in Reserve El Destino between 2002 and 2006. Bars represent the number of nesting attempts initiated (n = 160) or the total number of Screaming Cowbird eggs laid (n = 686) during the breeding season divided into weekly intervals.

Host incubation period was 13.0 ± 0.1 days with a range of 12–14 days and a mode of 13 (n = 42 clutches). Screaming and Shiny cowbirds had an incubation period of 12.0 ± 0.1 days (range = 11–13 days, n = 40 and 14 eggs of Screaming and Shiny cowbirds, respectively). Average number of Baywing chicks at hatching was 3.2 ± 0.1 (range = 0–5, n = 60). Nests parasitized by Screaming Cowbirds only, had 1.3 ± 0.2 parasite chicks at hatching (n = 37). Nests naturally parasitized by Shiny Cowbirds (n = 2) had one Shiny Cowbird and one Screaming Cowbird chick each. Combining host and parasitic chicks, Baywings reared, on average, 4.2 ± 0.2 chicks per nest (range = 1–8, n = 60 nests; Table 1). The mean nestling period was 14 days (range = 12–16; n = 20 nests).

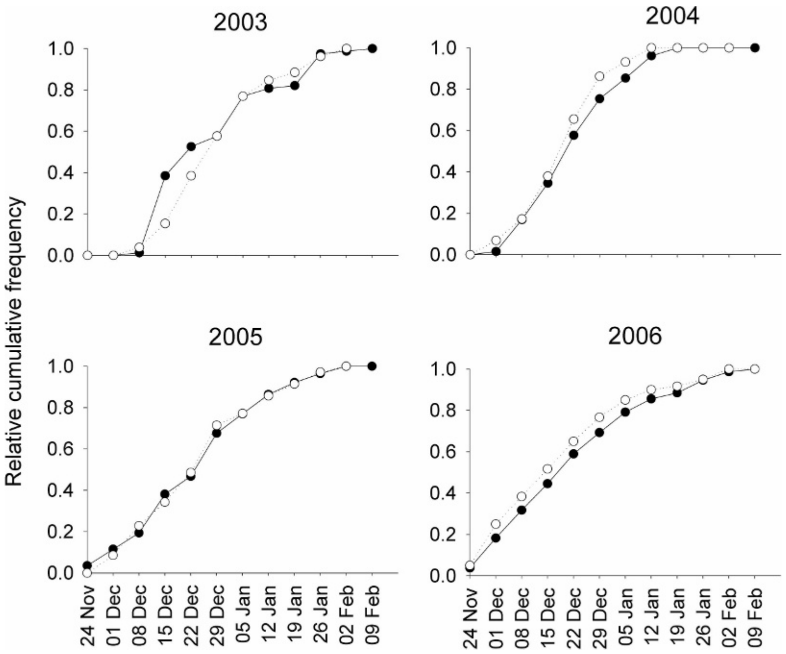

FIG. 2. Baywing and Screaming Cowbird breeding seasons. Curves represent the cumulative relative frequency of Baywing nesting attempts (white) and parasite eggs laid (black) along the breeding season. Sample sizes are: 2003 = 26 nests and 78 eggs, 2004 = 29 nests and 130 eggs, 2005 = 35 nests and 139 eggs, and 2006 = 60 nests and 312 eggs. Year 2002 was excluded due to small sample sizes.

Egg Size and Nestling Growth.—Egg size and volume differed between host and parasites (Table 2). Shiny Cowbird eggs were wider than those of Baywings and Screaming Cowbirds (ANOVA: $F_{2,552} = 76.8$, $P < 0.001$) and had greater volume (ANOVA: $F_{2,552} = 52.2$, $P < 0.001$; Tukey *post-hoc* test: $P < 0.05$). Egg length did not differ among species (ANOVA: $F_{2,552} =$

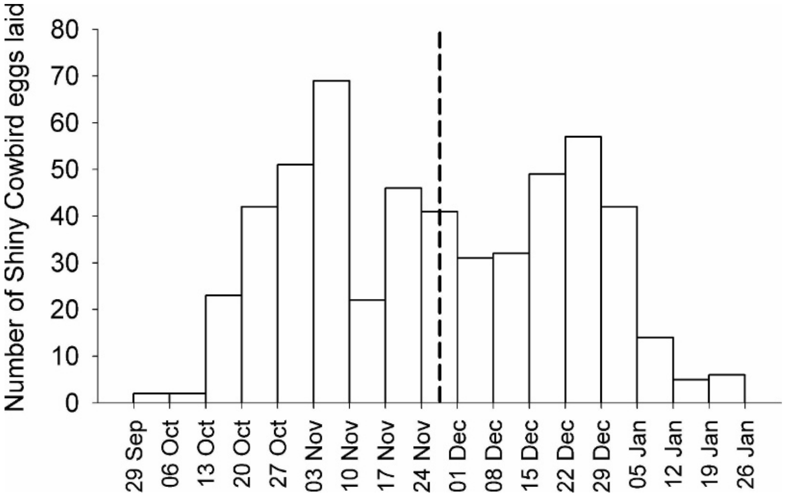

FIG. 3. Seasonal distribution of Shiny Cowbird parasitism in Reserve El Destino during the 2002–2006 breeding seasons. Bars represent the number of parasite eggs laid within each weekly interval in nests of Baywings, Chalk-browed Mockingbirds, and House Wrens ($n = 534$). The dashed line indicates clutch initiation date of the earliest Baywing nesting attempt during this study (27 Nov).

TABLE 2. Length, width, and volume ($\bar{x}$ ± SE) of Baywing, and Screaming and Shiny cowbird eggs. Values corresponding to host eggs represent average egg size and volume of all eggs in 98 clutches. Some Baywing (Bw) nests in our sample were artificially parasitized with Shiny Cowbird eggs collected from Chalk-browed Mockingbird (CbM) and House Wren (HW) nests, and we present data on size and volume of Shiny Cowbird eggs in the three host species. Data from Chalk-browed Mockingbird and House Wren nests were provided by V. D. Fiorini and D. T. Tuero (unpubl. data).

Species	Host	*n*	Length (cm)	Width (cm)	Volume (cm^3)
Baywing		346	2.36 ± 0.01	1.78 ± 0.00	3.87 ± 0.02
Screaming Cowbird	Bw	357	2.37 ± 0.01	1.79 ± 0.00	3.94 ± 0.02
Shiny Cowbird	Bw	11	2.30 ± 0.03	1.86 ± 0.00	4.11 ± 0.16
	CbM	61	2.43 ± 0.02	1.89 ± 0.01	4.49 ± 0.05
	HW	29	2.34 ± 0.00	1.86 ± 0.00	4.20 ± 0.10

1.6, $P = 0.20$). Differences in egg volume were not attributable to larger Shiny Cowbird eggs coming from Chalk-browed Mockingbird nests because the results did not change when these eggs were removed from the data set (ANOVA: $F_{2,491} = 8.9$, $P < 0.001$).

We found differences in growth parameters between host and parasite chicks, as well as between Screaming and Shiny cowbird chicks (Table 3, Fig. 4). Overall, both Screaming and Shiny cowbirds had higher growth constant (ANOVA: $F_{2,45} = 6.5$, $P = 0.003$), maximum instantaneous growth rate (ANOVA: $F_{2,45} = 45.8$, $P < 0.001$), and asymptotic weight ($F_{2,45} = 37.3$, $P < 0.001$) than Baywing nestlings (Tukey *post-hoc* test, $P < 0.05$). Shiny Cowbirds had a higher weight at hatching (ANOVA: $F_{2,45} = 6.7$, $P = 0.003$) and lower age of maximum growth ($F_{2,45} = 8.8$, $P < 0.001$; Tukey *post-hoc* test, $P < 0.001$) than both Screaming Cowbird and host nestlings.

Sex-specific growth curves for Screaming and Shiny cowbirds varied (Table 3, Fig. 4). Male Screaming Cowbird nestlings ($n = 4$) did not differ from females ($n = 6$) in weight at hatching (*t*-test: $t = -1.15$, df = 8, $P = 0.28$), growth constant (*t*-test: $t = -0.09$, df = 8, $P = 0.93$), and age of maximum growth (*t*-test: $t = -0.46$, df = 8, $P = 0.66$; Table 3). However, male nestlings had a higher maximum instantaneous growth rate (*t*-test: $t = -3.84$, df = 8, $P = 0.005$) and reached a higher asymptotic weight than females (*t*-test: $t = -5.53$, df = 8, $P < 0.001$; Table 3). Sample sizes for Shiny Cowbirds were too low for statistical analyses, but growth curves suggest that differences in males and females similar to those of Screaming Cowbirds might occur in this species (Table 3, Fig. 4).

Baywing Reproductive Success.—Only 35 (19%) of all nests fledged chicks and all but one produced host fledglings. The exception was a parasitized nest where all host eggs failed to hatch and only two Screaming Cowbird chicks fledged. The number of Baywing chicks fledged per nest was 3.0 ± 0.2 ($n = 34$ nests, range = 1–5). Overall, host productivity in nests that survived the entire nesting cycle was 0.78 fledglings per egg laid ($n = 25$ nests with known clutch size). Losses were mostly due to egg punctures by Screaming and Shiny cowbirds and hatching failures. On average, survival of host eggs was 0.92 ($n = 54$ nests). Egg survival was higher in

TABLE 3. Growth parameters ($\bar{x}$ ± SE) of Baywing, and Screaming and Shiny cowbird nestlings obtained from adjusted growth curves. Data for host nestlings were averaged over each brood. Data for parasite nestlings were based on individual nestlings of each gender. Sample sizes = 69 Baywings in 25 broods, 6 female and 4 male Screaming Cowbirds, and 5 female and 2 male Shiny Cowbirds.

		Screaming		Shiny	
Parameter	Baywing	Male	Female	Male	Female
Hatch weight, g	3.6 ± 0.1	3.8 ± 0.4	3.3 ± 0.2	4.9 ± 0.3	4.4 ± 0.2
Growth constant/day	0.47 ± 0.01	0.50 ± 0.02	0.49 ± 0.02	0.51 ± 0.03	0.51 ± 0.03
Maximum growth rate, g/day	4.25 ± 0.07	6.37 ± 0.14	5.23 ± 0.22	6.10 ± 0.14	5.31 ± 0.32
Age of maximum growth, days	5.8 ± 0.1	6.2 ± 0.2	6.0 ± 0.2	5.3 ± 0.2	5.2 ± 0.1
Asymptotic weight, g	36.7 ± 0.4	51.6 ± 1.9	42.5 ± 0.6	48.3 ± 1.8	41.4 ± 1.0

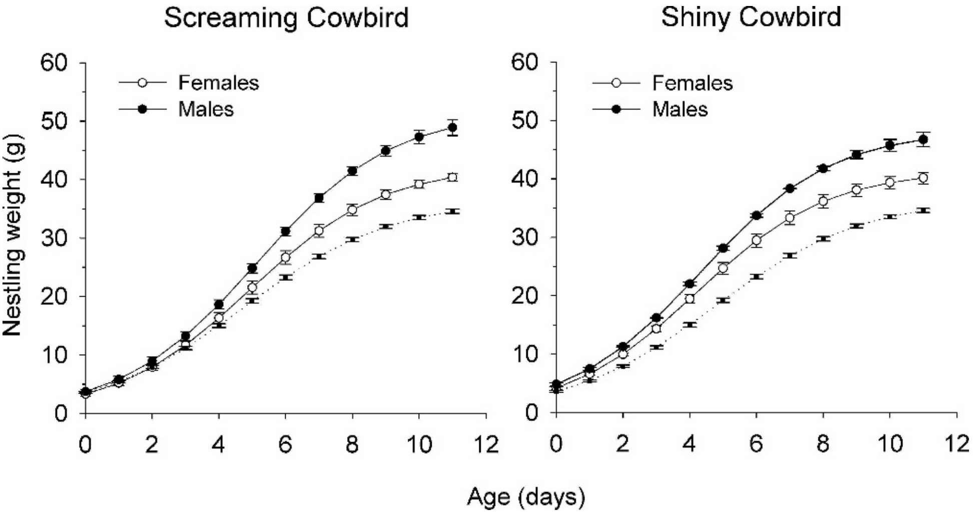

FIG. 4. Growth curves of Screaming and Shiny cowbird nestlings reared by Baywings. Points correspond to daily weights ($\bar{x}$ ± SE) as a function of age for male (black circles) and female (white circles) nestlings of each species, estimated from the corresponding adjusted logistic functions. The dotted line in each graph represents the growth curve of the host with adjusted daily weights ($\bar{x}$ ± SE) averaged across all host nestlings within the same brood (n = 25 broods with 1–5 host nestlings) Sample sizes were four and six female Screaming Cowbirds, and two and five female Shiny Cowbirds, respectively.

nests that were not parasitized during the egg stage than in parasitized nests (Mann-Whitney U-test: $Z = -2.03$, $P = 0.042$, $n = 10$ unparasitized and 44 parasitized nests). On average, hatching success was 0.88 ($n = 54$ nests). Hatching success did not differ between parasitized and unparasitized nests (Mann-Whitney U-test: $Z = 0.00$, $P > 0.99$). There were no statistical differences in survival of Baywing chicks between parasitized ($n = 20$) and unparasitized nests ($n = 8$; Mann-Whitney U-test: $Z = -1.52$, $P = 0.13$). Nestling survival was, on average, 0.94 ($n = 28$ nests). Brood reduction occurred in six parasitized nests where one ($n = 5$) or two ($n = 1$) host nestlings died due to starvation or nest crowding.

Screaming Cowbird Reproductive Success.—About 89% (615/694) of the Screaming Cowbird eggs in Baywing nests failed as a result of nest predation or desertion ($n = 146$ naturally parasitized nests found before or during host laying). Survival of Screaming Cowbird eggs in nests that survived until hatching was 0.93 ($n = 48$ nests). Hatching success was 0.62 ($n = 47$ nests), and hatching failures were mostly due to parasitic females laying eggs too late for successful incubation. Hatching success of Screaming Cowbird eggs laid during host laying was 0.92 ($n = 40$ nests). Overall nestling survival was 0.77 ($n = 20$ nests). Mortality of parasitic chicks occurred at six nests as a result of late hatching ($n = 4$ nests) and partial nest predation ($n = 2$ nests). Screaming Cowbird productivity was 0.14 fledglings per egg laid ($n = 20$ nests).

Shiny Cowbird Reproductive Success.—Nearly 91% of Shiny Cowbird eggs naturally laid (30/33, $n = 26$ nests) and 82% of those artificially placed in Baywing nests (40/49, $n = 49$ nests) failed due to nest predation or desertion. Combining natural and artificial parasitism, Shiny Cowbird egg survival was 0.95 ($n = 19$ nests) and hatching success was 0.94 ($n = 18$ nests). Nestling survival was 0.91 ($n = 11$ nests) and only one Shiny Cowbird chick died, presumably due to partial nest predation. Sample size was too small to estimate productivity. Only one of three Shiny Cowbird eggs naturally laid produced a fledgling ($n = 3$ nests). The others were laid before host laying and therefore rejected by hosts.

DISCUSSION

Nest Site Use.—Baywings used a wide variety of nesting sites, but the more commonly used were old, closed nests built by several furnarid species. This observation contrasts with a previous study in a nearby area, which reported that nest boxes and secondary cavities were preferred nesting sites (Fraga 1988, 1998). These differences, however, could be explained by local variation in abundance of suitable nesting sites at the time Baywings start to breed (Hoy and Ottow 1964). Some authors have observed Baywings fighting with owners to occupy their nests (Friedmann 1929, Jaramillo and Burke 1999), but we seldom observed nest piracy, suggesting that nesting sites were not limiting during our study (see also Hoy and Ottow 1964, Fraga 1988). It is not clear why in most cases Baywings use old nests of other species instead of building their own nests, but it is possible this behavior allows breeding pairs to save time and energy (Hauber 2002, Wiebe et al. 2007). Additionally, closed nests might offer better protection against predators than open cup nests (Martin and Li 1992, Auer et al. 2007).

Breeding Seasons.—Our results indicate the breeding season of Baywings typically starts in early December and may extend to early March, considering nestling and postfledgling stages of late nesting attempts. Fraga (1998), in the Province of Buenos Aires, observed laying as early as October, but we did not observe any sign of nesting activity before late November. The breeding season of Screaming Cowbirds overlapped extensively that of Baywings. However, female Screaming Cowbirds started parasitism in advance of host laying indicating that nest building and defense activities by the host may stimulate laying behavior of the parasite. It is also possible the parasite's breeding season began earlier if Screaming Cowbirds in our study area also parasitize Brown-and-yellow Marshbirds, which breed from October to December (Mermoz and Reboreda 1996, Mermoz and Fernández 2003). Shiny Cowbirds began to breed much earlier in our study area than Baywings, parasitizing other hosts such as Chalk-browed Mockingbirds and House Wrens starting in late September (Fiorini and Reboreda 2006, Tuero et al. 2007).

Friedmann (1929) suggested differences in time of breeding would be the cause of the low frequency of Shiny Cowbird parasitism in nests of Baywings. However, our data indicate only 10% of the nesting attempts of Baywings began after the Shiny Cowbird breeding season ended. Breeding seasons of Baywings and Shiny Cowbirds overlapped more extensively than previously estimated (90 vs. 65–80%; Fraga 1998), and female Shiny Cowbirds would have broad opportunities for parasitizing this host. An alternative explanation for the low frequency of Shiny Cowbird parasitism of this host is that the parasite would have low reproductive success with Baywings (Fraga 1998), but this hypothesis remains untested.

Incidence of Cowbird Parasitism.—Nearly all Baywing nests were parasitized by Screaming Cowbirds, and regularly more than once (Hoy and Ottow 1964, Mason 1980, Fraga 1998). These high levels of parasitism did not seem to be an artifact of nest boxes (Kattan 1997), as the frequency and intensity of parasitism by Screaming and Shiny cowbirds did not differ between nest boxes and natural sites. Our results did not appear to be influenced by the shortage of host nests in a particular year, as frequency and intensity of parasitism were consistent among consecutive breeding seasons. Females of other brood parasites parasitize nests within nearly exclusive breeding areas, which may allow them to reduce the costs associated with intraspecific competition (Langmore et al. 2007). Several observational and genetic studies indicate that cowbirds, however, lack territorial behavior (Kattan 1997, Hahn et al. 1999, Mermoz and Reboreda 1999, McLaren et al. 2003, Strausberger and Ashley 2005, Ellison et al. 2006). Thus, multiple parasitism can arise as a consequence of a limitation of suitable nests, high fecundity rates of female cowbirds, or high population density of the parasite relative to the number of host breeding pairs (Martínez et al. 1998, Strausberger 1998, McLaren et al. 2003, Ellison et al. 2006). Multiple parasitism by Screaming Cowbirds, which are constrained to locate and parasitize near a single host species, could also be the result of different females parasitizing the same nest and individual females parasitizing a nest more than once as a result of low nest availability.

Baywing Reproductive Success.—Cowbird parasitism reduces host fitness in several ways (Massoni and Reboreda 1998, Lorenzana and Sealy 1999, Zanette et al. 2005, Astié and Reboreda 2006). We found parasitized nests lost more host eggs than unparasitized nests, but hatching success and nestling survival did not differ between parasitized and unparasitized nests. Our results indicate survival of Baywing eggs and nestlings was higher than in previous reports (Fraga 1986, 1998), possibly because, during our study, most host egg and nestlings were lost due to nest desertion and predation rather than to egg punctures or competition with parasite nestlings.

We rarely observed brood reduction in parasitized nests and nestling mortality due to parasitic mites, as reported previously (Fraga 1986). Regular cleaning of nest boxes may have contributed to decrease the incidence of ectoparasite infestations in our study population. However, given that most nests occurred in natural sites, we have confidence that box cleaning had little influence on our estimates of nestling survival. Costs of parasitism for Baywings are similar to those observed in other host species of the Shiny Cowbird that are larger than the parasite (Mermoz and Reboreda 2003, Astié and Reboreda 2006). Productivity is often lowered in hosts larger than the parasite by puncture or removal of host eggs by female cowbirds rather than by nestling mortality, as host young are seldom outcompeted by parasitic nestlings (Eckerle and Breitwisch 1997, Lichtenstein 1998, Lorenzana and Sealy 1999, Astié and Reboreda 2006), unless a marked hatching asynchrony exists (Soler et al. 1996, Duré Ruiz et al. 2008). Baywings are smaller than Screaming and Shiny cowbirds; thus, it is expected that host nestlings compete strongly for food with the parasite young. However, Baywings are cooperative breeders (Fraga 1991) and it is possible that helpers at the nest contribute to ameliorate the costs of parasitism by increasing nest provisioning rates (Fraga 1991).

Nestling Growth.—We did not find differences in growth patterns between Screaming and Shiny cowbird nestlings in nests of Baywings. Overall, Screaming and Shiny cowbird nestlings did not differ in asymptotic weight, growth constant, and maximum instantaneous growth rate. This is consistent with similar comparisons between parasite nestlings of both species reared in Brown-and-yellow Marshbird nests (Mermoz and Fernández 2003). However, parasite nestlings differed in weight at hatching and age of maximum growth, which could be the result of differences in egg size between both species (Nolan and Thompson 1978). A higher weight at hatching combined with a shorter incubation period could provide Shiny Cowbird nestlings a head start to overcome competition, which can be particularly important in nests of host species larger than the parasite (Astié and Reboreda 2006, Fiorini et al. 2009). However, evidence for a positive effect of egg size on nestling performance is equivocal (e.g., Schifferli 1973, Magrath 1992, Reed et al. 1999).

Screaming Cowbird eggs and hatchlings were similar in mass to those of Baywings, although parasitic juveniles and adults are quite larger than the host (Mason 1987, Fraga 1998). Females in other parasite species have evolved eggs similar in size to those of the host, presumably in response to host discrimination against larger or smaller eggs (Mason and Rothstein 1986, Marchetti 2000). No experiments have been conducted on Baywings to test whether they are able to discriminate eggs by size. However, that they readily accepted larger Shiny Cowbird eggs artificially placed in their nests (this study) suggests Baywings do not discriminate foreign eggs on the basis of size. Screaming Cowbird eggs in Baywing nests usually have low chances of success as a consequence of poor synchronization of parasitism and high nest failure rates (Hoy and Ottow 1964, Fraga 1998, De Mársico and Reboreda 2008). Thus, a selective pressure may exist on female Screaming Cowbirds to increase the total number of eggs laid at the expense of laying smaller eggs (Fontaine and Martin 2006, Martin et al. 2006).

Screaming Cowbird nestlings were sexually dimorphic in size and presented sex-specific growth curves. Males grew faster and were larger than females over the entire nestling period, consistent with a recent study of Brown-headed Cowbirds (*Molothrus ater*) (Tonra et al. 2008, but see Weatherhead 1989). Our sample sizes were too small to compare growth parameters between male and female Shiny Cowbirds, but our data indicate that sex-specific growth patterns similar to that observed in Screaming Cowbirds may occur in this species. The occurrence of sex-specific growth curves among parasitic cowbirds implies that gender should be considered when analyzing the costs of competition and factors affecting nestling growth in host and parasite species.

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