The Auk 124(3):898–906, 2007

EARLY INFESTATION BY BOT FLIES (*PHILORNIS SEGUYI*) DECREASES CHICK SURVIVAL AND NESTING SUCCESS IN CHALK-BROWED MOCKINGBIRDS (*MIMUS SATURNINUS*)

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Abstract.—Bot flies (Diptera: Muscidae: *Philornis* spp.) are a group of flies comprising mostly species with a Neotropical distribution. Their larvae parasitize several species of birds, living subcutaneously on altricial chicks. We investigated the effect of parasitism by bot flies (*P. seguyi*) on the reproductive success of Chalk-browed Mockingbirds (*Mimus saturninus*) in temperate grasslands near the southern limit of bot fly distributions. We analyzed seasonal variation of bot fly prevalence during three consecutive years and how the timing and intensity of bot fly infestation affected growth and survival of Chalk-browed Mockingbird nestlings. Bot fly prevalence was 58.3%, 30.7%, and 45.5% each year, and in all years, it increased with time of breeding. Most of the infested nests fledged no chicks. In these nests, chicks had a lower tarsus growth rate than in noninfested nests and died 3–4 days after parasitism. The average time from hatching of the first chick until infestation was 4.4 days. The age of the chicks at the time of infestation was associated positively with nesting success and negatively with intensity of parasitism. Bot fly parasitism also reduced the survival of Shiny Cowbird (*Molothrus bonariensis*) chicks present in Chalk-browed Mockingbird nests, but the presence of Shiny Cowbird chicks did not affect timing of infestation or fledging success of Chalk-browed Mockingbird chicks. Our results show that an intermediate prevalence of bot fly parasitism produces an important decrease in the reproductive success of Chalk-browed Mockingbirds and suggest that bot flies may play an important role as selective agents in the evolution of host life-history strategies. *Received 14 November 2005, accepted 25 July 2006.*

Key words: bot fly parasitism, Chalk-browed Mockingbird, host–parasite interactions, *Mimus saturninus*, nesting success, *Philornis seguyi*.

La Infestación Temprana con Larvas de *Philornis seguyi* Disminuye la Supervivencia de los Pichones y el Éxito de Nidificación de *Mimus saturninus*

Resumen.—*Philornis* es un complejo grupo de moscas que incluye principalmente especies con una distribución Neotropical. Sus larvas parasitan varias especies de aves, desarrollándose en forma subcutánea en pichones nidícolas. Pocos estudios han analizado el impacto del parasitismo de *Philornis* sobre el éxito reproductivo del hospedador. Estos estudios han diferido en sus resultados, y en la mayoría de los casos fueron realizados en regiones tropicales o subtropicales. Investigamos el impacto del parasitismo de *Philornis seguyi* sobre el éxito reproductivo de *Mimus saturninus* en pastizales templados cerca del limite sur de la distribución de *Philornis*. Analizamos la variación estacional de la frecuencia de parasitismo en tres años consecutivos (1999–2001), y cómo el momento y la intensidad de la

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infestación de *Philornis* afectó el crecimiento y la supervivencia de los pichones de *M. saturninus*. La frecuencia de parasitismo fue 58.3%, 30.7% y 45.5% cada año y en los tres años aumentó durante el transcurso de la temporada reproductiva. En la mayoría de los nidos infestados no sobrevivió ningún pichón. En estos nidos, los pichones tuvieron una menor tasa de crecimiento del tarso y murieron 3–4 días después de ser parasitados. El tiempo transcurrido desde la eclosión del primer pichón hasta que el nido fue infestado fue en promedio de 4.4 días. Observamos una asociación positiva entre el éxito del nido y la edad de los pichones al momento de la infestación, y una asociación negativa entre la intensidad de parasitismo y la edad de los pichones al momento de la infestación. El parasitismo de *Philornis* también redujo la supervivencia de los pichones de *Molothrus bonariensis* presentes en nidos de *M. saturninus*, pero la presencia de pichones parásitos no afectó la edad a la que los pichones de *M. saturninus* fueron infestados o su supervivencia. Nuestros resultados muestran que una frecuencia intermedia de parasitismo de *Philornis* produce una reducción significativa del éxito reproductivo de *M. saturninus*, similar a la producida por la depredación de nidos o el parasitismo de cría, y sugieren que *Philornis* podría jugar un importante rol como agente de selección en la evolución de las estrategias de historia de vida de sus hospedadores.

Avian parasites play an important role as selective agents in the evolution of host life-history strategies. Therefore, measuring the costs of parasitism within host–parasite associations and understanding its variation is central to our knowledge of the evolution of these associations (Møller 1997, Moore and Clayton 1997). Many studies have used birds and haematophagous ectoparasites that live on birds or in their nest as a model system. These works have demonstrated detrimental effects of parasites on clutch size (Møller 1991, 1993), chick survival (Merino and Potti 1995), chick body condition (Hurtrez-Boussès et al. 1997), chick or parent behavior (Hurtrez-Boussès et al. 1997, Hurtrez-Boussès and Renaud 2000), juvenile dispersal (Brown and Brown 1992), and host future reproductive success (Richner and Tripet 1999) and survival (Brown et al. 1995). Most of these studies involved either colonial (Brown and Brown 1986) or hole-nesting (Hurtrez-Boussès et al. 1997) birds, which have been suspected of being particularly susceptible to parasites because of their social habits or reuse of old nests (Loye and Carroll 1995). In addition, most of these studies have been conducted in Paleartic and Neartic temperate regions.

Bot flies (Diptera: Muscidae: *Philornis* spp.) are a group of flies comprising mostly species with a Neotropical distribution (Dodge and Aitken 1968). Adult bot flies are free living, but their larvae parasitize several species of tropical and subtropical birds (Dodge and Aitken 1968, Couri 1985). In most species, the larvae live subcutaneously on altricial chicks and adult birds. Chicks can be infested as soon as they hatch (Smith 1968; Arendt 1985b; Delannoy and Cruz 1988, 1991; Young 1993). The larvae feed on red blood cells (Uhazy and Arendt 1986) and remain in the chick for 5–8 days (Arendt 1985b, Young 1993), after which they drop out as third instars and pupate in the nest material (Uhazy and Arendt 1986). Adult flies emerge after a pupation period of 1–3 weeks (Oniki 1983, Young 1993). Infestation by several cohorts of larvae are common (Arendt 1985b, Young 1993), and more than one bot fly species may infest the same host simultaneously (Oniki 1983, Nores 1995). Because bot fly larvae largely attack nestlings (Arendt 1985b), they are a good model to test the effect of parasitism on chick morbidity and mortality.

Few studies have analyzed the effect of bot fly parasitism on host reproductive success, and these have differed in results. Several studies showed that bot flies have sublethal or lethal effects on their hosts (Arendt 1985a, b; Delannoy and Cruz 1991; Nores 1995; Fessl and Tebbich 2002), but one study found no evidence of detrimental effects (Young 1993). Most of the previous studies were carried out in tropical or subtropical regions. In the present study, we investigated the effect of bot fly parasitism on the reproductive success of Chalk-browed Mockingbird (*Mimus saturninus*; hereafter "mockingbird"). This species has been described as frequently infested with bot flies (García 1952, Fraga 1985, Mason 1985), but the effect of bot fly parasitism has not been studied. We conducted our study in temperate grasslands near the southern limit of bot fly distribution. We analyzed seasonal variation of bot fly prevalence in three consecutive years and how the timing and intensity of bot fly infestation affected growth and survival of nestlings. We also analyzed the effect of bot fly parasitism in relation to nest predation and brood parasitism, two primary aspects that determine reproductive success of mockingbirds.

Methods

Study site.—The study was conducted in two semi-open grassland areas in the so-called "rolling pampa" (Soriano 1991) in the province of Buenos Aires, Argentina. Site A is located near the town of Lima (33°58′S, 59°19′W). The site consists of grassland with implanted pastures and isolated forest patches dominated by tala trees (*Celtis tala*). We collected data at site A from early September to late December 1999. Site B is located near the town of Magdalena (35°08′S, 57°25′W). The site is nearly flat and consists of marshy grassland with implanted pastures, and old and second-growth stands dominated by tala and coronillo (*Scutia buxifolia*). We collected data at site B from early September 2000 to mid-February 2001 and from early September 2001 to mid-February 2002. The distance between sites A and B is ~220 km. The range of mean monthly ambient temperatures during the study period was 14.3°C (September) to 23.4°C (December) in 1999, 12.9°C (September) to 23.9°C (February) in 2000, and 13.3°C (September) to 24.6°C (January) in 2001. Mean monthly rainfall during the study period was 129.2 mm (range: 67.6–195 mm) in 1999, 110.4 mm (range: 91.4–165.6 mm) in 2000, and 97.1 mm (range: 46.5–184.4 mm) in 2001.

Study species.—Mockingbirds begin laying during the second half of September and continue to the second half of January. They build open nests, and the most favored nest sites are shrubs or trees with dense foliage. At our study sites, most nests were built in tala, coronillo, and molle (*Schinus longifolius*) at a height of 1.5–2 m. The nest is a large open cup of twigs (outer diameter: 20–25 cm) lined with plant fibers and hair. Mockingbirds produce clutches of 3–4 eggs that are incubated for 13–14 days. Chicks leave the nests when they are 12–14 days old and weigh 50–55 g. Adult mass is approximately 70–75 g (Fraga 1985).

Mockingbirds are commonly parasitized by Shiny Cowbirds (*Molothrus bonariensis*; hereafter "cowbirds"). The proportion of nests parasitized by cowbirds during 1999, 2000, and 2001 was 0.18, 0.79, and 0.88, respectively. The intensity of brood parasitism (average number of parasitic eggs per parasitized nest) was 1.20, 1.78, and 1.83 for 1999, 2000, and 2001, respectively. Cowbird eggs hatch after 11–12 days of incubation, and their chicks leave the nest when they are 11–12 days old and weigh ~40 g (F. L. Rabuffetti and J. C. Reboreda unpubl. data). Adult mass is ~45 g (females) and ~50 g (males). Female cowbirds peck and destroy host eggs when they visit or parasitize mockingbird nests, but they also peck cowbird eggs in nests already parasitized (Sackmann and Reboreda 2003, Fiorini and Reboreda 2006). As a result, the number of hatchlings (either mockingbird or cowbird) differs markedly between nests (range: 0–5 mockingbirds and 0–3 cowbirds), with ≤7 chicks of both species per nest.

Data collection.—We found mockingbird nests either by inspecting potential nesting sites or by following potential breeding individuals. We found 54 nests in 1999 (10 during construction, 12 during egg laying, and 32 during incubation), 70 nests in 2000 (29, 18, and 23), and 83 nests in 2001 (41, 19, and 23). For the present study, we used only nests that survived at least two days after the first chick hatched (n = 36, 39, and 33 for 1999, 2000, and 2001, respectively). We used this criterion because the minimum chick age at which we detected bot flies was one day. The number of nests that hatched only mockingbird chicks, only cowbird chicks, or chicks of both species, respectively, was 32, 0, and 4 for 1999; 17, 3, and 19 for 2000; and 9, 6, and 18 for 2001.

We checked the nests daily or every other day until either the chicks fledged or the nest failed. After hatching, we marked the chicks with waterproof ink and put color bands on the tarsus of each chick. For each nest, we recorded (1) hatch day of each chick, (2) number of chicks hatched, (3) day each chick was infested with bot flies, (4) day the nest failed or fledged chicks, and (5) number of chicks fledged. During 2000 and 2001, we also measured tarsus length and intensity of parasitism (number of bot fly larvae per chick). We measured length of the right tarsus using a dial caliper (accuracy: ±0.1 mm). To control for daily variation in body size, we made all chick measurements between 1700 and 1900 hours.

Collection and identification of bot flies.—We collected ~100 bot flies from nests containing mockingbird chicks (three nests with six chicks), cowbird chicks (one nest with two chicks), or chicks of both species (three nests with six mockingbirds and four cowbirds). We collected the larvae from the chick by grasping each larva by its caudal spiracle with small forceps and removing it through the dermal opening in the chick. We put the larvae from each chick into a cylindrical plastic container (10 cm in height, 8 cm in diameter) with 1–2 cm of sand on the bottom and some nest-lining on the top. We covered the container with tulle (a soft, fine net-like material) and left it at room temperature. The larvae pupated in 14–16 days, and after that we collected the adult flies. We also collected bot flies from infested nests that had been depredated or deserted or had fledged chicks. We removed the nest and put it in a funnel 30 cm in diameter wrapped up with tulle. We left the funnel with the nest at room temperature for three weeks, and after that we collected the adult flies. M. Couri, at Museu Nacional, Federal University of Rio de Janeiro, Brazil, identified adult flies, which in all cases were *Philornis seguyi* (García 1952). Bot flies collected from other host species in the same study areas were also identified as *P. seguyi* (Couri et al. 2005). Specimens of adult flies were deposited at Museu Nacional, Federal University of Rio de Janeiro, and Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires.

Data analysis.—We considered a nest to be successful if it fledged at least one mockingbird or one cowbird chick. Alternatively, we considered it depredated if all chicks disappeared between two consecutive visits, and deserted if we found the chicks dead and no signs of mockingbirds attending the nest. In our study, most desertion events were associated with bot fly parasitism (see below). In these cases, we observed a progressive decline in the corporal condition of the chicks. The parents regularly attended the nest until all the chicks died. We are confident that these nests were deserted as a result of bot fly parasitism and not other causes (e.g., one parent was killed by a predator and the remaining parent subsequently abandoned the nest).

To estimate the effect of bot fly parasitism on the survival of chicks, we calculated the fledging success (proportion of hatchlings that fledged) of noninfested and infested nests. For this analysis, we excluded nests that had been depredated or deserted in circumstances other than bot fly parasitism. We determined the effect of bot fly parasitism on chick growth by comparing tarsus growth rate in noninfested and infested chicks. To avoid pseudoreplication, we used brood mean of tarsus growth rate. We estimated tarsus growth rate from the slope of a linear regression of tarsus length versus chick age for chicks one to nine days old (hatching day = age 0). During this period, tarsus growth rate was almost linear ($y = 7.25 + 2.96 \times x$; $r = 0.98$, $P < 0.001$, $n = 119$ data points from 25 noninfested nests).

Statistical analysis.—We used parametric tests only for normally distributed data. Otherwise, we used nonparametric tests with corrections for ties. For independent comparisons, we used Mann-Whitney *U* or Kruskal-Wallis tests. For analysis of contingency tables, we used Fisher's exact test or a chi-square test. Reported values are means ± SE. All tests were two-tailed, and differences were considered significant at $P < 0.05$. Statistical tests were done using STATVIEW, version 5.0 (SAS Institute, Cary, North Carolina).

Results

Bot fly prevalence during the breeding season.—Percentage of nests infested with bot flies (prevalence of parasitism at the nest level) during 1999, 2000, and 2001 was 58.3% (21 of 36 nests), 30.7% (12 of 39 nests) and 45.5% (15 of 33 nests), respectively ($\chi^2 = 5.8$, df = 2, $P = 0.06$). To test for an association between time of breeding and prevalence, we performed a logistic regression between occurrence of bot fly parasitism in a nest (0–1) as a dependent variable and day of the breeding season when the first chick hatched as an independent variable (day 1 corresponded to October 16). To control for seasonal differences in nest survival that may have influenced the probability of bot fly parasitism, we also included as an independent variable the number of days elapsed since the hatching of the first chick until the nest failed or fledged chicks. We also included as an independent variable the number of chicks (either mockingbird or cowbird) in the nest. There was a positive association between occurrence of bot fly parasitism and time of breeding for the three breeding seasons (logistic regression, 1999: $\chi^2 = 6.2$, $P < 0.01$; 2000: $\chi^2 = 5.4$, $P < 0.05$; and 2001: $\chi^2 = 5.9$, $P < 0.05$; Fig. 1). By contrast, bot fly parasitism was not associated with the number of days the nest survived (logistic regression, 1999: $\chi^2 = 0.68$, $P = 0.41$; 2000: $\chi^2 = 0.11$, $P = 0.74$; and 2001: $\chi^2 = 0.001$, $P = 0.99$), or with the number of chicks in the nest (logistic regression, 1999: $\chi^2 = 2.2$, $P = 0.14$; 2000: $\chi^2 = 0.55$, $P = 0.46$; and 2001: $\chi^2 = 0.03$, $P = 0.87$).

We also analyzed whether the seasonal increase in the prevalence of bot fly parasitism was associated with the decrease in the availability of mockingbird nests. We divided the breeding season into 15–day periods, and for each period we determined the number of nests with chicks and the proportion of nests that were parasitized by bot flies. Because of the small number of periods per year (6–7), we combined the data of the 1999–2001 breeding seasons. We found no association between number of nests with chicks and prevalence of parasitism (Spearman's rank correlation, $Z = 0.37$, $P = 0.75$, $n = 20$ periods).

Effect of bot fly parasitism on chick survival and nesting success.—Most of the nests infested with bot flies did not fledge any chicks (Table 1). In these nests, chicks died shortly after bot fly infestation (day the first chick was infested: 3.1 ± 0.38; day the nest failed: 6.2 ± 0.44; $n = 22$ nests). Chick survival was significantly lower in infested than in noninfested nests in 1999 and 2000 (Mann-Whitney *U*-tests, $Z = -3.11$, $P < 0.01$, and $Z = -2.05$, $P < 0.05$, respectively) but not during 2001 (Mann-Whitney *U*-test, $Z = -1.53$,

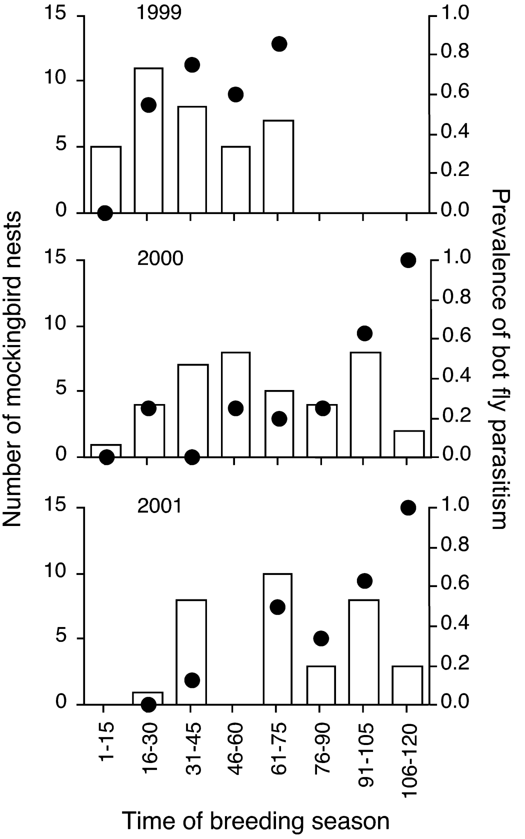

Fig. 1. Number of Chalk-browed Mockingbird nests with hatchlings (white bars) and proportion of those nests infested with bot flies (black circles) as a function of time of the breeding season when chicks hatched (day 1 = October 16). For graphical purposes, we grouped the data into 15-day intervals.

Table 1. Chalk-browed Mockingbird nests that hatched chicks and their fate for the breeding seasons, 1999–2001. Nests deserted as a result of bot fly infestation are in parentheses.

Breeding season	Bot fly parasitism	Fate: Depredated	Fate: Deserted	Fate: Successful
1999	no	5	1	9
	yes	3	12 (12)	6
2000	no	11	1	15
	yes	4	5 (5)	3
2001	no	8	3	7
	yes	4	5 (5)	6

P = 0.13; Fig. 2). When the data for the three years were combined, the proportion of chicks that fledged was significantly lower in infested than in noninfested nests (infested: 0.31 ± 0.07, n = 36; noninfested: 0.78 ± 0.05, n = 29; Mann-Whitney U-test, Z = –4.4, P < 0.001). When we repeated the analysis, excluding the nests that failed as a result of bot fly infestation (i.e., we considered only infested nests that fledged at least one chick), we did not detect any difference in fledging success (data of 1999–2001 combined, noninfested nests: 0.78 ± 0.05, n = 29; infested nests: 0.74 ± 0.07, n = 15; Mann-Whitney U-test, Z = –0.71 P = 0.48). Bot fly parasitism also reduced the fledging success of the cowbird chicks present in mockingbird nests (Mann-Whitney U-test, Z = –2.69, P < 0.01; Fig. 2). For this analysis, we grouped the data of 1999–2001 because of the small number of nests with cowbird chicks.

We analyzed whether bot fly parasitism affected chick growth by comparing tarsus growth rate in noninfested with that in infested nests. For infested nests, we analyzed separately nests that failed (all chicks died) and nests that fledged chicks. Tarsus growth rate was lower in infested nests that failed (1.9 ± 0.2 mm day^{-1}, n = 4 nests) than in infested nests that fledged chicks (2.9 ± 0.2 mm day^{-1}, n = 4 nests) or in noninfested nests (2.9 ± 0.1 mm day^{-1}, n = 20 nests; Kruskal-Wallis test, H = 8.76, P < 0.01, and contrasts).

Number of larvae per chick was, on average, 21.4 ± 4.3 (range: 1–79, n = 23 nests). Infested nests that failed had higher intensity of parasitism than infested nests that fledged chicks (37.3 ± 7.7, n = 7 vs. 9.7 ± 3.4, n = 9; Mann-Whitney U-test, Z = –2.75, P < 0.01). We also observed a negative association between intensity of parasitism and age of the chicks at the time they were parasitized (Spearman's rank correlation, Z = –1.92, P < 0.05, n = 23 nests).

Depredation rates did not differ between noninfested and infested nests for each of the three years analyzed independently (Fisher's exact tests, P = 0.24 for 1999, P = 0.55 for 2000, and P = 0.47 for 2001), or combined (χ^2 = 2.8, df = 1, P = 0.09; Table 1).

Timing of bot fly infestation and chick survival.— The time elapsed since the hatching of the first chick until the nest was infested was, on average, 4.4 ± 0.4 days (range: 1–11 days, n = 48 nests). We did not detect differences in timing of infestation between years (4.9 ± 0.6 days, n = 21 for 1999; 3.8 ± 0.6 days, n = 12 for 2000; and 4.2 ± 0.7 days, n = 15 for 2001; Kruskal-Wallis test, H = 1.25, P = 0.53).

To determine whether there was an association between nest survival and timing of infestation, we performed a logistic regression between nest success (0–1) as a dependent variable and day at which we detected the first chick infested (day 0 = day of hatching of the first chick) as an

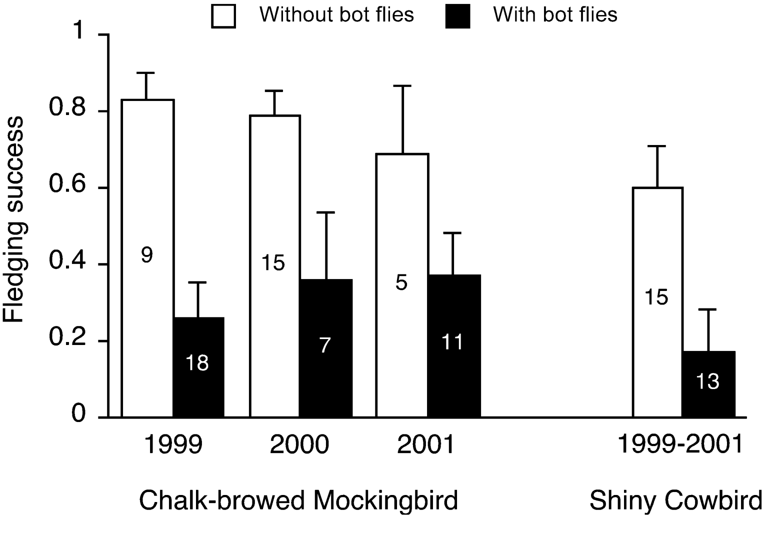

Fig. 2. Bars show mean ± SE of the proportion of Chalk-browed Mockingbird and Shiny Cowbird hatchlings that fledged (fledging success) from nests noninfested (white bars) and infested (black bars) with bot flies. Numbers inside bars indicate number of nests.

independent variable. We also included as independent variables the number of hatchlings in the nest and the year when we collected the data. For this analysis, we excluded nests that were depredated. There was a significant increase in the likelihood of nest success with day of infestation (logistic regression, $\chi^2 = 10.3$, $P < 0.001$, $n = 37$ nests; Fig. 3). Successful nests were infested, on average, three days later than nests in which all chicks died (6.7 ± 0.6 days, n = 15, vs. 3.1 ± 0.4 days, n = 22, Mann-Whitney U-test, Z = –3.82, P < 0.001). By contrast, the success of infested nests was not associated with number of hatchlings (logistic regression, χ^2 = 0.07, P = 0.78) or year (logistic regression, χ^2 = 1.8, P = 0.18).

Interactions between cowbird and bot fly parasitism.—Because some nests held both mockingbird and cowbird chicks, we tested whether the presence of cowbird chicks had any effect on the prevalence of bot fly parasitism, timing of bot fly infestation, or survival of mockingbird chicks in infested nests. The proportion of nests infested with bot flies did not differ between nests with or without cowbird chicks (16 of 41 vs. 29 of 58, χ^2 = 0.8, df = 1, P = 0.38). Similarly, timing of infestation and fledging success of mockingbird chicks did not differ between nests with and without cowbird chicks (timing of infestation: with: 4.9 ± 0.7 days, n = 16; without: 4.3 ± 0.5 days, n = 29; Mann-Whitney U-test, Z = –0.56, P = 0.57; fledging success: with: 0.55 ± 0.09, n = 24; without: 0.5 ± 0.07, n = 41; Mann-Whitney U-test, Z = –0.51, P = 0.61).

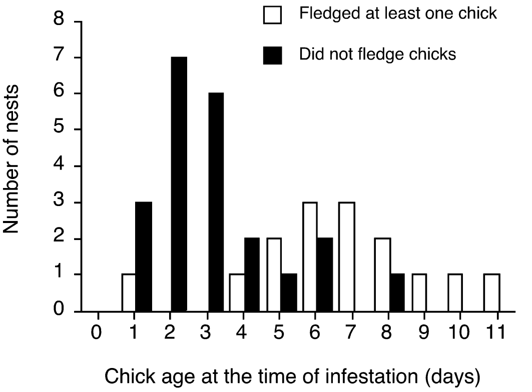

FIG. 3. Number of nests infested with bot flies that fledged chicks (white bars) or when all chicks died (black bars) as a function of the time when the first chick was infested (day 0 = day of hatching of the first chick in the nest).

DISCUSSION

Our results indicate that in mockingbirds (1) prevalence of bot fly parasitism increases with time of breeding, (2) bot fly parasitism decreases chick survival and nesting success, and (3) chick survival is negatively associated with intensity of bot fly parasitism and positively associated with chicks' age at the time they are infested. Probability and timing of bot fly parasitism were not affected by the number of hatchlings in the nest. Similarly, probability and timing of bot fly parasitism and fledging success of mockingbird chicks in infested nests were not affected by the presence of cowbird chicks.

Previous studies have shown that bot flies reduce host reproductive success (Arendt 1985b, Delannoy and Cruz 1991, Nores 1995, Fessl and Tebbich 2002; but see Young 1993). These studies were conducted in tropical and subtropical regions or on cavity-nesting birds, which may be particularly susceptible to parasites because of their reuse of old nests (Arendt 2000). Our results indicate that bot fly parasitism is also an important factor affecting reproductive success of hosts that breed in temperate regions and build open nests.

Mockingbird nests infested with bot flies can be divided into two groups that have markedly different outcomes: (1) nests that did not fledge any chicks and (2) nests that fledged at least one chick. We found that most nests that did not fledge chicks were infested shortly after chick hatching. In those nests, chick tarsus growth rate was lower than in infested nests that fledged chicks or in noninfested nests. Arendt (1985a, 2000) reported that bot flies significantly retarded nestling growth and that if larval infestation occurred at or just after hatching, even light larval loads caused chick death. By contrast, most infested nests that fledged at least one chick were infested late in the nestling period (after day 6). Fledging success and growth rate of chicks in these nests did not differ from that in noninfested nests.

We found that chick mortality was dependent on the age at which the chick was infested. However, chick mortality was also affected by intensity of parasitism, which in turn was negatively associated with chick age. One interpretation for the latter association would be that intensity of parasitism is higher in earlier-infested chicks, because bot fly larvae can penetrate the skin more easily before the chicks have developed their feathers. One previous study did not find a detrimental effect of bot fly parasitism (Young 1993), reporting only a slight negative effect of bot flies on nestling growth. In that study, most chicks were infested when they were between 6 and 12 days old. Thus, the difference between studies that show lethal effects of bot fly parasitism (Arendt 1985a, b; Delannoy and Cruz 1991; Nores 1995; present study) and the study of Young (1993) is likely explained by differences in the age at which the chicks were infested.

Bot fly parasitism also affected the fledging success of cowbird chicks present in mockingbird nests. Fledging success of infested cowbird chicks was lower than that of infested mockingbird chicks. This difference was probably the result of mockingbird chicks outcompeting cowbird nestmates for food, which happens in noninfested nests (Sackmann and Reboreda 2003). We did not find any evidence of interplay between brood and bot fly parasitism. Prevalence of parasitism, timing of infestation, and fledging success of mockingbird chicks did not differ between nests with and without cowbird chicks, which suggests that for bot flies, cowbird chicks were similar to mockingbird chicks.

Two important factors determining the reproductive success of mockingbirds are nest depredation and brood parasitism by cowbirds. In our study, ~50% of the nests failed during laying and incubation as a result of nest depredation or nest desertion after cowbirds punctured mockingbirds' eggs (F. L. Rabuffetti and J. C. Reboreda unpubl. data). In regard to nests that hatched chicks, 32% were depredated, whereas 20% failed as a result of bot fly parasitism (Table 1), which indicates that even an intermediate prevalence of parasitism (in our study, it was 39% on average) has a sublethal or lethal effect on this host.

In summary, our results show that bot flies have an important effect on host reproductive success and, therefore, may play an important role as selective agents in the evolution of host life-history strategies.

Acknowledgments

We thank C. Sackmann and the E. Shaw de Pearson Foundation for allowing us to conduct this study at Estancias "Casamu" (site A) and "El Destino" (site B), respectively. We are very grateful to M. Couri, at Museu Nacional, Federal University of Rio de Janeiro, who identified adult flies. We also thank V. Fiorini for field assistance and C. Dick and an anonymous reviewer for valuable comments on an earlier version of this manuscript. F.L.R. was supported by a FOMEC fellowship from the Department of Biological Sciences, University of Buenos Aires. J.C.R. is Research Fellow of the Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET). This work was supported by Agencia Nacional de Promoción Científica y Tecnológica (grant 01-09237) and University of Buenos Aires (grant X158).

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Associate Editor: K. P. Johnson