# Development of *Pseudacteon nocens* (Diptera: Phoridae) on *Solenopsis invicta* and *Solenopsis richteri* Fire Ants (Hymenoptera: Formicidae)

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**ABSTRACT**   We studied the developmental performance of the large morph of *Pseudacteon nocens* Borgmeier (Diptera: Phoridae), a prospective biological control agent of imported fire ants (Hymenoptera: Formicidae). We measured selected life history traits of this parasitoid as a function of 1) host species (*Solenopsis invicta* Buren versus *Solenopsis richteri* Forel), 2) temperature (22 versus 28°C), 3) source population of the fly (Corrientes and Santiago del Estero, Argentina), and 4) varied size distributions of offered host ants. Developmental periods were influenced by host species, although the populations responded in opposing manners. Developmental times, however, were most strongly influenced by temperature with total developmental periods lengthened by 17–32% at 22°C. Pupal mortality was also significantly lower at this temperature. Although numbers of progeny per female were significantly higher for the Corrientes population, we found no significant differences in progeny per female according to host species. Interestingly, we found that females were larger than males, and flies from Corrientes were larger than those from Santiago del Estero, even after statistical adjustments for host size. The modal frequency of host size elected in all treatment combinations tested was identical (0.6 mm), a size that represented the apparent threshold for producing female progeny. These laboratory and additional field observations demonstrate considerable interpopulational variation in *P. nocens* and lend further support to the applied approach focusing at the population, as opposed to the species level, with respect to both source and target areas for classical biological control introductions of *Pseudacteon* flies.

**KEY WORDS**   Argentina, biological control, body size, parasitoid, biotype

Exotic insects often become serious invasive pests as a result of escaping from natural enemies (Van den Bosch et al. 1982, Shea and Chesson 2002). One such invader is the imported fire ant, *Solenopsis invicta* Buren. After first leaving central South America in the 1930s, it is now found extensively through the southern United States (Callcott and Collins 1996, Dowell et al. 1997) and the Caribbean (Davis et al. 2001) as well as along the eastern Pacific brim in Australia and New Zealand (McCubbin and Weiner 2002) as well as Taiwan, Malaysia, Hong Kong, Macau, and southern China (Na and Lee 2001, Anon. 2005). All along much of this wide-ranging path, its high population densities and voracious appetite have caused serious ecological problems (Porter and Sauvignon 1990). Porter et al. (1997) compared a wide range of potential factors that might have contributed to fire ant-elevated densities in its new range relative to its source areas. By a process of elimination, they concluded that the higher abundance and diversity of natural enemies in the fire ant's home range was the most likely contributor to this relative difference in densities. In a situation that seems so clearly a result of reduced natural enemy regulation, classical biological control can be considered an important element of integrated pest management (Van den Bosch et al. 1982).

One group of natural enemies currently being used in classical biological control efforts for the red imported fire ant, and the related black imported fire ant, *Sopenopsis richteri* Forel, is the decapitating phorid flies in the genus *Pseudacteon* (Gilbert and Patrock 2002, Porter et al. 2004, Graham et al. 2003). Although these flies are unlikely to reduce fire ant populations by direct mortality (Morrison 2000, Morrison and Porter 2004), their potential role in limiting fire ants is thought to result from their mediation of ant–ant competition at food resources (Feener and Brown 1992, Orr et al. 1995, Folgarait and Gilbert 1999). Their safety has been a important contributor to their acceptance for classical biological control because these flies exhibit high levels of specificity toward their hosts (Porter and Gilbert 2004; Porter et al. 1995a,b; Gilbert and Morrison 1997; Porter and Alonso 1998; Morrison and Gilbert 1999; Folgarait et al. 2002b).

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The common name for *Pseudacteon* species, decapitating flies, stems from their life history as koinobiontic parasitoids of adult ants, that is, as immatures they feed on a living host before killing it (Disney 1994). The female is first attracted to worker ants under a number of conditions, such as at disturbed mounds, mating flights, or when they are foraging for food. When she has located an appropriate host, she injects in midflight an egg into the ant's thorax, by using species-specific ovipositors resembling tools such as knives or pitchforks. In a sequence of events described by Consoli et al. (2001), the larvae hatches from the egg, migrates to the head of the host, and feeds. At some point, however, the ant dies and its head falls off (decapitates), revealing the fly pupae within the severed head capsule. Adult emergence typically follows within weeks of this event. As might be expected from this description, individual and group fire ant worker behavior is dramatically affected when female flies are attacking (Wuellner et al. 2002) and forms the basis for how these flies may mediate food resource competition.

We assume that any classical biological control program incorporating decapitating flies will involve establishing a set of species because we do not think a single species will be sufficient to impact fire ant populations. Communities of these flies in South America, typically consist of five to 10 species (Orr et al. 1997; Folgarait et al. 2003, 2005a) with individual species affecting the ants in contrasting ways, including using different-sized workers (Campiolo et al. 1994), partitioning their time of attacks by day or season (Pesquero et al. 1996, Folgarait et al. 2003) or by the ants' activity, density, or location (Orr et al. 1997). Given this variation in attack modes, the introduction of complementary species should probably be designed to imitate the community structure and dynamics of the flies in the native range of the fire ants in South America.

Our work has been focused on the selection, rearing, and establishment of *Pseudacteon* species into central and southern Texas where climatic conditions are among the most extreme with respect to aridity within the range of imported fire ants (Gilbert and Patrock 2002, Morrison et al. 2004). To meet our long-range goals, we wanted to identify species that will be able to survive under a wide range of variable conditions, such as are found in southern Texas. This study is part of a series that examines how host and environmental conditions might affect immature performance of a candidate species, in this article, *P. nocens* Borgmeier. Below, we address some of the reasons for questions we are pursuing in our study.

Populational source of a *Pseudacteon* species can be an important consideration in the choice of a classical biological control introduction because of the observed wide-ranging populational variation in the genus with respect to use of host species and size and climatic tolerance. For example, *Pseudacteon curvatus* Borgmeier from the Rio Plata area of Argentina show little interest in *S. invicta*, but they are fond of *S. richteri* (Porter and Briano 2000). Conspecific flies

from the Formosa area of Argentina in comparison have the reverse preference as well as being much more host specific with respect to their ability to parasitize workers and their attraction to ants in the field (Vazquez et al. 2004). Introductions of this species have been successful only where their preferred hosts were predominant (Graham et al. 2003). Along with the differences in preferences toward the imported fire ants, flies associated with *S. richteri* showed lower aggressive activity toward native fire ants than those of Argentina and Brazilian populations associated with *S. invicta* (Porter and Gilbert 2004).

An important practical issue related to matching *Pseudacteon* species with *Solenopsis* fire ants in Texas is the distribution of worker sizes within a colony (Gilbert and Patrock 2002). Sex determination in three of the five documented species, *Pseudacteon tricuspis* Borgmeier, *Pseudacteon litoralis* Borgmeier and *Pseudacteon obtusus* Borgmeier, is size dependent (Morrison et al. 1999; Folgarait et al. 2005b) with females emerging from larger ants, whereas males emerge from smaller ants. Worker size in fire ants is related to social form with smaller ants being found in colonies with multiple queens (polygyne) and larger workers in colonies with single queens (monogyne) (Greenberg et al. 1985). In Texas, especially in the central and southern areas of the state, the polygyne form predominates and worker sizes available for oviposition can lead to progeny having very male biased ratios. Host size and sex ratios is therefore an important consideration in estimating reproductive performance of *Pseudacteon.* In addition, Morrison et al. (1999) found host size-related differences in the same populations of *P. tricuspis* and *P. litoralis* reared from different populations of ants (Brazil and Texas), suggesting that components of interpopulational variation in *Pseudacteon* might be induced by interpopulational host variation or other rearing conditions.

*P. nocens* is found across much of northern Argentina (Calcaterra et al. 2005; Folgarait et al. 2005a) in varying climatic conditions ranging from the mesic north central to the arid west. Whereas *S. invicta* is found throughout this distribution, other *Solenopsis* species, including *S. richteri* (Calcaterra et al. 2005), *Solenopsis macdonaghi* Santschi, *Solenopsis quinquecuspis* Forel (Folgarait et al. 2002b), and *Solenopsis interrupta* Santschi (P.J.F., personal observation) are potential hosts. We have been monitoring *Pseudacteon* for a number of years in two Argentinean locations that differ substantially in their phytogeography and climate (Schwerdtfeger 1976, Cabrera 1980). This study examines how contrasting environmental conditions such as host and temperature affect the immature performances of flies from these populations. Because host size affects resulting body size of *Pseudacteon* and body size is an important predictor of fecundity and other life history parameters (Calder 1984, Atkinson 1994), we examined the interplay between host and resulting parasitoid sizes as well.

## Materials and Methods

We discuss many of the details of our methods in Folgarait et al. (2002a) and in Folgarait et al. (2005b). Here, we provide a brief overview of our methodology and relate specific information that differs from those studies.

We compared two populations of Argentinean *P. nocens:* a northeastern population from Mercedes, Corrientes Province (27.78° S and 58.05° W) in the mesic Mesopotamia region and a population from the dry Chaco, near Brea Pozo, Santiago del Estero (28.27° S and 63.95° W). Specimens were collected in the field up to three times per month from June 2002 to June 2004. Once collected, the flies were placed in separate plastic vials (10 by 40 mm) and transported in a cooler at ≈10°C to our laboratory in Buenos Aires.

An oviposition trial consisted of releasing one to six female flies into flight boxes containing 0.8 g of either ant species (Folgarait et al. 2002a). Flies were typically tested the next day but no later than 72 h after field collection. The trials were run for 3–5 h or until the flies died. Ants used came from healthy, monogyne colonies kept for <3 mo in the laboratory. *S. invicta* colonies were obtained from the same general areas around Mercedes, Corrientes and Brea Pozo, Santiago del Estero as were their parasitoid flies, whereas *S. richteri* colonies derived from the Reserva Ecológica Costanera Sur (RECS) or the Hudson site, Buenos Aires (34.62° S and 58.37° W). Each fly population was reared and on *S. invicta* from its own locality (i.e., flies from Corrientes were reared on *S. invicta* from Corrientes) and on both of the two populations of *S. richteri* hosts.

Ant host size is an important component of oviposition choice in *Pseudacteon* (Morrison and Gilbert 1998). To examine the extent to which females elected to oviposit on particular size classes we offered them ants that had been sieved into one of four size distributions: big, mix1, mix2, and small. Big ants were those that failed to pass through soil sieve size #18; medium ants were those that passed through soil sieve size #18 but not through #20, and small ants were those that passed though both soil sieve size #18 and #20. Mix1 included ≈40% small ants by weight with the difference being equally distributed between the other two classes. Mix2 was represented by approximately an equal amount of big and medium ants by weight. A rank order of these offerings from largest mean ant size offered to the flies would be Big, Mix2, Mix1 and Small. The number of ants offered in a trial was determined by weights, which were adjusted so that the same approximate number of ants was offered in each choice.

The ants were placed in one of two temperature regimes, 22 and 28°C (Folgarait et al. 2002b, 2005b) after their removal from the attack arenas. All attacked ants were inspected daily for 45 d for the appearance of pupae in the heads of dead ants. Likewise, pupae in their host's head capsule were inspected daily until adult fly emergence. Rearing conditions follow that of Folgarait et al. (2002b). A fact not made explicit in that study was that the fly pupae were kept within tightly covered Tupperware containers on moistened plaster to maintain high relative humidities (typically >90%). Humidity conditions were therefore kept much higher for pupae than for the ants containing larvae. We measured directly three developmental intervals: 1) time from day of attack to the death of the ant (time to ant death), 2) time from ant death until the head decapitated and a pupae was seen (time to decapitation), and 3) the time between pupal appearance and adult emergence (pupal developmental time). From these data, we were able to estimate five time intervals: time to ant death, time to decapitation, egg–larval developmental time, pupal (puparial) developmental time, and total developmental time. Egg–larval developmental times were calculated as the sum of the first two periods. Time units were days.

We measured five additional aspects of performance other than developmental time: 1) thoracic width of the fly (millimeters), 2) percentage males per cohort, 3) direct pupal mortality, and 4 and 5) pupal and adult efficiencies. We calculated percentage of pupal mortality as the number of nonviable pupae divided by the total number of pupae resulting from an attack trial, or cohort. Efficiencies were ratios of either the number of pupae or adults divided by the number of their possible mothers in a given attack trial. Life cycle components inherent in both efficiency measures included oviposition rates as well as larval mortality, whereas adult efficiency also incorporated pupal mortality. Maximum host ant head widths (millimeters) were also measured to determine whether phorids elected to oviposit on a certain size class of ant and to determine the extent to which ant size influenced resulting fly size or other aspects of performance. Morphological measurements were made using an ocular micrometer calibrated in 0.03-mm increments on a stereoscopic microscope (Nikon model type 102).

The data from our study was unbalanced, particularly with respect to our 22°C treatment (Tables 1 and 2). Given this constraint and because developmental times between temperature regimes were largely exclusive of one another, we split our developmental time analysis of variance (ANOVA) analyses by temperatures and restricted our analysis of developmental time within our 22°C treatment to males. Other ANOVAs performed did not incorporate this restriction because they involved other variables, including our estimates of mortality and efficiencies (host = both, temperature = both, and population = both) and our assessment of host size on resulting fly size (host = both, population = both, sex = both, sieve class = big, mix1 and mix2). This latter test was done pooling temperature regimes after considering results from Folgarait et al. (2005b) with *P. obtusus.*

We compared head size distributions using Kolmogorov–Smirnov nonparametric tests. To evaluate the relationships between host and fly sizes, we ran a two-way analysis of covariance (ANCOVA) (host = *S. invicta*, population = both and sex = both) of the flies' thoracic widths with the host ant head widths as

**Table 1. Developmental times of the Corrientes and Santiago del Estero populations of *P. nocens* (large morph) on *S. invicta* and *S. richteri* at 22°C**

| *Solenopsis* host | Pop | Sex | *n* | Developmental time (d) ± SE | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Time to ant death | Time to decapitation | Larval | Pupal | Total |
| *S. invicta* | Corrientes | Female | 106 | 28.7 ± 0.75 | 1.6 ± 0.10 | 30.2 ± 0.76 | 26.0 ± 0.35 | 56.2 ± 0.81 |
| | | Male | 174 | 27.8 ± 0.45 | 1.5 ± 0.07 | 29.2 ± 0.45 | 25.7 ± 0.32 | 54.4 ± 0.62 |
| | Santiago del Estero | Female | 36 | 26.4 ± 0.64 | 2.1 ± 0.24 | 28.1 ± 0.64 | 28.4 ± 1.15 | 56.6 ± 1.34 |
| | | Male | 134 | 25.7 ± 0.38 | 2.2 ± 0.23 | 27.8 ± 0.37 | 26.6 ± 0.31 | 54.6 ± 0.53 |
| *S. richteri* | Corrientes | Female | 52 | 31.9 ± 0.92 | 1.7 ± 0.13 | 33.6 ± 0.97 | 27.8 ± 0.77 | 61.3 ± 1.32 |
| | | Male | 177 | 31.5 ± 0.34 | 2.1 ± 0.10 | 33.5 ± 0.35 | 27.0 ± 0.3 | 60.5 ± 0.42 |
| | Santiago del Estero | Female | 1 | 24.0 | 1.0 | 24.0 | 31.0 | 55.0 |
| | | Male | 32 | 23.6 ± 0.65 | 1.7 ± 0.15 | 25.3 ± 0.66 | 27.3 ± 0.73 | 45.3 ± 3.69 |

Data are presented only for individuals where data was collected for all life cycle components.

the covariate. The ANCOVA was performed after determining the parameter slopes were not significantly different from each other.

All data were transformed before analysis to meet assumptions of equality of variance and normality using logarithmic (head and thoracic widths), square-root (development times and efficiencies) or arcsine-square root (percentage data) transformations of the variables. Scheffé post hoc tests were used to discriminate contrasts. All multiple comparisons were adjusted using Bonferroni's method to keep the $\alpha$ level = 0.05 (Miller 1991). Given that two of our developmental time measures (larval and total time) were composites of other measures, we also examined the significance of Wilk's Lambda in multivariate ANOVA tests. Statistical analysis were done using SAS 9.1 (Delwiche and Slaughter 2003).

## Results

We followed the development of 6,198 individual *P. nocens* resulting from 448 attack trials, of which 3,978 (61.2%) adults emerged. Tables 1 and 2 give specific accounts of sample sizes and developmental times in each treatment regime.

**Host Species.** We obtained first generation adults of both populations of *P. nocens* reared from *S. richteri* (novel host) as well as *S. invicta* (source host). Developmental time, in general, was strongly affected by host in both temperature regimes, although the effect depended on the population: at 22°C, pupal and total

developmental time ($F_{1, 513} = 5.67$; $P = 0.018$ and $F_{1, 513} = 7.76$; $P = 0.0055$, respectively) both differed significantly between hosts; at 28°C, days to death, days to decapitation, and pupal time differed between hosts ($F_{1, 2784} = 4.43$; $P = 0.035$, $F_{1, 2784} = 4.1$; $P = 0.043$, and $F_{1, 2784} = 8.41$, $P = 0.0038$, respectively). The Corrientes population developed more slowly on *S. richteri* than on *S. invicta* in all stages (between 2.5 and 17.9% slower), whereas, in general, the Santiago del Estero population developed faster on *S. richteri* than *S. invicta* (between 1.5 and 20.7% faster).

Wilk's Lambda was significant with respect to host ($F_5 = 2.25$, $P = 0.048$ and $F_5 = 8.42$, $P < 0.0001$ for 22 and 28°C, respectively) and host by population ($F_5 = 9.71$, $P < 0.0001$ and $F_5 = 3.06$, $P < 0.0092$ for 22 and 28°C, respectively). We would expect a significant Lambda when the composites of the developmental times differ according to treatment. We also found significant differences in Wilk's Lambda with respect to population ($F_5 = 14.4$, $P < 0.0001$ and $F_5 = 13.8$, $P < 0.0001$ for 22 and 28°C, respectively) and sex ($F_5 = 2.51$, $P = 0.0285$ for 28°C only).

**Temperature Effects.** As expected, temperature had a large effect on developmental times for all stages. Considering phorids from both hosts and both populations together, we found that the lengths of the time to ant death, time to decapitation, larval and pupal periods as well as the total developmental time were 32.3, 17.4, 31.5, 27.5, and 29.7% longer, respectively, at 22°C compared with 28°C.

**Table 2. Developmental times of the Corrientes and Santiago del Estero populations of *P. nocens* (large morph) on *S. invicta* and *S. richteri* at 28°C**

| *Solenopsis* host | Pop | Sex | *n* | Developmental time (d) ± SE | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | | Time to ant death | Time to decapitation | Larval | Pupal | Total |
| *S. invicta* | Corrientes | Female | 144 | 22.7 ± 0.53 | 1.4 ± 0.06 | 24.1 ± 0.53 | 19.3 ± 0.29 | 43.4 ± 0.63 |
| | | Male | 333 | 21.0 ± 0.25 | 1.5 ± 0.09 | 22.5 ± 0.27 | 19.1 ± 0.25 | 41.5 ± 0.38 |
| | Santiago del Estero | Female | 407 | 22.9 ± 0.47 | 1.4 ± 0.04 | 24.2 ± 0.48 | 19.7 ± 0.34 | 44.0 ± 0.59 |
| | | Male | 1,279 | 19.7 ± 0.19 | 1.5 ± 0.03 | 21.2 ± 0.20 | 18.6 ± 0.17 | 39.8 ± 0.27 |
| *S. richteri* | Corrientes | Female | 125 | 22.7 ± 0.5 | 1.5 ± 0.07 | 24.1 ± 0.5 | 21.5 ± 0.28 | 45.6 ± 0.52 |
| | | Male | 418 | 22.1 ± 0.26 | 1.6 ± 0.04 | 23.6 ± 0.26 | 19.9 ± 0.15 | 43.5 ± 0.31 |
| | Santiago del Estero | Female | 17 | 17.5 ± 1.22 | 1.7 ± 0.24 | 19.9 ± 1.40 | 19.5 ± 0.33 | 39.5 ± 1.46 |
| | | Male | 69 | 18.1 ± 0.56 | 1.7 ± 0.12 | 20.1 ± 0.65 | 19.2 ± 0.25 | 39.2 ± 0.69 |

Data are presented only for individuals where data was collected for all life cycle components.
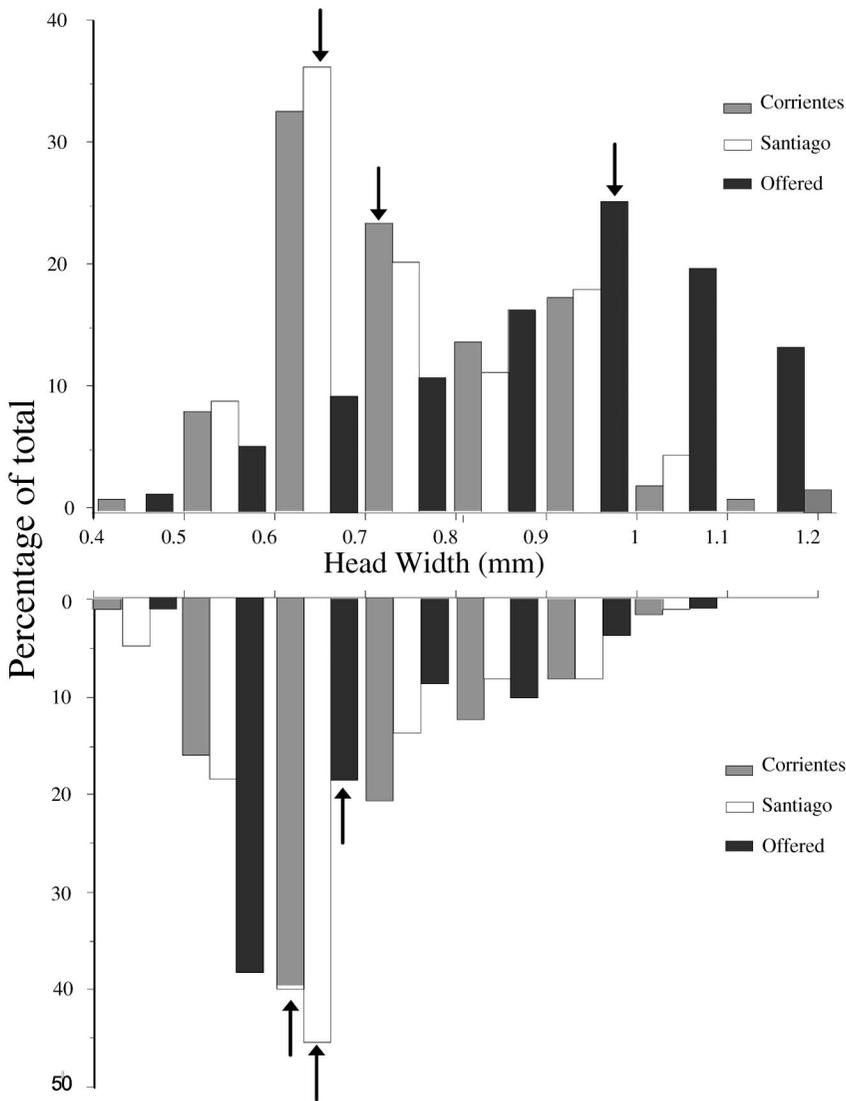
**Fig. 1.** Percentages of sieved big (top) and mixed size (bottom) of *S. invicta* ants discriminated by size classes offered to flies from the Corrientes and Santiago del Estero populations and those elected by *P. nocens*. Arrows point out the size class at which the median offered and elected fall. There were significant differences between ants offered and elected in both treatments (for further details, see text).

Developmental times within temperatures differed significantly by population and sex (within 28°C) as well as host species (host species section). Corrientes flies took significantly longer to ant death ($F_{1, 513} =$ 15.74; $P < 0.0001$), larval time ($F_{1, 513} = 59.7$; $P < 0.0001$), and total time ($F_{1, 513} = 25.4$; $P < 0.0001$) at 22°C than did flies from Santiago del Estero and significantly longer time to ant death ($F_{1, 2784} = 26.9$; $P < 0.0001$), larval time ($F_{1, 2784} = 25.1$; $P < 0.0001$), pupal time ($F_{1, 2784} = 4.65$; $P < 0.032$), and total developmental time ($F_{1, 2784} = 22.96$; $P < 0.0001$) at 28°C than did the Santiago population. Females, in general had significantly longer developmental times than males ($P < 0.026$ at both temperatures and for all variables except for time to decapitation).

**Host Size and Election.** Head widths chosen by *P. nocens* differed significantly by host, population, and sex in our three-factor ANOVA (host, population, and sex). *S. richteri* heads were larger ($0.70 \pm 0.12$ mm [mean $\pm$ SD], $F_{1, 3678} = 11.5$; $P = 0.0007$) than those of *S. invicta* ($0.67 \pm 0.13$ mm). Measured host heads of Corrientes flies ($0.71 \pm 0.12$ mm; $F_{1, 3678} = 27.1$; $P < 0.0001$) were larger than those from Santiago del Estero ($0.66 \pm 0.13$ mm) and host heads of females ($0.83 \pm 0.11$ mm; $F_{1, 3678} = 871.1$; $P < 0.0001$) were larger than those of males ($0.63 \pm 0.09$ mm).

The size distribution of heads of those workers found parasitized by *P. nocens* differed significantly from that offered for both host species ($P < 0.005$ for all combinations of host and ant size classes; Kolmog-
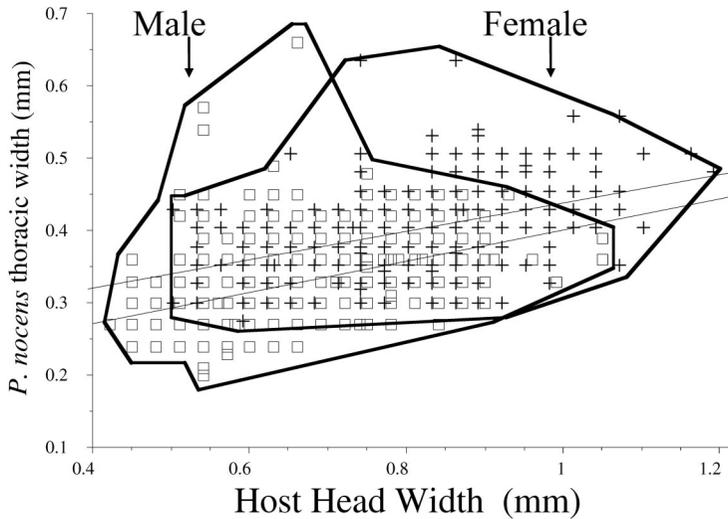
**Fig. 2.** Regressions of host ant head size against the resulting fly thoracic width. Female thoracic widths and the head sizes of the ants they emerged from were both significantly larger than those for males. Male thoracic widths and host ant head sizes, however, overlap the size distribution of the females. The regression equations are 1) for males: fly thoracic width (mm) = 0.21 * host head width (mm) + 0.19 ($r^2$ = 0.23, $P$ < 0.0001); and 2) for females: fly thoracic width (mm) = 0.22 * host head width (mm) + 0.24 ($r^2$ = 0.20, $P$ < 0.0001. Flies used in these analyses were from all treatments. Polygons isolate the distributional ranges of the male and female data. Host head width distribution shared by males and females is ≈70.4% of the entire range observed.

orov–Smirnov tests) (Fig. 1). The elected head width modal frequencies were exactly the same (0.6 mm) in all host, temperature, population, and sieve class combinations (where samples were >100). The overall median elected head width was 0.67 mm and varied within combination from 0.60 to 0.77 mm. When *P. nocens* was offered "big" ants, they attacked smaller ants ($P$ < 0.0001; elected 0.67–0.78 mm and offered 0.90–0.98 mm) for all host–population combinations. When offered "small" ants, they attacked larger ants, ($P$ < 0.0001; elected 0.65–0.68, offered 0.57–0.62 mm). The medians of offered and elected for the "mixed1" size ants, however, were not significantly different ($P$ > 0.05; elected 0.6–0.69 mm and offered 0.62–0.65 for all species population combinations).

Emerging fly size, as measured by (log) thoracic width (millimeters) depended significantly on our two-way ANCOVA on fly sex ($F_{1, 2427}$ = 181.1; $P$ < 0.0001), source population of the fly ($F_{1, 2427}$ = 24.1; $P$ < 0.0001), and the covariate (log) host ant head width ($F_{1, 2649}$ = 387.2; $P$ < 0.0001). Males (0.32 ± 0.04 mm) were significantly smaller than females (0.42 ± 0.05 mm). Emerging flies from the Corrientes source population were ≈5.1% larger for females (0.44 ± 0.05 mm) and 6.6% larger for males (0.34 ± 0.04 mm) than those in the Santiago del Estero population (0.40 ± 0.05 and 0.31 ± 0.03 mm for females and males, respectively). Females developed in all host sizes except in the smallest ants, whereas males developed in almost the entire range of ant head width classes offered, except in the biggest ants (Fig. 2). Accordingly, the size of ant heads with emerging females was significantly larger than those yielding males in both species of ants. This result was obtained with all sieve

ant size class treatments ($P$ < 0.01 in all population by head size class combinations).

**Mortality.** To examine other nontemporal aspects of performance, we looked at pupal mortality, percentage of males per cohort, and our two measures of production rates (pupal and adult efficiencies) by using three-factor ANOVAs (host, temperature, and population). None of the variables were significantly different according to host. All were slightly higher in *S. richteri* than in *S. invicta* (by 3.8, 9.7, 8.0, and 20% for pupal mortality, percentage of males per cohort, and pupal and adult efficiencies, respectively).

Temperature had a significant effect on pupal mortality ($F_{1, 366}$ = 8.1; $P$ = 0.004) (Fig. 3), pupal efficiency ($F_{1, 323}$ = 12.5; $P$ = 0.0005) (Fig. 3), and adult efficiency ($F_{1, 323}$ = 9.9; $P$ = 0.0018) with 34.7, 54.9, and 47.3% higher pupal mortality and pupal and adult efficiencies in the 28 than in the 22°C treatment. Although not significantly different, percentage of males per cohort was higher (by ≈30.1%) in the 28°C treatment.

With respect to the population sources, Corrientes had significantly lower percentage of males per cohort (by ≈15%; $F_{1, 366}$ = 12.0; $P$ = 0.0006), higher pupal efficiency (by ≈20%; $F_{1, 323}$ = 12.2; $P$ = 0.0006), and higher adult efficiency (by ≈28%; $F_{1, 323}$ = 12.3; $P$ = 0.0005) than Santiago del Estero. Pupal mortality was lower (by 28%) in the Corrientes than in the Santiago del Estero population but not significantly so ($P$ = 0.06).

There was a highly significant correlation between our untransformed efficiency measures ($r$ = 0.97, $n$ = 283, $P$ < 0.0001), suggesting these measures were quantifying much of the same variation. Pupal effi-
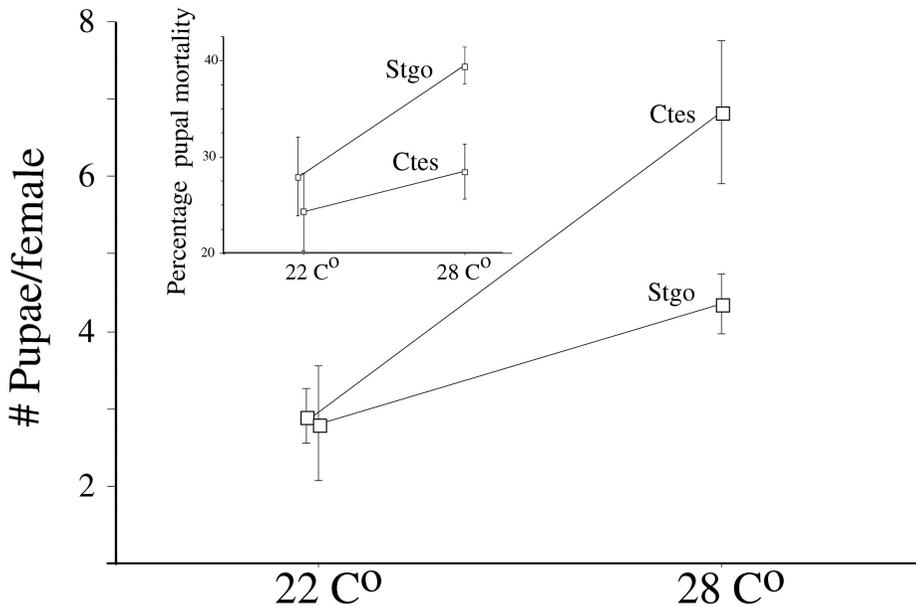
**Fig. 3.** Means and SEMs for Corrientes and Santiago del Estero fly populations according to temperature. Main figure shows pupal efficiency (number of pupae per cohort per female). Inset shows percentage of pupal mortality.

ciency was also correlated significantly with percentage pupal mortality ($r = 0.19$, $n = 283$, $P < 0.0012$). Other correlations between efficiencies, mortality, and percentage males per cohort were not significant ($P > 0.10$ for all combinations tested).

**Field Observations.** *P. nocens* has been collected across northern to central Argentina and southern Paraguay, including Entre Rios in the Mesopotamia through the dry Chaco regions of Santiago del Estero into the Andean Northwest around Salta, a distributional range of $\approx$20 to 32° S and 58 to 65° W (Borgmeier 1926, Calcaterra et al. 2005, Folgarait et al. 2005a). *P. nocens* is hosted by a number of different *Solenopsis* fire ants in addition to *S. invicta*, including *S. interrupta* in Santiago del Estero, and *S. macdonaghi* and *S. quinquecuspis* in Corrientes (P.J.F., unpublished data 1997–2003; Folgarait et al. 2002b). *S. invicta* is a common host in both of our source populations and *P. nocens* is one of the most common phorid species on all *Solenopsis* in Santiago del Estero (P.J.F., unpublished data 2000–2003; Azzimonti et al. 2004). Its temporal activity pattern is very wide; it can be found ovipositing on ants from morning until twilight, depending on the locality and season and has been found year-round in both Corrientes and Santiago del Estero (P.J.F., unpublished data 1997–2005). In western Argentina, *P. nocens* is the most frequent and abundant phorid at disturbed mounds as well as at experimentally placed baits (Azzimonti et al. 2004; R.J.W.P., unpublished observations 2003–2004). Additionally, fire ant responses to *P. nocens* can be dramatic; the ants often abandon or hide under the baits in the presence of ovipositing females. Typically, one or at most two females have been found attacking ants foraging on a bait (R.J.W.P., unpublished observations 2003–2004),

although many females are attracted to and attack ants that are set out in open tray arenas in the field.

**Discussion**

This study reports specific information on immature developmental rates and other performance measures for the *Solenopsis*-specific parasitoid *P. nocens.* Although other studies in this series (Folgarait et al. 2002a,b, 2005b; Porter et al. 1997; Porter and Briano 2000) compare performances of *Pseudacteon* species on both fire ant species (*S. invicta* and *S. richteri*) that are exotic pests in North America and examine host size and temperature effects, the novelty of this study is to document interpopulational variation in performance according to host species size and temperature.

As with all other Argentinean *Pseudacteon* we have tested, *P. nocens* was able to successfully develop on both species of imported fire ants, *S. invicta and S. richteri*, although immature performances differed substantially across populations and temperature regimes, and to some extent according to hosts. Population source had the greatest effect on fly performance, with higher production of females from Corrientes and larger flies produced as well. Higher temperatures speeded development as expected, but there were significant differences in fly production, depending on temperature and stage of immature development. Although we found differences in developmental time parameters between hosts, these differences were also dependent on the source of the population. In general, the performance of the Corrientes population as indicated by developmental times was faster on *S. invicta* than on *S. richteri,* although overall production did not differ significantly

between hosts. This difference in development fits a pattern suggested by results in Folgarait et al. (2002b) and Porter and Briano (2000) where *Pseudacteon* performed more poorly on the novel host *S. richteri.* However, because we found the population from Santiago del Estero developed significantly more quickly on *S. richteri* than *S. invicta,* host novelty per se may be an insufficient explanation for the developmental differences seen across populations. Given the fact that our efficiencies did not differ according to hosts, introductions of *P. nocens* from areas without *S. richteri* may do equally well if introduced into the southern United States for control of either imported fire ant.

An interesting aspect of *P. nocens* performance across populations was that the resulting fly size differed between populations: the flies from Corrientes were larger than those from Santiago del Estero. Because we reared the flies on hosts from their own locality, we cannot be sure whether the flies were doing better in Corrientes because of their own intrinsic abilities or because of host qualities that may differ between these disjunct populations. Finding that host species was not significantly different in our ANCOVA ($P = 0.48$) analyses with respect to pupal or adult efficiencies and knowing that both fly populations were presented with the same sources of *S. richteri,* we do not think that any potential populational differences in *S. invicta* contributed substantially to the differences in size across fly populations. Given that the flies from the more arid area of Santiago del Estero used the same-sized hosts less efficiently, that is, producing smaller flies with fewer progeny per female than flies from the more mesic area of Corrientes, it is likely that classical biological control introductions of *P. nocens* also may differ across localities, or differ from this study according to the populational origin of the fly. It has been argued previously (Folgarait et al. 2005a) that matching biotypes from climatically similar sites of origin to sites of release should be appropriate for successful introductions of *Pseudacteon.* Data from this study, however, suggests that even with climatic matching, although arid area biotypes may do better in arid areas than mesic biotypes, we might expect overall lower performance compared with mesic area biotypes in mesic conditions. If biotypes are used for the control of imported fire ants, follow-up cross-populational rearing studies may be needed to determine whether host locality effects exist after introduction.

Although pupal mortality was increased in the higher temperature regime, we also observed concomitant increases in pupal and adult efficiencies at 28°C (Fig. 3) in all the treatment combinations (host by temperature by population by ant sieve). Our measures of efficiency represent rates of population growth because they are based on the number of pupae or adults per cohort divided by the number of possible mothers for each cohort. We can reconcile the apparent contradiction between lower pupal survivorship yet higher pupal and adult numbers in the higher temperature regime by suggesting that *P. nocens* mortality rates are stage dependent according to

temperature. It is not likely that differential oviposition rates would account for these differences because we placed our ants into one of the two temperature regimes only *after* the oviposition trials. Ongoing experiments rearing larvae and pupae at appropriate temperature regimes will test our hypothesis of a temperature-dependent difference according to developmental stage.

Many aspects of *S. invicta* worker activity and survivorship are temperature dependent (Pinson 1980, Potts 1982), and 22°C is toward the lower end of performance for foraging (Porter and Tschinkel 1987) and colony growth (Porter 1988, Porter and Tschinkel 1993). One possible reason for higher pupal production in the higher temperature regime might be that the ant hosts do better at this temperature, allowing for higher survivorship of the flies to the pupal stage. This would certainly be the case if the parasitized ant kept close to the majority of other ants in the thermoregulated nest. Once the fly has detached from its dead host, however, it is not likely to follow the movement of the colony that provides this thermoregulation, and the pupae would have to face lower and probably less consistent temperatures. This latter aspect of lower pupal mortality at lower temperatures is consistent with other tested *Pseudacteon,* including *Pseudacteon cultellatus* Borgmeier (Folgarait et al. 2002), *P. obtusus* (Folgarait et al. 2005b), and *P. tricuspis* (Porter et al. 1997). The data in this article suggest that husbandry of *P. nocens,* at least, and for other species as well, might be improved by splitting the life stages of the flies according to the specific needs of the host and then the best ambient conditions of the fly.

Our finding that the laboratory mortality of *P. nocens* pupae was significantly lower in the lower temperature treatment is similar to the one we found for *P. obtusus.* In that study, we had examined *P. obtusus* only from Corrientes, where the mean annual temperature is slightly <22°C and a fit between mortality and general field conditions could be approximated. In this study, we found the same increased pupal mortality in the higher temperature regime for our Santiago del Estero population. Although this area is substantially more arid, it also has a similar mean annual temperature of ≈20.5°C (Fig. 4). We found female *P. nocens* ovipositing year-round when air temperatures ranged from 18 to >40°C, demonstrating they have a polyvoltine or continual overlapping population generation pattern. Analysis of *P. nocens* mortality by season (Albioni Montenegro et al. 2005) indicates that there may be strong seasonal effects with respect to mortality schedules, specifically in the detached pupal stage as suggested by our data.

Initial studies of *Pseudacteon* sexual dimorphism in *P. tricuspis* and *P. litoralis* indicated a clear pattern of environmental sex determination (Morrison et al. 1999b). In these two species, males and females use hosts that are largely exclusive of one another with respect to size. *P. cultellatus* (Folgarait et al. (2002a) and *P. curvatus* (Chirino et al. 2004), however, showed no gender differences in host sizes used, whereas host
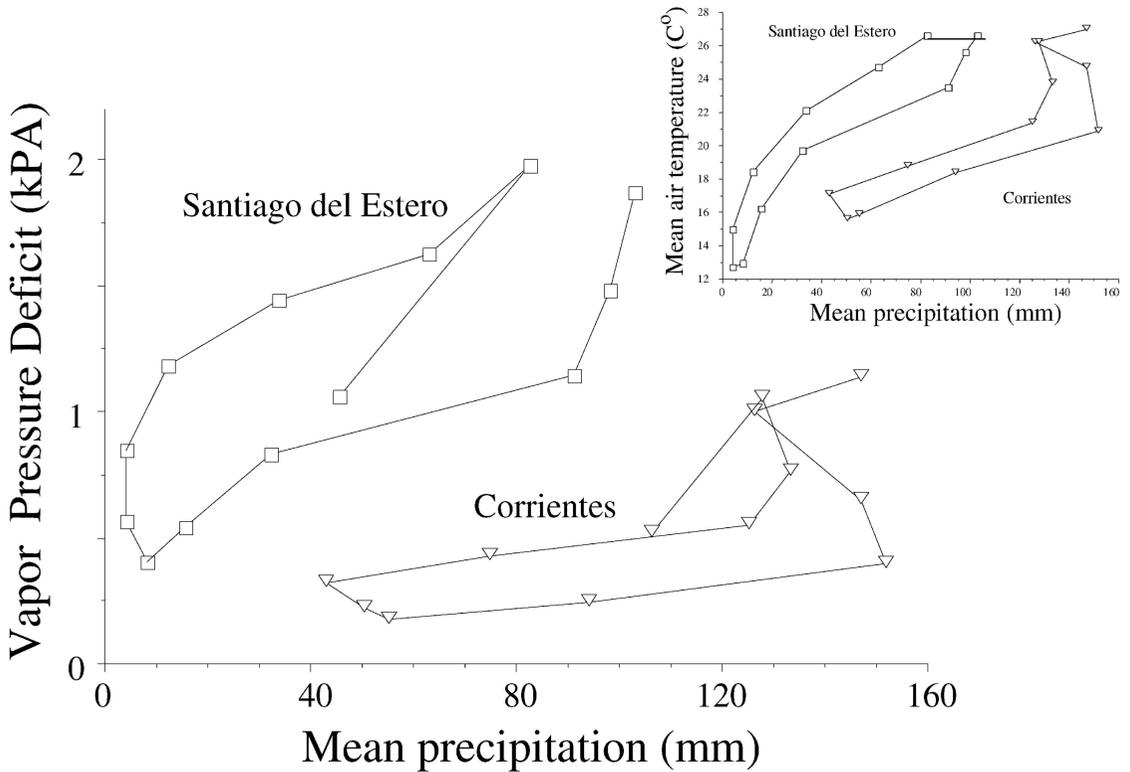
**Fig. 4.** Climatograms of Corrientes and Santiago del Estero, Argentina. Bottom, mean monthly vapor pressure deficit (kPA) against the mean monthly precipitation. Inset shows the monthly mean temperature (°C) against the mean monthly precipitation. Although the mean temperatures of the two areas are similar, the vapor pressure deficits demonstrate the higher aridity of the dry Chaco relative to the Mesopotamian region of Argentina.

size distributions in *P. obtusus* (Folgarait et al. 2005b) was predominately overlapping, although females did not use the smallest ants. This study shows that *P. nocens* is an intermediate case with respect to overlapping host use between males and females. Male development was excluded only in the largest ants, whereas females did not develop in the smallest ants (Fig. 2).

Within *Pseudacteon* to date, there have been descriptions of four syndromes with respect to how sex ratio at emergence is influenced by host size: 1) host size has no apparent influence on which sex emerges (*P. cultellatus* and *P. curvatus;* Fig. 5); 2) only females are influenced by host size (*P. obtusus*); 3) both sexes are influenced, but only at the outer margins of host sizes (*P. nocens*); and 4) both sexes depend on host size, but the influence is represented in the middle range of the species host use distribution (*P. tricuspis* and *P. litoralis*). Our data also suggest that these syndromes will each have different outcomes with respect to how much of a constraint host size can place on population growth (Morrison et al. 1999; Folgarait et al. 2002b, 2005b). Gilbert and Patrock (2002) suggested that classical biological control efforts in Texas using *P. tricuspis* could have been affected by the predominance there of polygyne colonies because most ants in a polygyne colony are too small to host

female *P. tricuspis*, leading to heavily male-biased sex ratios and low effective population sizes of the flies. The host size distribution we found that can produce female *P. nocens*, however, is in the majority of a typical polygyne colony (Greenberg et al. 1985) and should not by itself be limiting.

The sex ratios were influenced significantly by size distributions of hosts offered ($F_{1, 367} = 6.22$; $P = 0.0004$), however, in the same relative way as that found for *P. tricuspsis*. All of the sieve class offerings gave rise to male-skewed sex ratios, including big ($55 \pm 36\%$ [SD]; $n = 32$), whereas the others were decidedly more male-biased (mix1: $73 \pm 25\%$, $n = 223$; Mix2: $68 \pm 38\%$, $n = 47$; and small: $73 \pm 35\%$, $n = 20$). The resulting male-biased ratios may partly arise from the observed behavior of the flies to attack ants in the lower range of the size distribution than that which can produce females. We found that the elected modal frequency for host head width regardless of host, population or ant sieve offering was 0.6 mm, which was near the threshold for producing females, with <4% of the females emerging from smaller heads. When we consider that the median for the elected host head width was 0.67 mm, we still found <10% of females produced from smaller head widths. It is striking that the modes, or the most frequently elected host head sizes for small flies such as *P. cultellatus* and *P. curvatus*
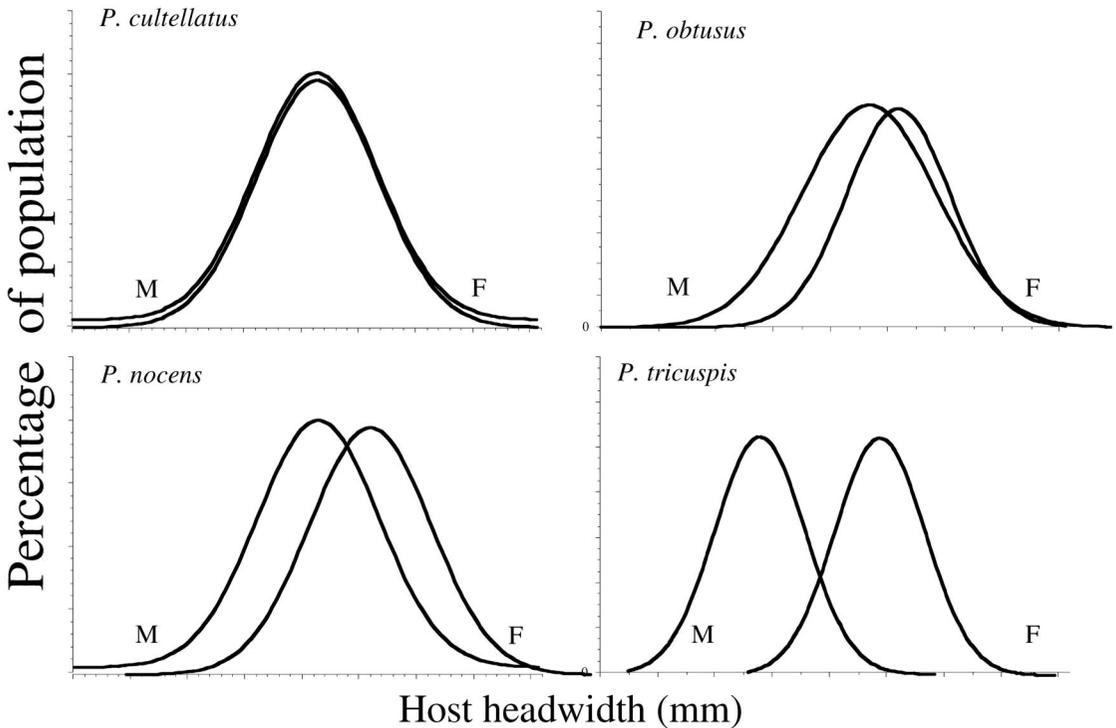
**Fig. 5.** Normalized distributions of host head widths used by different species of *Pseudacteon*. Figures drawn from original data from Folgarait et al. 2002b (top left), Folgarait et al. 2005b (top right), this study (bottom left), and Morrison et al. 1999 (bottom right).

(Folgarait et al. 2002a; Chirino et al. 2004; M. Chirino, unpublished data) is about the same (0.6–0.66 mm) as that of the larger *P. nocens* (this study). Such a similarity suggests that these species of *Pseudacteon* are opportunistic regarding the size of flies chosen for oviposition in that they take advantage of the most numerous size classes found in field nests (Chirino et al. 2004), regardless of what size distributions are offered.

A conspicuous finding regarding body size relationships observed in this study was that the resulting size of the fly, as measured by thoracic width differed by both population and sex after statistical adjustment for host size. That is, females were on average larger than males, and flies from Corrientes were larger than those from Santiago del Estero when emerging from the same sized hosts. In addition to the possible host effects we discuss above in dealing with absolute size differences between the populations, we might expect such a difference with respect to sex if 1) females are more likely to emerge from higher quality hosts than males, 2) females use the same size host more efficiently than males, or 3) females have a lower body mass/thoracic width ratio than males. Although we consider the last prospect unlikely, all three possibilities could be examined by looking at the allometric relationships between fly and ant body weights and linear dimensions. The first prospect also would need to consider host qualities such as age or "health." These questions also could be addressed with *P. ob-*

*tusus.* We reanalyzed the data from Folgarait et al. (2005b) for this species and found that females were also larger (by 25.5%) than males when using the same host head width (ANCOVA: $F_{1,\ 226} = 8.16$; $P = 0.005$).

We have been able to rear up to three generations of *P. nocens* in the laboratory, but mass production of this species is not practical at this time. We consider the time and effort to examine issues related to husbandry extremely worthwhile because this species has many qualities that would make it an ideal candidate for classical biological control introductions. *P. nocens* is an aggressive parasitoid that attacks *Solenopsis* fire ants under both disturbed mound and food resource recruitment situations. Our field experience indicates that *P. nocens* can be found very early in the ant recruitment trajectory, it can be one of the most frequent phorids at experimentally placed baits, and its impact at baits can be described as dramatic because fire ants often abandon the food resource or their numbers are substantially reduced once the fly is present. *P. nocens* is aggressive against other ants, however, and has been seen striking at other nonhosts such as large *Ectatomma* and *Camponotus* when these competitor ants become involved in bait fights with *S. invicta.* In one instance, the *Ectatomma* immediately left and the *P. nocens* returned to chasing a fire ant. This heightened aggression has been observed in host specificity tests with *Solenopsis geminata* (F.), although only when presented first with *S. invicta* in

nonchoice sequential tests (L.E.G., manuscript in preparation; Porter and Gilbert 2004).

As an addition to the community of *Pseudacteon*, introduced for biological control of imported fire ants, *P. nocens* would fill in important ecological gaps not covered by other species. Its size-based election of hosts lies intermediate between two of the currently introduced species of *Pseudacteon*, *P. curvatus* and *P. tricuspis* (Gilbert and Patrock 2002, Graham et al. 2003, Porter et al. 2004). Moreover, we have consistently collected a small morph of *P. nocens* that we have found is able to use smaller ants than even *P. curvatus* (P.J.F. et al., unpublished data 2002–2005; Chirino et al. 2004). The periodicity of *P. nocens* is also different from that of other *Pseudacteon* species. Its ovipositional periods, for example, in the hottest months are most frequent when other flies are not found or are much less common. We have been monitoring for a number of years two remote populations that differ in their seasonal phenological patterns (Azzimonti et al. 2004; P.J.F., et al., manuscript in preparation) as well as their host use and performance in the field and in the laboratory (this study). The broad range of this species across mesic and xeric areas in northern Argentina suggests that there can be additional interpopulational dimensions of variation that could be exploited in matching populations to appropriate sites for introductions into areas where these fire ants have become naturalized.

## Acknowledgments

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