LETHAL AND SUBLETHAL EFFECTS OF BOTFLY (*PHILORNIS SEGUYI*) PARASITISM ON HOUSE WREN NESTLINGS

Martín A. Quiroga[1,3] and Juan C. Reboreda[2]

[1]*Instituto Nacional de Limnología (INALI-CONICET-UNL), Santo Tomé, 3016 Santa Fe, Argentina*
[2]*Departamento de Ecología, Genética y Evolución, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EGA, Buenos Aires, Argentina*

Abstract. We studied the effect of botfly (*Philornis seguyi*) parasitism on survival and growth of House Wren (*Troglodytes aedon*) nestlings. We investigated whether nestling survival was related to (1) the intensity of botfly infestation, (2) age of the nestling at the time it was parasitized, and (3) the order in which a chick hatched within a brood. The prevalence of botfly parasitism was 25%; the mean intensity and age at parasitism were 12.8 larvae per nestling and 3.9 days, respectively. Nestling survival was 42% lower in infested than in noninfested broods. Nestling survival was negatively associated with the mean intensity of parasitism of the brood and positively associated with the age of the nestling at the time it was parasitized. Within infested broods, nestling survival was higher in chicks hatched first than in chicks hatched last. Infested nestlings that survived until fledging grew at lower rates and remained in the nest longer than did nestlings in noninfested broods. Our results reveal that *P. seguyi* has lethal and sublethal effects on House Wren nestlings and that the intensity of parasitism, age of nestlings at the time they are infested, and sequence of hatching are important factors that influence the survival of parasitized nestlings.

Key words: botfly, ectoparasite, House Wren, Philornis seguyi, Troglodytes aedon.

Efectos Letales y Subletales del Parasitismo de *Philornis* sobre los Pichones de *Troglodytes aedon*

Resumen. Estudiamos el efecto del parasitismo de *Philornis seguyi* sobre la supervivencia y el crecimiento de pichones de *Troglodytes aedon*. Analizamos si la supervivencia de pichones estuvo relacionada a: (1) la intensidad de parasitismo, (2) la edad de los pichones cuando el nido fue parasitado, y (3) el orden de eclosión de los pichones dentro de la nidada. La prevalencia de parasitismo de *Philornis* fue de 25%, mientras que las medias de intensidad y edad de parasitismo fueron 12.8 larvas por pichón y 3.9 días, respectivamente. La supervivencia de los pichones fue un 42% menor en nidos infestados que en no infestados. La supervivencia de los pichones estuvo negativamente asociada con la intensidad de parasitismo de la nidada y positivamente asociada con la edad de los pichones cuando fueron parasitados. Dentro de cada nidada infestada, los pichones que eclosionaron primero tuvieron una mayor probabilidad de sobrevivir que el que eclosionó último. Los pichones infestados que sobrevivieron tuvieron tasas de crecimiento menor y permanecieron más tiempo en el nido que los pichones de nidadas no infestadas. Nuestros resultados indican que *P. seguyi* produce efectos letales y sub-letales sobre los pichones de *T. aedon* y que la intensidad de parasitismo, la edad de los pichones al momento de la infestación y el orden de eclosión son factores importantes que influencian la supervivencia de los pichones parasitados.

INTRODUCTION

Avian ectoparasites, ranging from feather lice (Clayton et al. 1992), mites (Proctor and Owens 2000), fleas (Tripet and Richner 1999), and cimicid bed bugs (Brown and Brown 2004) to various flies (Hurtrez-Boussès et al. 1997), are common. Among ectoparasitic flies, interactions between blowflies (genus *Protocalliphora*) and their hosts have been studied relatively well (Johnson and Albrecht 1993, Hurtrez-Boussès et al. 2000, O'Brien and Dawson 2008), but fewer studies have analyzed the interactions between botflies (*Philornis* spp.) and their hosts. These parasites are not present in the North Temperate Zone, and their effects have been studied mostly in tropical and subtropical regions (Arendt 1985a,b,

Delannoy and Cruz 1991, Dudaniec et al. 2006, Fessl et al. 2006). Our study adds to the relatively meager information available on these parasites in the temperate southern cone of South America (but see Nores 1995, Rabuffetti and Reboreda 2007, Antoniazzi et al. 2010).

Larvae of most species of botflies live subcutaneously on altricial nestlings, feeding on serous fluids, tissue debris, and blood cells (Uhazy and Arendt 1986, Teixeira 1999). Larvae complete growth in 4–8 days, after passing through three instars (Fraga 1984), dropping then from the host to the base of the nest, where they pupate for approximately 2 weeks (Teixeira 1999). Larvae detach from the nestling to pupate either when fully grown or immediately after the nestling's death, and pupae with the developmental period thus truncated

produce smaller adult flies (Spalding et al. 2002). Adult bot-flies feed on decaying organic matter (Teixeira 1999).

Although some studies have reported negative effects of botfly parasitism on the survival of nestlings (Arendt 1985a,b, Delannoy and Cruz 1991, Fessl et al. 2006, Dudaniec et al. 2006, Rabuffetti and Reboreda 2007), others have reported no such effect (Nores 1995) or only a slight adverse effect on their growth (Young 1993). One possible explanation for this discrepancy is differences in host resistance to botflies or in botfly virulence. In addition, the effect of botfly parasitism on the growth and survival of nestlings likely depends on other factors, such as the number of larvae per nestling (intensity of parasitism), age of nestlings at the time they are infested, brood size, and parental behavior (Dudaniec and Kleindorfer 2006). For example, Dudaniec et al. (2006) reported that, in the Small Ground-Finch (*Geospiza fuliginosa*), nestling survival and hemoglobin concentration were negatively associated with intensity of *P. downsi* parasitism, and intensity of parasitism was negatively associated with number of nestlings in a brood. Similarly, Rabuffetti and Reboreda (2007) found a negative association between intensity of parasitism by *P. seguyi* and survival of Chalk-browed Mockingbird (*Mimus saturninus*) nestlings, as well as a positive association between age at parasitism and nestling survival. These results were obtained through comparisons of infested broods, which may differ in other variables, such as time or parental quality.

We investigated the effects of intensity and age of botfly parasitism on the survival of House Wren (*Troglodytes aedon*) nestlings (lethal effects) and whether botfly parasitism reduces growth rates of infested wren nestlings that survived until fledging with respect to growth rates of uninfested nestlings (sublethal effects). The House Wren is one few species in which nestling survival is not affected negatively by botfly infestation (Young 1993). Therefore, our results will help to elucidate whether this host is more resistant to botflies or the lack of effect can be attributed to low intensity of parasitism or age at parasitism. We also examined whether the intensity of parasitism and order in which chicks hatch are associated with the survival of infested nestlings. To our knowledge, no previous study has analyzed the effect of intensity of parasitism or age at parasitism on the survival of individual nestlings from within the same brood. Taking into account previous studies (Dudaniec and Kleindorfer 2006, Rabuffetti and Reboreda 2007), we expect that nestling survival should be negatively correlated with the intensity of parasitism and positively correlated with the age of nestlings at the time of infestation. These predictions should hold both across multiple broods and among the chicks within one brood.

METHODS

STUDY SITE

Our study was conducted at two sites near the city of Santa Fe, Argentina, during the breeding seasons (October–February) of 2004–2005, 2005–2006, 2006–2007, and 2007–2008. Site A was located on the campus of University of Litoral (31° 38′ S, 60° 40′ W) and site B at a private cattle ranch about 10 km from site A and close to the Colastiné River (31° 38′ S, 60° 35′ W).

HOST AND ECTOPARASITE SPECIES

House Wrens nest in natural and artificial cavities. We placed 60 and 56 nest boxes at sites A and B, respectively, on poles at a height of 1.6 m and at least 20 m apart. House Wrens began laying during early October and continued through early January. Clutches consisted of 3–5 eggs (modal clutch size = 4) that were incubated for 13–14 days. As this species begins incubation with the penultimate egg, eggs hatched asynchronously (most eggs hatched on the same day and the last-laid egg the following day). Nestlings fledged at an age of 14–15 days old, weighing approximately 12 g at that time.

House Wrens were parasitized by botflies of the species *Philornis seguyi* (Couri et al. 2009, see below). The larvae lived subcutaneously and developed in their host for 5–6 days, reaching a length of approximately 8–9 mm, with a mass of 0.11–0.13 g. At that stage, they dropped from the host to pupate at the base of the nest. Adult flies emerged from the pupae after 9–10 days of pupal development (Quiroga 2009).

DATA COLLECTION

The numbers of nests studied during 2004–2005, 2005–2006, 2006–2007, and 2007–2008 were 34, 46, 35, and 43, respectively. We checked nests daily near the time of hatching and every 2 or 3 days thereafter until nestlings were 12 days old. After day 12 we observed the nest every 1 or 2 days and recorded parental activity but stopped physically checking the nest to avoid premature fledging. For each nest, we recorded the day of each nestling's hatching, number of nestlings hatched, the day each nestling was infested with botflies, the maximum number of botflies per nestling, and the day each nestling died or left the nest. We marked nestlings with waterproof ink on the bill immediately after hatching. During each visit, we recorded the number of larvae on each nestling, and on days 3, 6, 9, and 12, we weighed the nestlings with a 30-g Pesola scale (±0.25 g; recalibrated before each visit to a nest), measured the length of head plus bill with calipers (±0.1 mm), and measured wing length with a ruler (±0.5 mm). After a nest was abandoned or nestlings fledged, we removed the nest from the box and put it in a plastic bag with small holes. We left the bag at room temperature until flies emerged. We collected four adult botflies from each infested brood (*n* = 39 broods and 156 botflies), all of which Márcia Couri (Museu Nacional, Federal University of Rio de Janeiro, Brazil) identified as *P. seguyi* (Garcia 1952, Couri et al. 2009). Specimens of adult flies and puparia were deposited at the Museu Nacional, Federal University of Rio de Janeiro, Brazil, and Museo Argentino de Ciencias Naturales Bernardino Rivadavia, Buenos Aires, Argentina.

DATA ANALYSIS

To measure the prevalence of parasitism (percentage of broods infested with botflies), we used only nests that remained active at least 6 days after the first nestling hatched because >95% of parasitized nests were infested by this age. The prevalence of parasitism at sites A and B did not differ (29/132 vs. 10/25, contingency test $\chi^2 = 2.76$, $P = 0.10$), so for most analysis we pooled the data from the two sites. We used a brood's mean of intensity of parasitism (the mean maximum number of botflies over all the nestlings in the brood) to avoid pseudoreplication. We also calculated the coefficient of variation of intensity of parasitism within a brood as an index of the variability of intensity of parasitism among nestlings in the same brood. We calculated the age at parasitism as the number of days elapsed between the hatching of the first nestling and the detection of the first botfly larva and the time of breeding as the day the first egg was laid.

To estimate the effect of botfly parasitism on nestling survival by brood, we compared the proportion of hatchlings that fledged in noninfested vs. infested broods. For this analysis, we excluded nests that had been preyed upon. We also analyzed the effect of botfly parasitism on infested nestlings that fledged by comparing their growth rates to those of nestlings in noninfested broods. We estimated the growth rate of each nestling from the slope of a linear regression for each variable (head plus bill, wing length, mass) with the age of the nestling between the ages of 3 and 12 days. We compared these growth rates of infested vs. noninfested nestlings with means for each brood.

STATISTICAL ANALYSIS

Because of lack of normality of the data in most cases we used nonparametric statistical tests with corrections for ties (Siegel and Castellan 1988). When the comparisons yielded a nonsignificant result we report the 95% confidence interval (Zand Ruxton 2003), and when they yield a significant result we also report Cohen's d to indicate effect sizes (Cohen 1977). For nonparametric statistical tests we used StatView 5.0 (SAS Institute 1998). We tested the effects of botfly parasitism on nestling survival by using a generalized linear model (GLM) with a binomial error structure and logit-link function (Crawley 2007). We also included as fixed effect the site (A or B). For this analysis we used the package Rcmdr from R software, version 2.13.0. All tests were two-tailed, and we considered differences significant at $P < 0.05$. Reported values are means ± SE.

RESULTS

PREVALENCE AND INTENSITY OF BOTFLY PARASITISM

The prevalence of botfly parasitism did not differ significantly by year (goodness of fit: $G_3 = 5.9$, $P = 0.18$) and averaged 25%. The intensity of parasitism was lower in 2006 than in the other three years (Table 1; Kruskal–Wallis: $H_3 = 12.3$, $P = 0.006$, and contrasts, $P < 0.05$). There was no association between time of breeding and probability of parasitism (logistic regression: $\chi^2 = 2.8$, $n = 157$ nests, $P = 0.09$) or between time of breeding and intensity of parasitism (Spearman $\rho = -0.06$, $Z = -0.35$, $n = 39$ nests, $P = 0.73$).

In parasitized broods, all nestlings had botflies. The coefficient of variation of intensity of parasitism across broods was 0.59, whereas among nestlings within a brood it was on average 0.35 ± 0.03 (4 years combined, Table 1). We found no association between intensity of parasitism and number of nestlings in the brood (range 2–5, Spearman $\rho = -0.11$, $Z = 0.68$, $n = 39$ nests, $P = 0.5$).

TABLE 1. Botfly (*Philornis seguyi*) parasitism of House Wren nestlings in Santa Fe Province, Argentina, during the breeding seasons 2004–2005 to 2007–2008. Values of prevalence of parasitism (% of infested broods), total intensity of parasitism (number of larvae per brood in infested broods), mean intensity of parasitism (brood averages of number of larvae per nestling in infested broods), mean coefficient of variation of within brood intensity of parasitism, age of the nest at the time it was parasitized (number of days elapsed since hatching of the first nestling until we detected the first botfly larvae in the brood), and date of hatching in the first infested brood.

	2004–2005	2005–2006	2006–2007	2007–2008
Prevalence	25	32.6	11.1	27.9
Infested/total	8/32	15/46	4/36	12/43
Total intensity	57.3 ± 6.8	41.4 ± 5.9	20.3 ± 1.2	55.9 ± 9.9
Range	40–92	16–99	17–22	20–128
Mean intensity	15.6 ± 1.4	11.9 ± 1.6	5.1 ± 0.3	14.5 ± 2.5
Range	8.3–23	4.3–24.8	4.3–5.8	4.3–30.3
Coefficient of variation of within brood intensity	0.30 ± 0.04	0.36 ± 0.04	0.32 ± 0.05	0.39 ± 0.06
Age (days)	3.0 ± 0.0	4.1 ± 0.4	5.3 ± 0.8	3.8 ± 0.5
First brood infested	13 November	23 October	25 December	24 November

EFFECT OF PARASITISM ON NESTLING SURVIVAL
AND GROWTH RATES

The number of hatchlings in infested and noninfested broods did not differ (infested: 3.77 ± 0.14, $n = 39$, noninfested: 3.66 ± 0.10, $n = 118$; Mann–Whitney $U = 2389.5$, $Z = 0.38$, $P = 0.7$; 95% confidence interval: (–0.48, 0.26), but the proportion of nestlings that survived was significantly lower in infested than in noninfested broods (Fig. 1A; GLM $Z = –7.6$, $P < 0.001$). There was no significant effect of site on nestling survival (GLM $Z = 1.72$, $P = 0.09$). Among infested broods, nestling survival was negatively associated with intensity of botfly parasitism (Fig. 1B; Spearman $\rho = –0.55$, $Z = 3.4$, $n = 39$ nests, $P < 0.001$) and positively associated with age at parasitism (Spearman $r = –0.39$, $Z = 2.4$, $n = 39$ nests, $P = 0.02$). Intensity and age at parasitism were not significantly associated (Spearman $r = –0.26$, $Z = 1.6$, $n = 39$ nests, $P = 0.12$).

Of 39 infested nests, all nestlings survived in five (13%) and all nestlings died in 13 (33%). In the 21/39 nests (54%) where not all nestlings died, the intensity of parasitism of nestlings that fledged and those that died did not differ (11.0 ± 1.1 vs. 12.9 ± 1.6 larvae; Wilcoxon signed-rank test: $Z = 1.6$, $P = 0.12$, $n = 21$ broods; 95% confidence interval: (–2.15, 6.12). However, first-hatched nestlings had a higher probability of survival than those hatched one day later (0.59 ± 0.07 vs. 0.06 ± 0.06; Wilcoxon signed-rank test: $Z = 3.0$, $P = 0.002$, $n = 18$ broods; 95% confidence interval: (0.35, 0.72; Cohen's $d = 2.0$).

The growth rates of head plus bill and wing length were significantly lower in infested nestlings that survived than in nestlings of noninfested broods (Fig. 2; head plus bill: Mann–Whitney $U = 347.5$, $Z = –5.88$, $P < 0.001$; 95 % confidence interval: (0.26, 0.45; Cohen's $d = 1.6$); wing: $U = 618.5$, $Z = –4.3$, $P < 0.001$; 95 % confidence interval: (0.4, 0.95; Cohen's $d = 1.07$). Similarly, the rate of body-mass increase was significantly lower in infested nestlings that survived than

in noninfested nestlings (1.09 ± 0.05 g day^{-1}, $n = 26$ vs. 1.20 ± 0.02 g day^{-1}, $n = 105$; Mann–Whitney $U = 922$, $Z = –2.56$, $P = 0.01$; 95% confidence interval: (0.016, 0.22; Cohen's $d = 0.66$), although the mass of the former included the mass of larvae. As a result of this, infested nestlings had longer nestling periods than did noninfested nestlings. On average, infested nestlings that survived spent 17.9 ± 0.6 days in the nest ($n = 12$ broods with 3–5 nestlings), while nestlings in noninfested broods spent 16.1 ± 0.2 days ($n = 79$ broods with 3–5 nestlings; Mann–Whitney $U = 262.5$, $Z = –2.48$, $P = 0.01$; 95% confidence interval: (–3.2, –0.51; Cohen's $d = 0.85$).

DISCUSSION

Young (1993) analyzed the effect of parasitism the botfly *P. carinatus* on the House Wren's reproductive success and found that infestation did not affect nestlings' survival and only had a slight adverse effect on the growth of the nestlings. The discrepancy between Young's results and ours could be due to differences in virulence between the two species of botflies (our study investigated parasitism by *P. seguyi*). In our study, however, the higher intensity of parasitism and lower age of the chicks at the time they were parasitized likely explain the stronger negative effects.

Nores (1995) studied the effect of parasitism by *P. seguyi* and *P. pici* on nestlings of the Brown Cacholote (*Pseudoseisura lophotes*) and Firewood-gatherer (*Anumbius annumbi*). Even though Nores observed parasitism of intensity similar to that we observed (9–11 vs. 12.8 larvae per chick), he found no effect of botfly parasitism on nestling survival. This difference may be explained by these species' chicks being larger than those of the House Wren combined with the fact that larger nestlings survive *Philornis* parasitism better (Dudaniec and Kleindorfer 2006, Kleindorfer and Dudaniec 2009). However, Rabuffetti and Reboreda (2007) found that *P. seguyi*
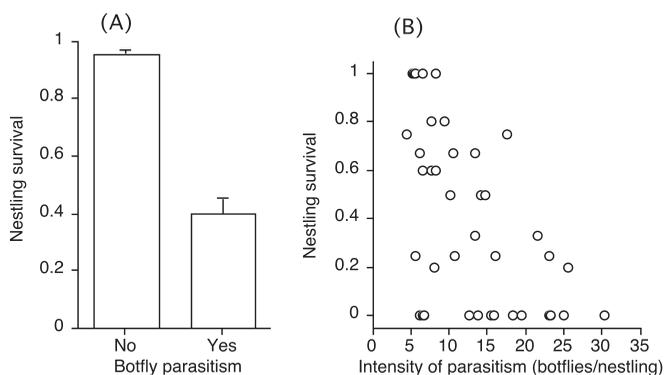
FIGURE 1.   (A) Mean (±SE) proportion of House Wren hatchlings that fledged in broods that were not parasitized ($n = 106$) and parasitized ($n = 39$) by botflies (*P. seguyi*). (B) Proportion of hatchlings that fledged (chick survival) in broods ($n = 39$) of House Wrens parasitized with botfly larvae as a function of intensity of parasitism (brood averages of number of larvae per chick).
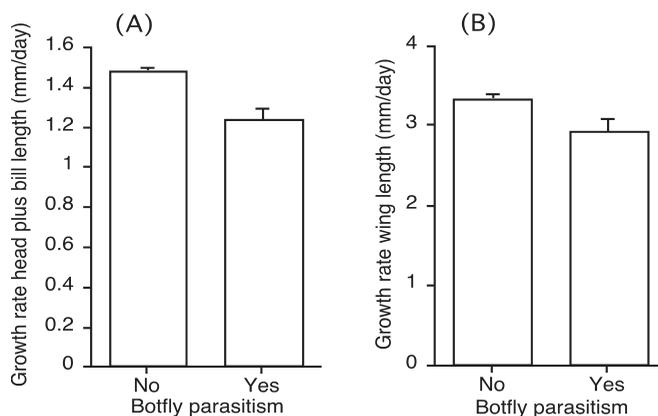
FIGURE 2.   Mean (±SE) of average growth rates of length of (A) head plus bill and (B) wing of nestlings in unparasitized broods ($n = 105$) and nestlings that survived in broods parasitized by botflies ($n = 26$).

parasitism decreased survival of nestlings of the Chalk-browed Mockingbird (*Mimus saturninus*) and Shiny Cow-bird (*Molothrus bonariensis*), both of which are larger than the House Wrens (mockingbird 70–75 g, cowbird 45–50 g). *P. seguyi* apparently has negative effects on hosts over a wide range of body masses. One alternative explanation for the discrepancy between our results and those of Nores may be that the hosts he studied were infested with larvae of two species of botfly (*P. seguyi* and *P. pici*), and perhaps *P. pici* has weaker effects on host nestlings than does *P. seguyi*.

We found that nestling survival was positively associated with the age of the chick at the time of infestation. Similarly, Rabuffetti and Reboreda (2007) found a positive association between nestling survival and age at parasitism. Arendt (1985a, 2000) reported that if larval infestation occurred at or just after hatching, even light larval loads killed the chick. We also found that nestling survival was negatively associated with intensity of parasitism, a result similar to those reported by other authors who found that chick survival decreased as the number of larvae in the chicks or the brood increased (Arendt 1985b, Delannoy and Cruz 1991, Fessl and Tebbich 2002, Dudaniec et al. 2007, Reboreda and Rabuffetti 2007). We did not find a negative association between nestling survival and intensity of botfly parasitism within infested broods, probably because the variance in intensity of parasitism was lower within than among broods.

Within infested broods the time of hatching was a good predictor of nestling survival: nestlings hatched last rarely survived, as they were infested when they were one day younger. Because we obtained this result through comparisons within infested broods, it allowed us to control for other variables such as breeding time or parental quality. Similarly, among broods there was a positive association between age at parasitism and nestling survival. Thus results within and among broods indicate that the age of a nestling when it is infested is an important factor affecting ne nestling survival.

In addition to increasing nestling mortality, botfly infestation significantly reduced the growth rate of infested nestlings that survived, which resulted in longer nestling periods than for noninfested broods. Because we did not follow the young after they left the nest, we cannot rule out the possibility that infested nestlings that fledged had higher mortality immediately after leaving the nest, as shown by Streby et al. (2009). Those authors found that blowflies (*Protocalliphora* spp. and *Trypocalliphora braueri*) did not affect the mortality of Ovenbirds (*Seiurus aurocapilla*) during the nestling period, but fledglings' survival and minimum distance traveled the first day after fledging were significantly lower for infested than for uninfested fledglings.

To summarize, our results show that *P. seguyi* has lethal and sublethal effects on House Wren nestlings and that the intensity of parasitism, age at infestation, and order in which the chick hatches are all factors that influence nestling survival and therefore should be considered in future studies of the detrimental effects of botflies on their hosts.

LITERATURE CITED

ANTONIAZZI, L. R., D. E. MANZOLI, D. ROHRMANN, M. J. SARAVIA, L. SILVESTRI AND P. M. BELDOMENICO. 2010. Climate variability affects the impact of parasitic flies on Argentinean forest birds. Journal of Zoology 283:126–134.

ARENDT, W. J. 1985a. *Philornis* ectoparasitism of Pearly-eyed Thrashers I. Impact on growth and development of nestlings. Auk 102:270–280.

ARENDT, W. J. 1985b. *Philornis* ectoparasitism of Pearly-eyed Thrashers II. Effects on adults and reproduction. Auk 102: 281–292.

ARENDT, W. J. 2000. Impact of nest predators, competitors, and ectoparasites on Pearly-eyed Thrashers, with comments on the potential implications for Puerto Rican Parrot recovery. Ornitología Neotropical 11:13–63.

BROWN, C. R., AND M. B. BROWN. 2004. Group size and ectoparasitism affect daily survival probability in a colonial bird. Behavioral Ecology and Sociobiology 56:498–514.

CLAYTON, D. H., R. D. GREGORY, AND R. D. PRICE. 1992. Comparative ecology of neotropical bird lice (Insecta, Phthiraptera). Journal of Animal Ecology 61:781–795.

COHEN, J. 1977. Statistical power analysis for behavioral sciences (revised ed.), Academic Press, New York.

COLEGRAVE, N., AND G. D. RUXTON. 2003. Confidence intervals are a more useful complement to nonsignificant tests than are power calculations. Behavioral Ecology 14:446-450.

COURI, M. S., L. R. ANTONIAZZI, P. BELDOMENICO, AND M. QUIROGA. 2009. Argentine *Philornis* Meinert species (Diptera: Muscidae) with synonymic notes. Zootaxa 2261:52–62.

CRAWLEY, M. J. 2007. The R book. Wiley, Chichester, UK.

DELANNOY, C. A., AND A. CRUZ. 1991. *Philornis* parasitism and nestling survival of the Puerto Rican Sharp-shinned Hawk, p. 93–103. *In* J. E. Loye and M. Zuk [EDS.], Bird–parasite interactions: ecology, evolution and behaviour. Oxford University Press, Oxford, UK.

DUDANIEC, R. Y., AND S. KLEINDORFER. 2006. Effects of the parasitic flies of the genus *Philornis* (Diptera: Muscidae) on birds. Emu 106:13–20.

DUDANIEC, R. Y., S. KLEINDORFER, AND B. FESSL. 2006. Effects of the introduced ectoparasite *Philornis downsi* on haemoglobin level and nestling survival in Darwin's Small Ground Finch (*Geospiza fuliginosa*). Austral Ecology 31:88–94.

DUDANIEC, R. Y., S. KLEINDORFER, AND B. FESSL. 2007. Interannual and interspecific variation in intensity of the parasitic fly, *Philornis downsi*, in Darwin's finches. Biological Conservation 139: 325–332.

FESSL, B., AND S. TEBBICH. 2002. *Philornis downsi*—a recently discovered parasite on the Galapagos Archipelago—a threat for Darwin's finches? Ibis 144: 445–451.

FESSL, B., S. KLEINDORFER, AND S. TEBBICH. 2006. An experimental study of the fitness costs of *Philornis downsi* in Darwin's ground finches. Biological Conservation 127:55–61.

Fraga, R. M. 1984. Bay-winged Cowbirds (*Molothrus badius*) remove ectoparasites from their brood parasites, the Screaming Cowbird (*M. rufoaxillaris*). Biotropica 16:223–226.

García, M. 1952. Las especies argentinas del género *Philornis* Mein. con descripción de especies nuevas. Revista de la Sociedad Entomológica Argentina 15:277–293.

Hurtrez-Boussèz, S., and F. Renaud. 2000. Effects of ectoparasites of young on parents' behavior in a Mediterranean population of Blue Tits. Journal of Avian Biology 31:266–269.

Hurtrez-Boussèz, S., P. Perret, F. Renaud, and J. Blondel. 1997. High blowfly parasitic loads affect breeding success in a Mediterranean population of Blue Tits. Oecologia 112:514–517.

Johnson, L. S., and D. J. Albrecht. 1993. Effects of hematophagous ectoparasites on nestling House Wrens, *Troglodytes aedon*: who pays the cost of parasitism? Oikos 66:255–262.

Kleindorfer, S., and R. Y. Dudaniec. 2009. Love thy neighbour? Social nesting pattern, host mass and nest size affect ectoparasite intensity in Darwin's tree finches. Behavioral Ecology and Sociobiology 63:731–739.

Nores, A. I. 1995. Botfly ectoparasitism of the Brown Cacholote and the Firewood-gatherer. Wilson Bulletin 107:734–738.

O'Brien, E. L., and R. D. Dawson. 2008. Parasite-mediated growth patterns and nutritional constraints in a cavity-nesting bird. Journal of Animal Ecology 77:127–134.

Proctor, H., and I. Owens. 2000. Mites and birds: diversity, parasitism and coevolution. Trends in Ecology and Evolution 15:358–364.

Quiroga, M. 2009. Host–parasite interactions between the parasitic fly *Philornis seguyi* (Diptera: Muscidae) and his host *Troglodytes aedon* (Aves: Troglodytidae): parasite life cycle and impact on host. Ph.D. dissertation, Universidad de Buenos Aires, Buenos Aires.

Rabuffetti, F. L., and J. C. Reboreda. 2007. Early infestation by botflies (*Philornis seguyi*) decreases chick survival and nesting success in Chalk-browed Mockingbirds (*Mimus saturninus*). Auk 124:898–906.

SAS Institute Inc. 1998. StatView user´s guide 5.0 SAS Institute Inc., Cary, NC.

Siegel, S., and N. Castellan Jr. 1988. Nonparametric statistics for the behavioral sciences, 2nd edition. McGraw-Hill, London.

Spalding, M. G., J. W. Mertins, P. B. Walsh, and K. C. Morin. 2002. Burrowing fly larvae (*Philornis porteri*) associated with mortality of Eastern Bluebirds in Florida. Journal of Wildlife Diseases 38:776–783.

Streby, H. M., S. M. Peterson, and P. M. Kapfer. 2009. Fledging success is a poor indicator of the effects of bird blow flies on Ovenbird survival. Condor 111:193–197.

Texeira, D. M. 1999. Myasis caused by obligatory parasites, Ib. General observations on the biology of species of genus *Philornis* Meinert, p. 51–70. *In* J. H. Guimaraes and N. Papavero [eds.], Myasis in man and animals in the Neotropical Region. Pleidae, São Paulo.

Tripet, F., and H. Richner. 1999. Density-dependent processes in the population dynamics of a bird ectoparasite *Ceratophyllus gallinae*. Ecology 80:1267–1277.

Uhazy, L. S., and W. J. Arendt. 1986. Pathogenesis associated with philornid myiasis (Diptera: Muscidae) on nestling Pearly-eyed Thrashers (Aves: Mimidae) in the Luquillo rain forest, Puerto Rico. Journal of Wildlife Diseases 22:224–237.

Young, B. E. 1993. Effects of the parasitic botfly *Philornis carinatus* on nestling House Wrens, *Troglodytes aedon*, in Costa Rica. Oecologia 93:256–262.