Sexual Differences in Life History Traits of *Philornis seguyi* (Diptera: Muscidae) Parasitizing House Wrens (*Troglodytes aedon*)

M. A. QUIROGA[1,2] AND J. C. REBOREDA[3]

Ann. Entomol. Soc. Am. 106(2): 222–227 (2013); DOI: http://dx.doi.org/10.1603/AN12084

ABSTRACT We studied life history traits of *Philornis seguyi* García, 1952 (Diptera: Muscidae) parasitizing house wrens, *Troglodytes aedon* (Vieillot) (Passeriformes: Troglodytidae), and analyzed sexual differences in the size of larvae, pupae, and adults, as well as in the length of larval and pupal stages and in adult survival. Males were larger than females at the larval, pupal, and adult stages, but there were no sexual differences in the length of larval and pupal stages, or in the time adults survived. Larvae developed in 5–6 d and started the larval-pupal molt within 24 h after abandoning the host. Pupal stage lasted for 9 d and its length was positively associated with size of the pupa. The size of the pupa was positively associated with that of the larva and the size of the adult with that of the pupa. In laboratory conditions, 86% of the larvae pupated and 75% of the pupae emerged as adults. In natural conditions, the proportion of unsuccessful pupae increased by the end of host's breeding season. The proportion of males and females that survived until the adult stage did not differ from random. Our results show that *P. seguyi* has a relatively short generation time, which would allow it a rapid population growth during the host breeding season, and indicate that intrasexual selection may have selected for large body size in *P. seguyi* males.

KEY WORDS bot ffly, *Philornis seguyi*, *Troglodytes aedon*, sexual difference

The genus *Philornis* Meinert (Diptera: Muscidae) includes 49 species of bot flies. Adults of this genus feed on decaying matter, fruits, or flowers (Teixeira 1999, Fessl et al. 2001), whereas their larvae parasitize nestling birds (Couri and Carvalho 2003). Larval habits are known for 22 species and can be divided into three groups: coprophagous, semihaematophagous, and subcutaneous. Most *Philornis* species (82%, Dudaniec and Kleindorfer 2006) are subcutaneous parasites. Each larva feeds on serous fluids, tissue debris, and blood of the host, and breathes through a small aperture it cuts in the host's integument (Skidmore 1985, Uhazy and Arendt 1986, Young 1993). In some species, larval development is completed in a 4–8-d period (Teixeira 1999) in which the larvae grow up to 1 cm or more in length and pass through three larval instars (Fraga 1984, Arendt 1985a, Skidmore 1985, Delannoy and Cruz 1991, Spalding et al. 2002). After completing its development, the larva detaches from the host and moves beneath the nest material, where it forms a puparium and pupates (Dodge 1971, Skidmore 1985, Couri et al. 2005). Larvae abandon the host either when they complete development or immediately after the host dies (Teixeira 1999, Spalding et al. 2002) and can start pupation before they are fully developed (Kinsella and Winegarner 1974, Spalding et al. 2002). Adults usually emerge from the puparium after 2 wk (Glasgow and Henson 1957, Oniki 1983, Delannoy and Cruz 1991, Spalding et al. 2002), but the length of the pupal stage can vary between 5 and 20 d depending on the species.

Most works conducted on bot flies have focused on taxonomical issues (e.g., Dodge 1955, 1968; Couri 2000; Couri and Carvalho 2003; Couri et al. 2007), or in the interactions with their hosts (e.g., Fraga 1984; Arendt 1985a, b; Delannoy and Cruz 1991; Nores 1995; Teixeira 1999; Couri et al. 2005, 2007; Rabuffetti and Reboreda 2007; Antoniazzi et al. 2011; Quiroga and Reboreda 2012). Up to now, available data for this genus is limited to 28 species, and for most of them, many aspects of the life history are unknown (Teixeira 1999, Carvalho et al. 2005, Dudaniec and Kleindorfer 2006). In particular, no previous studies have analyzed sexual differences in morphological and life history traits in bot flies.

Sexual differentiation is a fundamental characteristic of life, affecting almost every aspect of an organism (Badyaev 2002, Blanckenhorn 2005). Sexual differences in morphometric and life history variables should be considered in population models, because fecundity (Roff 1992) and mortality (Calder 1983, Peters 1983) are often positively associated with body size (Fox and Czesak 2000), which may differ between sexes. Proximate mechanisms that result in sexual di-

[1] Instituto Nacional de Limnología, Ciudad Universitaria Universidad Nacional del Litoral, Santa Fé, 3000, Santa Fe, Argentina.

[2] Corresponding author: M. A. Quiroga, Laboratorio de Ecología de Enfermedades (Facultad Ciencias Veterinarias-UNL), R. P. Kreder 2805, Esperanza, S3080HOF (e-mail: mquiroga@inali.unl.edu.ar).

[3] Departamento de Ecología, Genética and Evolución, Facultad de Ciencias Exactas and Naturales, Universidad de Buenos Aires, Pabellón II Ciudad Universitaria, C1428EGA.

morphism in insects are sexual differences in growth rates, development time or both, but these mechanisms are not well understood in insects in general (Jarošík and Honek 2007) and in bot flies in particular.

We analyze life history traits of the bot fly *Philornis seguyi* García, 1952 (Diptera: Muscidae) parasitizing house wrens, *Troglodytes aedon* (Vieillot) (Passeriformes: Troglodytidae) and 1) provide information on sexual differences in size of larvae, pupae, and adults; 2) estimate sexual differences in the length of larval and pupal stages; and 3) analyze the association between length of these stages and body size.

Materials and Methods

Study Site. The study was conducted at two sites near the city of Santa Fe, Argentina. Site A is located on the campus of Universidad del Litoral (31° 38′ S, 60° 40′ W) and site B at a private cattle ranch ≈10 km from Site A and close to the Colastiné River (31° 38′ S, 60° 35′ W). Mean monthly temperatures at our study sites are 27.6°C in January (midsummer) and 13.9°C in July (midwinter) and average annual rainfall is 1,146 ± 76 mm (mean ± SE for the period 1997–2006).

Host and Parasite Species. House wrens commonly are parasitized by bot flies (Young 1993, Couri et al. 2005) and at our study site they are parasitized by *P. seguyi* (Couri et al. 2009). We conducted our study during the host's breeding seasons (October–February) in 2004–2005, 2005–2006, 2006–2007, and 2007–2008. House wrens nest in natural and artificial cavities (Johnson 1998, Tuero et al. 2007). To facilitate data collection 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. Modal clutch size was four eggs that were incubated for 13–14 d. Nestlings fledged at 14–15 d of age with body mass of ≈12 g. Prevalence of bot fly parasitism during the study period was 25% (range: 11–33), mean intensity of parasitism was 12.8 larvae per nestling (range: 5–15), and the age of chicks at the time they were parasitized was on average 3.9 d (range, 3–6) (Quiroga and Reboreda 2012). Survival of house wren chicks is negatively associated with intensity of bot fly parasitism (Quiroga and Reboreda 2012) as occurs in most bird species parasitized by *Philornis* spp (i.e., Fessl and Tebich 2002, Rabuffetti and Reboreda 2007). Besides, bot fly parasitism may reduce mass gain (i.e., Young 1993, Fessl et al. 2006), lower hemoglobin levels (Dudaniec et al. 2006) and delay growth and development (Arendt 1985b) of host chicks.

Data Collection. The number of nests parasitized during the breeding seasons 2004–2005, 2005–2006, 2006–2007, and 2007–2008 were 8 out of 34, 15 out of 46, 4 out of 35, and 12 out of 43, respectively. For each parasitized nest we recorded the hatch day of each nestling, the day each nestling was infested with bot flies, and the maximum number of bot flies per nestling. After the nest was abandoned (i.e., all the chicks died as a result of bot fly infestation or the 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. Bot flies at the study area were determined as *Philornis seguyi* (Couri et al. 2009, Quiroga and Reboreda 2012), the same species identified for this study. Specimens of adult flies and puparia were deposited at the Museo Provincial de Ciencias Naturales Florentino Ameghino, Santa Fe, Argentina (Accessing no. MFA-ZI-9455). After the breeding season finished (i.e., end of March), we took the small sticks of each nest apart and searched for puparia. We examined each puparium under stereomicroscope (20–80×), determined whether it was empty (i.e., it was an exuvium) or not, and calculated the proportion of pupae from which adults emerged.

During the 2007–2008 breeding season we collected larvae of *Philornis seguyi* from nine parasitized broods. We put gauze (15 by 15 cm) over the incubation chamber of the nest and collected the larvae after they dropped from the chicks to pupariate. We collected larvae daily and took them to the laboratory, where they were put into individual containers of 20 cm^3 with a small piece of cotton in the bottom. The containers were kept at an ambient temperature of 15–30°C and a photoperiod of ≈14:10 (L:D) h. We visually inspected each larva daily and recorded the day each larva started pupariation and the day each adult emerged from the puparium. At 2 d of age we recorded the weight (±0.01 g), length, and width (±0.1 mm) of the puparia. After emergence we transferred the adult to individual containers (60 cm^3) that contained ≈10–20 cm^3 of cow dung. We kept the adult in the container until it died and then, we determined its weight (±0.01 g), the lengths of body and right wing, the width of the thorax (±0.1 mm), and the sex under a stereomicroscope (20–80×) by using the methods of Couri (1999). We used the sex of adults to assign sex to pupae and larvae.

We calculated the length of the larval period for each brood as the time elapsed (in days) because we detected the presence of larvae in the chicks until 50% of the larvae dropped from the chicks. For each larva we calculated the length of the pupation period as the time elapsed because we observed the first evidence of pupa formation and adult emergence. Finally, we calculated the longevity of each adult as the time elapsed because it emerged from the pupa until it died.

Statistical Analysis. We tested sexual differences in morphometric and life history variables using analysis of variance (ANOVA) with sex nested with brood, as larvae from the same brood are not independent. We considered the brood from which larvae emerged as a random variable (brood), the sex of each larva as an independent variable (sex), and the morphometric and life history variables as dependent variables. To analyze if the sex ratios differed from random and if morphometric variables had an effect on larval pupation and rates of adult emergence and survival we used a generalized linear model (GLM) with a binomial error structure and logit-link function (Crawley 2007). We also included sex as a fixed effect and nest

Table 1. Values of morphometric variables for male and female larvae, pupae, and adults of the bot fly *P. seguyi* from season 2007–2008

	Larvae		Pupae		Adults	
	Males	Females	Males	Females	Males	Females
Weight (grams)	0.12 ± 0.002 (64)	0.10 ± 0.002 (95)	0.08 ± 0.001 (121)	0.06 ± 0.002 (150)	0.04 ± 0.003 (109)	0.02 ± 0.001 (120)
Length (millimeters)	—	—	9.04 ± 0.118 (121)	8.39 ± 0.103 (150)	8.97 ± 0.098 (109)	7.77 ± 0.081 (120)
Width	—	—	4.23 ± 0.049 (121)	3.89 ± 0.042 (150)	3.54 ± 0.046 (109)	3.16 ± 0.032 (120)
Development (d)	5.46 ± 0.106 (148)	5.44 ± 0.099 (160)	9.08 ± 0.096 (148)	8.93 ± 0.089 (157)	—	—
Wing length (millimeters)	—	—	—	—	8.68 ± 0.089 (109)	7.57 ± 0.062 (120)
Survival (d)	—	—	—	—	5.77 ± 0.154 (114)	5.16 ± 0.156 (119)

Values between parentheses indicate sample size.

as a random effect. For this analysis we used the package lme4 from r software, version 2.13.0.

To analyze the association among variables we used partial correlations that described the linear relationship between two variables while controlling for brood and sex. The number of bot flies used in different analysis varied because 1) not all the larvae we collected ($n = 461$) pupariated and not all pupae resulted in emerging adults, and 2) we did not measure every variable in all cases. All statistical tests were two-tailed with α set at 0.05 and reported values are mean ± SE.

Results

Table 1 shows values for morphological and life history variables of male and female bot flies from season 2007–2008. The length of the larval period was 5.5 ± 0.07 d (range, 2–8 d, $n = 321$ larvae) and did not differ between males and females, but differed among broods (nested ANOVA; sex: $F = 1.25$; df = 1,8; $P = 0.27$; brood: $F = 39.8$; df = 1,8; $P < 0.001$). At the time of abandoning the chicks, male larvae were significantly heavier than female larvae and there were weight differences among broods (nested ANOVA; sex: $F = 10.59$; df = 1,8; $P = 0.005$; brood: $F = 3.98$; df = 1,8; $P = 0.03$).

The percentage of larvae that pupariated in laboratory conditions was 86.3% (398 out of 461) and we found no differences in mass between larvae that pupated and those that did not (GLM $Z = -0.21$; $P = 0.834$). In 78% of the cases, the larval-pupal molt started within 24 h of the larvae abandoning the chick, whereas in the remaining 22% of the cases, it started between 24 and 48 h. There was a positive association between the mass of the pupae and that of the larvae (partial correlation: $R = 0.213$; df = 154; $P = 0.007$). Male pupae were significantly heavier (nested ANOVA; sex: $F = 26.46$; df = 1,8; $P < 0.001$), longer (nested ANOVA; sex: $F = 13.15$; df = 1,8; $P < 0.001$), and wider (nested ANOVA; sex: $F = 13.92$; df = 1,8; $P < 0.001$, Table 1) than female pupae. We also detected differences among broods in mass (nested ANOVA; brood: $F = 3.5$; df = 1,8; $P = 0.05$), length (nested ANOVA; brood: $F = 45.83$; df = 1,8; $P < 0.001$), and width (nested ANOVA; brood: $F = 20.77$; df = 1,8; $P < 0.001$). The length of the pupal stage in laboratory conditions was on average 9.0 ± 0.07 d (range, 6–12 d, $n = 305$) and did not differ between males and females (nested ANOVA; sex: $F = 0.385$; df = 1,8; $P = 0.54$. Table 1), but there were differences among broods (nested ANOVA; brood: $F_{1,8} = 14.2$, $P < 0.001$). There was a positive association between the length of the pupal stage and the size of the pupa (partial correlation: mass: $R = 0.25$, df = 267, $P < 0.001$; length: $R = 0.16$, df = 267, $P = 0.01$; width: $R = 0.223$, df = 267, $P < 0.001$).

We observed that for larvae that underwent pupation on the base of the nest in natural conditions, there was a positive association between the date (time of the breeding season) at which the brood was parasitized and the proportion of pupae from which adults did not emerge (Spearman rank correlation, $r = 0.38$, $n = 31$ nests, $Z = -2.08$, $P = 0.04$. Figure 1). The percentage of pupae from which adults emerged was 75% (346 out of 461). Pupae from which adults emerged were not morphologically different compared with those from which adults did not emerge (mass: GLM $Z = -0.562$, $P = 0.574$; length: GLM $Z = -0.34$, $P = 0.729$; width: GLM $Z = 1.44$, $P = 0.15$).

The sex ratio of adults did not differ from random when considering all broods together (males: GLM $Z = 0.27$, $P = 0.79$; females: GLM $Z = -0.27$, $P = 0.79$. Table 2), but in three of nine broods the sex ratio was biased (in two broods male biased and in one brood female biased).

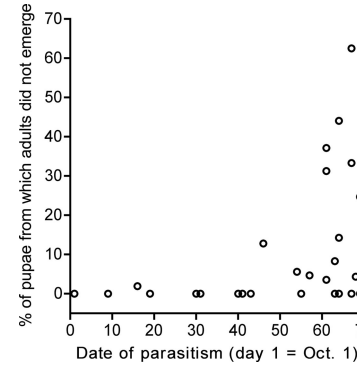

Fig. 1. Percentage of pupae from which did not emerge adults as the breeding season of the host progresses. Data correspond to 31 house wren (*T. aedon*) nests that were parasitized at different times of the breeding season of the host (from 2 October to 9 December).

Table 2. Number of larvae collected sexed as adults and proportion of males in nine broods of house wrens (*T. aedon*) parasitized by bot flies (*P. seguyi*). The *P* value indicates if the sex ratio (proportion of males versus proportion of females) differs significantly from random

Brood	No. larvae	Proportion of males	*P*
C22	36	0.53	0.43
C23	45	0.49	0.5
C4	33	0.61	<0.0001
C44	29	0.55	0.35
F4	31	0.77	0.002
P69	60	0.43	0.18
P92	40	0.48	0.43
P152	41	0.37	0.05
P165	30	0.37	0.1
All broods	346	0.53	

There was a positive association between the size of the pupae and that of adults (partial correlation of body mass of pupae and dry body mass of adults $R = -0.20$, df = 181, $P = 0.006$; length of the pupa versus length of adult body: $R = 0.39$, df = 181, $P < 0.001$; and width of the pupa versus width of adult body: $R = 0.31$, df = 181, $P < 0.001$). Adult males were significantly heavier (nested ANOVA; sex: $F = 13.75$; df = 1,8; $P = 0.008$), longer (nested ANOVA; sex: $F = 282.81$; df = 1,8; $P < 0.001$), and wider (nested ANOVA; sex: $F = 14.59$; df = 1,8; $P = 0.007$) and had longer wings (nested ANOVA; sex: $F = 70.77$; df = 1,8; $P < 0.001$) than females. For all variables except body mass, there were significant differences among broods (body length: $F = 44.41$; df = 1,8; $P < 0.001$; body width: $F = 4.02$; df = 1,8; $P = 0.042$; wing length: $F = 4.41$; df = 1,8; $P = 0.025$; body mass: $F = 2.09$; df = 1,8; $P = 0.176$). Adult bot flies survived on average 5.46 ± 0.11 d (males and females combined, range 2–10, $n = 233$) and there were no sexual differences in the time they survived (nested ANOVA; sex: $F = 0.68$; df = 1,8; $P = 0.43$), but there were differences in survival among individuals coming from different broods (nested ANOVA; $F = 4.72$; df = 1,8; $P = 0.017$). We did not find any association among morphological variables and the time adults survived (partial correlation; body mass: $R = 0.005$, df = 224, $P = 0.937$; width: $R = 0.042$, df = 224, $P = 0.533$; body length: $R = 0.085$, df = 224, $P = 0.204$; wing length: $R = 0.036$, df = 224, $P = 0.595$).

Discussion

We describe for the first time sexual differences in life history traits of one bot fly species (*Philornis seguyi*) and analyze sexual differences in morphological and life history variables. We found 1) males were larger than females at the larval, pupal, and adult stages, but there were no sexual differences in the length of the larval and pupal stages or in the time adults survived; 2) the size of the adult was positively associated with that of the pupa, and the size of the pupa with that of the larva; 3) larvae developed in 5–6 d and started the larval-pupal molt within 24 h after abandoning the host; 4) the pupal stage lasted for 9 d and its length was positively associated with its size of the pupa; 5) in laboratory conditions 86% of the larvae pupated and 75% of the pupae emerged as adults; 6) in natural conditions, the proportion of pupae from which adults did not emerge increased as the date of the breeding season of the host advanced; and 7) the proportion of males and females that survived until the adult stage did not differ from random.

Sexual size dimorphism is widespread in the animal kingdom (Shine 1989, Fairbairn 1997) and in most insect taxa is female-biased (Blanckenhorn et al. 2007). Contrary to this general pattern, we found that in *P. seguyi*, males were larger than females at the larval, pupal, and adult stages. For any particular species, which sex is larger depends on differing selection for or against large body size in the two sexes (Andersson 1994, Fairbairn 1997, Blanckenhorn 2000). Generally, an increase in female fecundity with body size selects for larger females than males, and intrasexual selection selects for larger males than females; whereas viability selects against body size in both sexes. Hence, it seems reasonable to postulate that intrasexual selection has selected for large body size in *P. seguyi* males. Further studies analyzing male–male competition in natural or experimental conditions are necessary to confirm this hypothesis. Although there were clear sexual differences in size, we did not find sexual differences in duration of the larval and pupal stages. Hence, sexual size dimorphism was likely to arise as a result of different growth rates of males and females. However, we cannot completely exclude the possibility that sexual size dimorphism was likely a result of sexual differences in length of the larval or pupal periods, as our estimation for the length of these periods was measured in days and not in hours.

We did not detect sexual differences in adult survival. Other studies in Diptera have reported a positive association between adult size and survival (i.e., Ohgushi 1996, Antonaci Gama et al. 2005, Salavert et al. 2011). However, is it possible that the laboratory conditions in which we kept adults affected our measurement of adult survival. The only study on adult survival of bot flies was conducted by Lincango and Causton (2008), who reared *Philornis downsi* (Dodge & Aitken) in Galapagos Islands and were able to kept alive females for 130 d and males for 55 d. In this study, adults were fed on a mixture of papaya juice, powdered milk, and hydrolyzed proteins and reared in larger cages than the ones we used (i.e., 126,000 versus 60 cm^3). These differences in rearing conditions may explain, in part, differences in survival between *P. downsi* and *P. seguyi.*

We observed a significant effect of the host brood on the length of larval and pupal stages and on adult longevity as well as on sexual differences in size at the larval, pupal, and adult stages. Because of the relatively small number of broods we did not have enough power to analyze the possible causes of these differences, but it seems likely that intensity of parasitism or how long host chicks survived bot fly infestation have affected morphological and life history variables of bot flies.

Our results show that for this species, the period elapsed since chicks were parasitized and adult emergence was ≈15 d. If we assume that female bot flies mate soon after emergence, the generation time for this species would be <20 d. This relatively short generation time would allow a rapid population growth, particularly in temperate zones, where is expected that very few adults had survived through winter. This rapid population growth is consistent with the pattern observed in temperate bot fly populations of a positive association between date of the breeding season and frequency and intensity of bot fly parasitism (i.e., Rabuffetti and Reboreda 2007, Segura and Reboreda 2011). In addition, the increase in the proportion of pupariae from which adults did not emerge, as the host breeding season advances, may indicate that the probability of pupariae entering diapause increases as the end of the host breeding season approaches. Thus, one interpretation for the increase in frequency and intensity of parasitism with date of the breeding season is that at the beginning of the season there are very few adults (those emerging from pupae that entered in diapause at the end of the previous breeding season), but as the breeding season progresses and new adult bot flies parasitize host chicks, the population increases and consequently, frequency and intensity of parasitism increases.

Finally, we found that in laboratory conditions ≈86% of the larvae pupated and 75% of the pupae emerged as adults. Because we only could determine the sex after the adults emerged, we could not determine whether there were sexual differences in survival along the larval or pupal stages. However, considering all the broods analyzed, the sex ratio of emerging adults did not differ from 1:1. Therefore, if we assume that the primary sex ratio was 1:1, then survival in larval and pupal stages would not differ between sexes.

To summarize, this work shows that males of *P. seguyi* are larger than females at the larval, pupal, and adult stages and that this species has a relatively short life cycle, which would allow rapid population growth.

Acknowledgments

We thank the University Nacional del Litoral (UNL), Centro Regional de Investigación y Desarrollo de Santa Fe Consejo Nacional de Investigaciones Científicas y Técnicas (CERIDE-CONICET), and Francisco Caminos for allowing us to conduct this study on their grounds. We are very grateful to M. Couri, at the Museu Nacional, Federal University of Rio de Janeiro, who helped us identify adult flies. We also thank L. Auce and R. Lorenzon for field assistance and R. Regner, E. Lordi, and E. Creus, Instituto Nacional de Limnología-Consejo Nacional de Investigaciones Científicas y Técnicas-University Nacional del Litoral (INALI-CONICET-UNL) for their invaluable help setting up and maintaining nest boxes.

References Cited

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ.

Antonaci Gama, R., K. Carvalho Alves, R. Ferreira Martins, A. Eiras, and M. Carvalho de Resende. 2005. Efeito da densidade larval no tamanho de adultos de *Aedes aegypti* criados em condições de laboratório. Rev. Soc. Bras. Med. Trop. 38: 64–66.

Antoniazzi, L., D. Rohrmann, M. Saravia, L. Silvestri, and P. Beldomenico. 2011. Climate variability affects the impact of parasitic flies (*Philornis torquans*) on Argentinean forest birds. J. Zool. 753: 1–9.

Arendt, W. 1985a. *Philornis* ectoparasitism of pearly-eyed thrashers I. Impact on growth and development of nestlings. Auk 102: 270–280.

Arendt, W. 1985b. *Philornis* ectoparasitism of pearly-eyed thrashers II. Effects on adults and reproduction. Auk 102: 281–292.

Badyaev, A. 2002. Growing apart: an ontogenetic perspective on the evolution of sexual size dimorphism. Trends Ecol. Evol. 17: 369–378.

Blanckenhorn, W. 2000. The evolution of body size: what keeps organisms small? Q. Rev. Biol. 75: 385–407.

Blanckenhorn, W. 2005. Behavioral causes and consequences of sexual size dimorphism. Ethology 111: 977–1016.

Blanckenhorn, U., A. Dixon, D. Fairbairn, M. Foellmer, P. Gibert, K. van der Linde, R. Meier, S. Nylin, S. Pitnick, C. Schoff, et al. 2007. Proximate causes of Rensch's rule: does sexual size dimorphism in arthropods result from sex differences in development time? Am. Nat. 169: 245–267.

Calder, W. 1983. Body size, mortality and longevity. J. Theor. Biol. 102: 135–144.

Carvalho, C., A. Pont, D. Pamplona, and S. Lopes. 2005. A catalogue of the Muscidae (Diptera) of the Neotropical region. Zootaxa 860: 1–282.

Couri, M. 1999. Myiasis caused by obligatory parasites. Ia. *Philornis* Meinert (Muscidae), pp. 51–70. *In* J. Guimaraes and N. Papavero (eds.), Myasis in man and animals in the Neotropical region. Pleidae, São Paulo, Brazil.

Couri, M. 2000. A new species of *Philornis* Meinert from Galapagos Is. (Diptera, Muscidae). Bol. Museo Nac. Serie Zool. 414: 1–6.

Couri, M., and C. Carvalho. 2003. Systematic relations among *Philornis Meinert, Passeromyia* Rodhain and Villeneuve and allied genera (Diptera, Muscidae). Braz. J. Biol. 63: 223–232.

Couri, M., F. Rabuffetti, and J. Reboreda. 2005. New data on *Philornis seguyi* García, 1952 (Diptera, Muscidae). Braz. J. Biol. 65: 29–41.

Couri, M., M. Troy, and P. Hoebeke. 2007. *Philornis fasciventris* (Wulp) (Diptera: Muscidae): description of the male, larva and puparium, with notes on biology and host association. Neotrop. Entomol. 36: 889–893.

Couri, M., L. Antoniazzi, P. Beldomenico, and M. Quiroga. 2009. Argentine *Philornis* Meinert species (Diptera: Muscidae) with synonymic notes. Zootaxa 2261: 52–62.

Crawley, M. 2007. The R book. Wiley Ltd., Chichester, United Kingdom.

Delannoy, C., and A. Cruz. 1991. *Philornis* parasitism and nestling survival of the Puerto Rican sharp-shinned hawk. Bird–parasite interactions, pp. 93–103. *In* J. Loye and M. Zuk (eds.), Ecology, evolution and behaviour. Oxford University Press, Oxford, United Kingdom.

Dodge, H. 1955. New muscid flies from Florida and West Indies. Fla. Entomol. 38: 147–151.

Dodge, H. 1968. Some new and little known species of *Philornis* (Diptera: Muscidae). J. Kans. Entomol. Soc. 41: 155–164.

Dodge, H. 1971. Revisional studies of flies of the genus *Philornis* Meirnret (Diptera: Muscidae). Stud. Entomol. 14: 458–459.

Dudaniec, R., and S. Kleindorfer. 2006. Effects of the parasitic flies of the genus *Philornis* (Diptera: Muscidae) on birds. Emu 106: 13–20.

Dudaniec, R., 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 Ecol. 31: 88–94.

Fairbairn, D. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annu. Rev. Ecol. Syst. 28: 659–687.

Fessl, B., and S. Tebich. 2002. *Philornis downsi* – a recently discovered parasite on the Galápagos archipelago – a threat for Darwin's finches? Ibis 144: 445–151.

Fessl, B., M. Couri, and S. Tebbich. 2001. *Philornis downsi* Dodge and Aitken, new to the Galapagos Islands (Diptera, Muscidae). Stud. Dipterol. 8: 317–322.

Fessl, B., S. Kleindorfer, and S. Tebbich. 2006. An experimental study of the fitness costs of *Philornis downsi* in Darwin's ground finches. Biol. Conserv. 127: 55–61.

Fox, C., and M. Czesak. 2000. Evolutionary ecology of progeny size in arthropods. Annu. Rev. Entomol. 45: 341–369.

Fraga, R. 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. Rev. Soc. Entomol. Argent. 15: 277–293.

Glasgow, L., and R. Henson. 1957. Mourning dove nestlings infested with larvae of *Philornis.* Wilson Bull. 69: 183–184.

Jarošík, V., and A. Honek. 2007. Sexual differences in insect development time in relation to sexual size dimorphism, pp. 205–211. *In* D. Fairbairn, W. Blanckenhorn, and T. Székely (eds.), Sex, size and gender roles. Oxford University Press, Oxford, United Kingdom.

Johnson, L. 1998. House wren (*Troglodytes aedon*). *In* A. Poole and F. Gill (eds.), The birds of North America no. 380. The birds of North America Inc., Philadelphia, PA.

Kinsella, J., and C. Winegarner. 1974. Notes on the life history of *Neomusca porteri* (Dodge), parasitic on nestlings of the great crested flycatcher in Florida. J. Med. Entomol. 11: 633.

Lincango, P., and C. Causton. 2008. Crianza en cautiverio de *Philornis downsi*, en las islas Galápagos - Internal Report. Charles Darwin Foundation, Puerto Ayora, Ecuador.

Nores, A. 1995. Botfly ectoparasitism of the brown cacholote and the firewood-gatherer. Wilson Bull. 107: 734–738.

Ohgushi, T. 1996. Consequences of adult size for survival and reproductive performance in a herbivorous ladybird beetle. Ecol. Entomol. 21: 47–55.

Oniki, Y. 1983. Notes on fly (Muscidae) parasitism of nestlings of South American birds. Le Gerfaut 73: 281–286.

Peters, R. 1983. The ecological implications of body size. Cambridge University Press, Cambridge, United Kingdom.

Quiroga, M., and J. Reboreda. 2012. Lethal and sublethal effects of botfly (*Philornis seguyi*) parasitism on house wren (*Troglodytes aedon*) nestlings. Condor 114: 197–202.

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

Roff, D. 1992. The evolution of life histories: theory and analysis. Chapman & Hall, New York.

Salavert, V., C. Zamora-Muñoz, M. Ruiz-Rodriguez, and J. Soler. 2011. Female-biased size dimorphism in a diapausing caddisfly, *Mesophylax aspersus:* effect of fecundity and natural and sexual selection. Ecol. Entomol. 36: 389–395.

Segura, L., and J. Reboreda. 2011. Botfly parasitism effects on nestling growth and mortality of red-crested cardinals. Wilson J. Ornithol. 123: 107–115.

Shine, R. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Q. Rev. Biol. 64: 419–461.

Skidmore, P. 1985. The biology of the Muscidae of the world. Junk Publishers, Dordrecht, the Netherlands.

Spalding, M., J. Mertins, P. Walsh, and K. Morin. 2002. Burrowing fly larvae (*Philornis porteri*) associated with mortality of eastern bluebirds in Florida. J. Wildl. Dis. 38: 776–783.

Teixeira, D. 1999. Myasis caused by obligatory parasites, Ib. General observations on the biology of species of genus *Philornis* meinert, pp. 51–70. *In* J. Guimaraes and N. Papavero (eds.), Myasis in man and animals in the Neotropical region. Pleidae, São Paulo, Brazil.

Tuero, D., V. Fiorini, and J. Reboreda. 2007. Effects of shiny cowbird *Molothrus bonariensis* parasitism on different components of house wren *Troglodytes aedon* reproductive success. Ibis 149: 521–529.

Uhazy, L., and W. Arendt. 1986. Pathogenesis associated with philornid myiasis (Diptera: Muscidae) on nestling pearly-eyed thrashers (Aves: Mimidae) in the Luquillo Rain Forest, Puerto Rico. J. Wildl. Dis. 22: 224–237.

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

Received 12 July 2012; accepted 30 October 2012.