Developmental Rates and Host Specificity for *Pseudacteon* parasitoids (Diptera: Phoridae) of Fire Ants (Hymenoptera: Formicidae) in Argentina

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ABSTRACT   This study extends our comparative knowledge of *Pseudacteon* interactions with *Solenopsis* fire ant workers. Reported in this work are development times for seven Argentinean parasitoid species reared on two hosts, *Solenopsis richteri* Forel and *Solenopsis invicta* Buren, under laboratory temperature regimes comparable with those of the climatic zones occupied by these host species. Developmental times spanned 31–66 d across phorid species, and in general did not differ between genders or host species, but were longer at lower temperatures. The size distribution of flies reared was bimodal, with a group of large (*Pseudacteon borgmeieri*, *Pseudacteon nocens*, *Pseudacteon obtusus*, and *Pseudacteon tricuspis*) and small (*Pseudacteon cultellatus*, *Pseudacteon curvatus*, and *Pseudacteon nudicornis*) species. *P. borgmeieri* was exceptional with respect to length of developmental time. Also reported are results of initial oviposition and developmental studies of some of these phorid species on other Argentinean *Solenopsis* ant species; *P. curvatus* was the only species able to complete its development on nonhost fire ants. These results support the concept of incorporating several complementary species of *Pseudacteon* in the biological control of pest fire ants.

KEY WORDS   Argentina, biological control, host ant acceptability, *Pseudacteon*, *Solenopsis*

Solenopsis richteri FOREL (black imported fire ant) and *Solenopsis invicta* Buren (red imported fire ant) were accidentally introduced into the United States between 1920 and 1940. The undesirable effects of these pests extend from purely ecological and economic to health hazards for humans (Taber 2000). The study of *Pseudacteon* parasitoids as biological control agents of exotic fire ants in the United States is relatively recent. Indeed, most work on *Pseudacteon* biology and *Pseudacteon/Solenopsis* interactions has been generated since the publication of Disney's (1994) general review of phorid biology (for a review, see Porter 1998a).

Most data on the development of *Pseudacteon* (e.g., *Pseudacteon curvatus* Borgmeier, *Pseudacteon tricuspis* Borgmeier, *Pseudacteon litoralis* Borgmeier, *Pseudacteon wassmani* Schmitz, and *Pseudacteon borgmeieri* Schmitz) are from studies using *S. invicta* as hosts (Porter et al. 1995b, Porter et al. 1997, Gilbert and Morrison 1997, Morrison et al. 1997, Porter 1998a, Porter and Alonso 1999, Morrison and Gilbert 1999, Porter 2000). To date, only two studies exist on the growth and development of *Pseudacteon* on *S. richteri*

(Porter and Briano 2000 for *P. curvatus*, Folgarait et al. 2002 for *Pseudacteon cultellatus* Borgmeier).

While the phylogeny of *Pseudacteon* has yet to be established, it is clear from known host associations that a major part of the genus diversified in an adaptive zone provided by *Solenopsis* fire ants that possess polymorphic workers. Latest estimates of the number of *Pseudacteon* specializing on *Solenopsis* indicate that 80% (24 of ≈30 total New World species) of these parasitoids restrict their attacks to *geminata* and/or *saevissima* species groups of the genus *Solenopsis*. Of these 24, 19 are specifically associated with the South American *saevissima* group (Porter and Pesquero 2001; P.J.F., unpublished data), including both of the imported species with which we are mainly concerned. Previous laboratory and field studies to determine host specificity and suitability, as well as behavioral impacts, lead to several important conclusions about particular species of fire ant-attacking *Pseudacteon.*

First, with the possible exception of *Pseudacteon convexicauda* Borgmeier (P.J.F., unpublished data), fire ant-attacking *Pseudacteon* do not attack ant genera other than *Solenopsis* in nature (Porter et al. 1995a) or in the lab (Porter and Alonso 1999). To our knowledge, *Pseudacteon* have never been observed to switch ant host genera when attacking *Solenopsis* at mounds

or baits with other ant genera nearby. Second, different *Pseudacteon* species display different levels of host specificity. In the laboratory, females of several species strongly discriminate between species groups of fire ants, always preferring their normal host complex, while others fail to strongly discriminate. For example, in laboratory tests, *Pseudacteon obtusus* Borgmeier (Brazil) chose *S. invicta* over *Solenopsis geminata* Forel, while *P. curvatus* (Brazil) freely attacked both species (Gilbert and Morrison 1997, Porter 2000). However, the species whose hosts include the United States native fire ant, *S. geminata*, have not switched to *S. invicta* or *S. richteri* despite over seven decades of coexistence (Morrison et al. 1997, Morrison and Gilbert 1998). Our field observations (unpublished data) indicate that some *Pseudacteon* species discriminate between different sympatric *Solenopsis* within a species complex as defined by Trager (1991), but appropriate laboratory choice experiments have not been conducted. Third, oviposition in laboratory arenas does not predict developmental success. For instance, *P. curvatus* (Argentina) develops poorly in the native species *Solenopsis xyloni* MacCook, but attack rates on this host were not significantly different than those on *S. invicta* (Porter 2000). Fourth, reproductive success in the laboratory does not predict success in the field. Thus, Argentinean populations of *P. curvatus* can be mass reared on *S. invicta*, but to date these flies have only become established in release areas in which *S. richteri* × *S. invicta* hybrids are the pest taxon (S. D. Porter, personal communication). In fact, laboratory studies with *P. curvatus* demonstrated a clear preference for *S. richteri*, even after being efficiently reared for many generations on *S. invicta* (Porter and Briano 2000).

The complex interplay of *Pseudacteon* and *Solenopsis* diversity outlined above is the basis for our interest in carefully exploring the details of host interactions for many of the *Pseudacteon* species that use *saevissima* group *Solenopsis* in Argentina. It is anticipated that this approach will help to determine the best candidates among phorids for control of imported fire ants in the United States. Therefore, in this study, we report on laboratory studies of seven *Pseudacteon* species, five of which (*P. borgmeieri*, *P. cultellatus*, *Pseudacteon nocens* Borgmeier, *Pseudacteon nudicornis* Borgmeier, and *P. obtusus*) were virtually unknown. Because of their significance as pests, *S. richteri* and *S. invicta* were used as hosts in most of these phorid-rearing experiments. These results constitute the first data collected to date on the development of six phorid species on *S. richteri* and four *Pseudacteon* species on *S. invicta*. However, we also report on *Pseudacteon* interactions with two other *Solenopsis* species that occur in Argentina.

Materials and Methods

Insects. Adult *Pseudacteon* used in this study were collected during 1998–2000 from the Reserva Ecológica Costanera Sur and the Estación de Cría de Animales Silvestres in Buenos Aires, Argentina (34° 55′ S and 57° 57′ W), and during 2000–2001 from Mercedes, Corrientes (29° 47′ S and 58° 03′ W), Argentina. The flies were then transported, in individually ventilated plastic vials (10 × 40 mm) with a lid made with cotton moistened in 50% sugar solution, and held in a cooler maintained at ≈10°, to the phorid laboratory at The National University of Quilmes. *Solenopsis* ants were attacked within 36 h after collection of flies in the field. *S. richteri* colonies were collected in Buenos Aires, whereas the other *Solenopsis* colonies were collected in Mercedes, Corrientes. In Corrientes, the ranges of both *Solenopsis macdonaghi* Santschi and *Solenopsis quinquecuspis* Forel overlap that of *S. invicta*. Because phorids were reared on these species before obtaining final identifications on host vouchers, and to better understand patterns of host preference, these *Solenopsis* were included in this study. Ant colonies were kept in the laboratory for a maximum of 6 mo.

Bioassays. Oviposition tests were conducted in flight boxes similar to those used by Porter and Alonso (1999). The boxes were white plastic trays (45 × 35 × 25 cm) covered with glass roofing and lined floors (2 cm deep) of plaster (SEMIROCK; Synthetic Dental Hard Plaster, BK Giulini Corp., Quedlinburg, Germany) moistened to maintain humidity. Each box was ventilated by ant-proof mesh-covered openings on both of the two longest sides. Lighting during attacks was provided by 500-watt halogen lights situated on the sides of flight boxes and by fluorescent lights placed over the top. Fans were used to maintain the temperature of flight boxes between 25 and 30°C. Humidifiers provided high humidity. Oviposition tests were carried out in a flight box containing two to six female flies, depending on how many were caught in the field (although generally only a couple of flies actively attacked), with 0.8 g of ants (representing ≈1,000 ants) for 3–5 h. Actual attack times within flight boxes depended on female oviposition motivation and survivorship. For *P. borgmeieri*, *P. cultellatus*, *P. curvatus*, *P. nocens*, *P. nudicornis*, *P. obtusus*, and *P. tricuspis*, there were a total of 38, 23, 20, 10, 20, 11, and 9 attacks on *S. richteri*; 23, 29, 2, 19, 3, 34, and 1 attacks on *S. invicta*; 11, 0, 7, 0, 7, 2, and 5 attacks on *S. macdonaghi*; and 1, 0, 1, 0, 3, 0, and 1 attacks on *S. quinquecuspis*, respectively.

Attacked ants were maintained in Tupperware-type plastic containers (22 × 22 × 6 cm) with mesh-covered windows to provide ventilation, moistened plaster floors to provide humidity, and food (2–3 g of animal protein, carabid larvae, earthworms, and/or crickets per week was provided, plus sugar water ad libitum). Attacked ants were placed in rooms maintained at 22, 25, or 27°C mean temperature and 60–80% RH by using cold/heat air conditioning systems (Toshiba RAS-07 NKHX, Tokyo, Japan) and controlled humidifiers (Herrmidifier 707, Sanford, NC).

All attacked ants were inspected daily for 60 d for appearance of pupae in the heads of dead ants. The duration of egg plus larval development was calculated as the time elapsed from the date of attack to the date pupae were observed. Pupal development time was calculated as the number of days from appearance

Table 1. Egg-larval, pupal, and total development for males, females, and nonviable egg larvae of several *Pseudacteon* species reared on *Solenopsis richteri*

Development period			*borgmeieri*	*cultellatus*	*curvatus*	*nocens*	*nudicornis*	*tricuspis*	*obtusus*
Egg-larval	Males	Median	27.0	21.0a	14.0ab	34.0	25.0		16.5ab
		1st–3rd quartile	(21.0–38.3)	(20.0–22.8)	(12.5–25.5)	(29.0–38.0)	(19.3–37.5)		(12.5–19.2)
		n	22	52	9	6	22		14
	Females	Median	26.0	20.5a	13.0a	32.0	20.0	19.0	15.0a
		1st–3rd quartile	(23.0–34.0)	(19.0–22.0)	(12.0–14.0)	(31.2–47.7)	(16.3–26.5)	(19.0–24.0)	(12.0–17.5)
		n	27	64	61	6	20	9	17
	Nonviable	Median	25.5	22.0b	14.0b	34.5	22.0	19.0	20.0b
		1st–3rd quartile	(21.0–38.0)	(20.0–24.0)	(12.0–20.0)	(32.0–38.0)	(17.0–39.3)	(17.3–20.0)	(16.5–24.0)
		n	86	213	320	16	54	4	22
		P	0.74	0.001	0.01	0.79	0.39		0.005
		H	0.60	16.7	8.74	0.46	1.91		10.0
Pupal	Males	Median	27.5	27.0	18.0	31.5	17.0		20.0
		1st–3rd quartile	(22.0–31.3)	(24.0–28.0)	(17.5–20.0)	(30.7–33.2)	(16.0–19.0)		(17.0–24.5)
		n	22	52	9	6	21		14
	Females	Median	30.0	27.0	18.0	32.5	19.0	17.0	23.0
		1st–3rd quartile	(24.0–32.0)	(25.0–28.0)	(17.0–19.0)	(31.0–33.0)	(17.0–22.0)	(14.5–20.0)	(20.0–24.0)
		n	27	63	57	6	20	9	17
		P	0.47	0.54	0.76	0.64	0.07		0.24
		U	268	1529	240	12.5	140		89.5
Total	Males	Median	55.5	47.0	32.5	66.0	45.0		34.5
		1st–3rd quartile	(50.5–64.3)	(45.0–49.8)	(30.8–48.0)	(59.7–70.5)	(34.0–56.0)		(32.7–39.2)
		n	22	52	9	6	21		14
	Females	Median	56.0	47.0	31.0	65.0	42.0	38.0	38.0
		1st–3rd quartile	(52.0–62.0)	(45.0–50.0)	(30.0–31.3)	(63.0–79.2)	(35.0–47.5)	(36.8–42.0)	(35.0–38.0)
		n	27	63	57	6	20	9	17
		P	0.92	0.93	0.07	0.686	0.50		0.175
		U	292	1624	185	11.5	193.5		85

Probabilities for Kruskal-Wallis statistical comparisons (H) among males, females, and nonviable for egg-larval development times, as well as probabilities for Mann-Whitney U test comparison between genders for pupal and total development times. Medians within a column followed by different letters denote significant contrasts ($P < 0.008$).

of a pupa to adult eclosion. Each pupa was followed individually until adult emergence.

It should be pointed out that many observations reported in this work were ancillary to trials to improve laboratory rearing. The opportunistic nature of our ability to collect various phorid species has prohibited optimal design in these experiments. However, it is valid to report developmental rates with respect to temperature as well as host species for all phorid species for which such information was obtained.

Statistical Analyses. Nonparametric statistics were used to compare group medians, because data distributions did not fit the assumptions of parametric analyses (Siegel 1974). Kruskal-Wallis (H) was used to compare more than two groups (as in cases of developmental periods or parasitoid sizes across phorid species); if statistical differences were found, a posteriori contrasts were performed using Bonferroni adjustments (reported as Z values) to maintain an experimental error of 0.05 (Daniel 1990). Mann-Whitney U tests were used to compare strictly two groups (as in the case of fire ant host comparisons or temperature comparisons). Statistical comparisons were made only in those cases in which sample sizes were greater than $n = 5$. Spearman correlations were used to associate developmental periods with phorid sizes. Median values were reported with the appropriate (for nonparametric statistics) measures of dispersion (first and third quartile). Statistical analyses were performed with Statistix 2.0 (Analytical Software 1998).

Results

S. richteri Host. Median total developmental times for all phorid species and rearing conditions spanned 31–66 d. No significant differences were found between females and males for any phorid species (Table 1).

Median egg-larval development times ranged from 13 to 34 d for all temperature regimes and species (Table 1). Across phorid species, female development times were always slightly less than for males, although none were significant. Nonviable parasitoids had similar egg-larvae developmental times compared with viable ones, although tendencies were not the same across species. Pupal development times varied from 17 to 32 d. Across taxa, female times tended to be longer than those of males, although for some species medians of pupal development were exactly the same between genders (Table 1). Ratios of egg-larval to pupal development times ranged from 0.79 for *P. obtusus* to 1.43 for *P. nudicornis*. Success rates of development, as measured by percentage of viable to nonviable pupae, ranged between 17.9% for *P. curvatus* and 69.2% for *P. tricuspis*.

Interspecific statistical comparisons were restricted to those cases in which phorid species were reared at the same temperature and had an adequate sample size ($n \geq 5$). With respect to the six species reared at 22°C, total developmental periods were significantly different among species tested ($H = 150.9$, $P < 0.0001$, df = 5). Three groups of species pairs were catego-
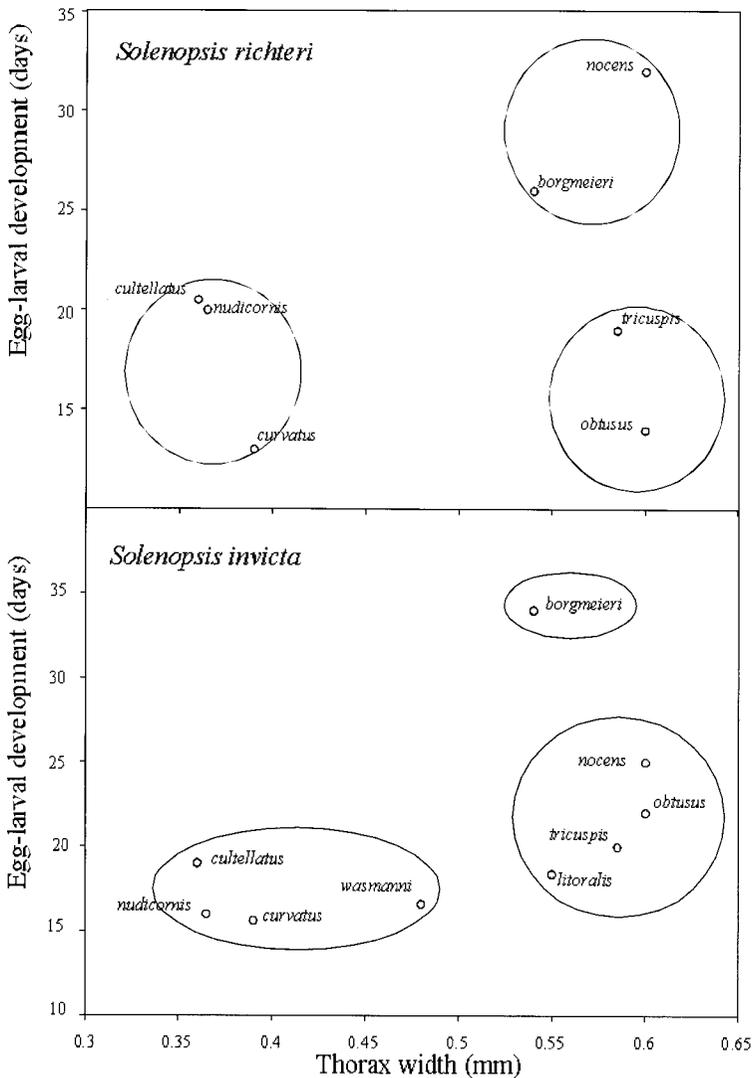
Fig. 1. (A) Egg-larvae developmental times versus thorax width for females of several *Pseudacteon* species reared on *S. richteri*. (B) Egg-larvae developmental times versus thorax width for females of several *Pseudacteon* species reared on *S. invicta*. (See Table 2 for sources of data not from this study; sizes for *Pseudacteon wasmanni* and *P. litoralis* gathered from Morrison et al. 1997.)

rized with respect to developmental times; one pair had the longest development (*P. borgmeieri* [59 d] and *P. nocens* [65 d]), another pair was intermediate (*P. cultellatus* [48 d] and *P. nudicornis* [44 d]), and a third was the most rapid (*P. nudicornis* [44 d] and *P. obtusus* [38 d]) (each contrast, $Z = 2.81$, $P < 0.0042$, df = 1).

Four phorid species reared at 27°C had significantly different total developmental times across species ($H = 57.33$, $P < 0.0001$, df = 3), and were categorized into two groups. The first group contained *P. borgmeieri* (53 d), *P. tricuspis* (38 d), and *P. nudicornis* (40 d), each having significantly longer developmental times compared with the second group that included only *P. curvatus* (31 d) (each contrast, $Z = 2.81$, $P <$

0.0042). Flies differed in their size (thorax width) across species ($H = 144.47$, $P < 0.0001$, df = 6). The distribution of flies reared from the black imported fire ant was clearly bimodal; one group included *P. cultellatus*, *P. curvatus*, and *P. nudicornis*, which were significantly smaller (each contrast, $Z = 3.1$, $P < 0.0012$) than the second group of *P. borgmeieri*, *P. nocens*, *P. obtusus*, and *P. tricuspis* (Fig. 1a). There was a weak tendency for the smaller species to develop more quickly than the larger taxa (Fig. 1a). Two species did not conform to this trend. *P. obtusus* and *P. tricuspis* developed much more quickly than would be predicted by their relative sizes, even after accounting for temperature differences in rearing conditions (Fig.

Table 2. Egg-larval, pupal, and total development for males, females, and nonviable egg larvae of several *Pseudacteon* species reared on *Solenopsis invicta*

Development period			*Pseudacteon* species						
			borgmeieri	cultellatus	curvatus	nocens	nudicornis	tricuspis	obtusus
Egg-larval	Males	Median	29.0	17.0	14.6[a]	22.0a		15.9[a]	19
		1st–3rd quartile	(24.2–41.2)	(16.0–20.0)	(± 1.1)	(22.0–26.0)		(± 2.4)	(19.0–23.0)
		n	14	29	5	27		82	49
	Females	Median	34.0	19.0	15.6[b]	25.0a	16.0	20.0[c]	22
		1st–3rd quartile	(25.7–44.2)	(17.0–20.0)	(± 0.5)	(20.7–29.5)		(± 5.0)	(18.0–24.0)
		n	14	23		18	1	12	27
	Nonviable	Median	43	19		29b			21
		1st–3rd quartile	(25.0–49.0)	(16.0–20.0)		(25.0–30.0)			(21.0–26.7)
		n	29	78		15			15
		P	0.290	0.805		0.004			0.212
		H	2.23	0.44		11.3			1.29
Pupal	Males	Median	28.0	22.0		21.0		17.2[a]	20
		1st–3rd quartile	(26.5–40.0)	(21.0–27.0)		(21.0–25.0)		(± 1.6)	(20.0–28.0)
		n	14	29		27		22	49
	Females	Median	29.0	23.0		26.5	19.0	19.0[c]	27.0
		1st–3rd quartile	(27.5–30.0)	(22.4–24.0)		(22.0–32.0)		(± 2.0)	(21.0–29.0)
		n	13	23		18	1	12	27
		P	0.86	0.888		0.001			0.116
		U	69.5	326		196			517
Total	Males	Median	56.0	41.0		43.0			49.0
		1st–3rd quartile	(52.2–77.0)	(38.0–46.0)		(43.0–50)			(42.0–52.5)
		n	14	29		27			49
	Females	Median	62.0	42.0		51.5	35.0	39.0[c]	49.0
		1st–3rd quartile	(55.0–76.5)	(39.0–43.0)		(44.0–58.5)		(± 4.0)	(49.0–52.0)
		n	13	23		18	1	12	27
		P	0.644	0.717		0.002			0.135
		U	81.5	314		202.5			524

Probabilities for Kruskal-Wallis statistical comparisons (*H*) among males, females, and nonviable for egg-larvae development times, as well as probabilities for Mann-Whitney *U* test comparison between genders for pupal and total developmental times. Medians within a column followed by different letters denote significant contrasts ($P < 0.008$).

[a] Morrison et al. 1997.
[b] Porter and Briano 2000.
[c] Porter et al. 1997.

1a). As a result, the correlation between egg-larvae development time and fly size (thorax width) was not significant ($r = 0.53$, $P > 0.25$, $n = 7$).

S. invicta Host. Median total development for all *Pseudacteon* taxa ranged from 39 to 62 d, with a general tendency of being longer for females than males, although this was significant only for *P. nocens* (Table 2). For this host species, we have included published records to compare with our results (see references in the footnotes of Table 2).

Egg-larval development varied from 15 to 34 d (Table 2). Female development was slower than males in all cases, although not significant in any case. For *P. nocens* and *P. borgmeieri*, nonviable larval developmental times were longer (although significant only for *P. nocens*) than for viable parasitoids; other species did not appear to differ. Pupal development spanned 17–29 d, showing a smaller range in comparison with *S. richteri*. There was a tendency for females to develop more slowly than males, although female pupal development was significantly longer only for *P. nocens* (Table 2). Pupal success rates ranged from 40 to 50%, except for *P. nocens* and *P. obtusus*, which were much higher (75 and 83.5%, respectively). All success rates, in which pupae were found, were higher on *S. invicta* compared with the same phorid taxa reared on *S. richteri*. There was a tendency for larger species to develop more slowly than smaller taxa (Fig. 1b), which has previously been reported for another suite of phorids (Morrison et al. 1997), including North American species. One species, *P. borgmeieri*, did not conform to this trend, developing more slowly than would be predicted by its relative size. In fact, the correlation between phorid development time and size became significant only when *P. borgmeieri* data were not included (including *P. borgmeieri*, $r = 0.52$, $P < 0.15$, $n = 9$; without *P. borgmeieri*, $r = 0.75$, $P < 0.03$, $n = 8$).

Host Specificity. *S. macdonaghi* workers were offered to *P. borgmeieri*, *P. curvatus*, *P. nudicornis*, *P. tricuspis*, and *P. obtusus* (Table 3). Oviposition attempts were made and pupae obtained for all phorid species except *P. obtusus*. Adult *Pseudacteon* species were reared from these pupae for all phorid species except for *P. borgmeieri*. Although *S. quinquecuspis* workers were offered to all *Pseudacteon* species except *P. obtusus*, development to pupae occurred only for *P. curvatus* and *P. nudicornis*, and adults solely for *P. curvatus*. Very few attacks were observed by *P. borgmeieri* on *S. quinquecuspis* and *P. obtusus* on *S. macdonaghi* (1 and 2, respectively). Because these were done simultaneously with other phorid species, these rearing results are preliminary.

To make statistical comparisons of median total developmental periods across hosts, comparisons were restricted by temperature and phorid species. Tem-

Table 3. Oviposition attempts and development of nonimported fire ants from United States (*Solenopsis geminata*, *Solenopsis xyloni*) and from Argentina (*Solenopsis macdonaghi*, *Solenopsis quinquecuspis*) attacked by different species of *Pseudacteon* parasitoids (most are from this study; otherwise, sources are specified by superscript letters)

Pseudacteon species	Attacked nonimported fire ants				Life cycle completed in nonimported fire ants			
	S. geminata	*S. xyloni*	*S. macdonaghi*	*S. quinquecuspis*	*S. geminata*	*S. xyloni*	*S. macdonaghi*	*S. quinquecuspis*
borgmeieri	Yes[a]		Yes	Yes			Pupae	No
curvatus	Yes[b,c]	Yes[c]	Yes	Yes	Yes[b,c]	Yes[c]	Yes	Yes
nudicornis			Yes	Yes			Yes	Pupae
tricuspis	Yes[b,d]		Yes	Yes	No[b,d]		Yes	No
obtusus	No[a]		Yes				No	
litoralis	Yes[b,d]				No[b]			
wassmani	Yes[e,b,f]				No[b]			

[a] Morrison and Gilbert 1999.
[b] Gilbert and Morrison 1997.
[c] Porter 2000.
[d] Porter and Alonso 1999.
[e] Porter et al 1995a.
[f] Porter 1998b.

perature effects were best described in *S. richteri*, for *P. borgmeieri* and *P. nudicornis* (between 27°C and 22°C), and for *P. obtusus* and *P. cultellatus* (between 25°C and 22°C). Total developmental times were shorter at higher temperature regimes, but were never faster than by a few days ($\approx$15% of total development time), and differences were only significant for *P. cultellatus* on both *S. richteri* ($U = 115$, $n_{25} = 12$, $n_{22} = 103$, $P < 0.0001$, df = 1) and *S. invicta* ($U = 33$, $n_{25} = 41$, $n_{22} = 11$, $P < 0.0001$, df = 1).

As to significant differences across hosts by phorid species and temperature, a significantly longer development period ($U = 340.5$, $n_{Si} = 48$, $n_{Sr} = 27$, $P < 0.0007$, df = 1) was necessary for *P. obtusus* at 22°C reared on *S. invicta* (47.5 d) than on *S. richteri* (38 d), and longer periods for *P. curvatus* at 27°C on *S. macdonaghi* and *S. quinquecuspis* versus *S. richteri* (33 and 34 d, respectively, versus 31 d) ($H = 22.95$, $P < 0.001$, df = 2; each contrast, $Z = 2.39$, $P < 0.0083$). There were no differences in developmental periods for *P. cultellatus* reared on *S. invicta* or *S. richteri* at either 22°C ($U = 415$, $n_{Si} = 11$, $n_{Sr} = 103$, $P > 0.14$, df = 1) or 25°C ($U = 217.5$, $n_{Si} = 41$, $n_{Sr} = 12$, $P > 0.54$, df = 1) (for *S. invicta*, 41 and 46 d; *S. richteri*, 40 and 48 d, respectively). Similarly, no differences in development times were observed at 27°C for *P. tricuspis* ($U = 340.5$, $n_{Sm} = 5$, $n_{Sr} = 10$, $P > 0.59$, df = 1) or *P. nudicornis* ($U = 126$, $n_{Sm} = 9$, $n_{Sr} = 33$, $P > 0.67$, df = 1) reared on *S. macdonaghi* (41 and 36 d) or *S. richteri* at (38 and 40 d).

Discussion

Among the seven *Pseudacteon* species tested, there were basically two size classes: small species including *P. cultellatus*, *P. nudicornis*, and *P. curvatus*, and distinctively larger species *P. borgmeieri*, *P. nocens*, *P. obtusus*, and *P. tricuspis*, as has been described in Brazilian phorid communities containing different sets of species (Orr et al. 1997). Typically, both across and within species, phorid adult size correlated with host ant head size (Feener 1978, Morrison et al. 1997, Morrison and Gilbert 1998, Folgarait et al. 2002). Thus,

in nature a greater size range of workers can be expected to be attacked when *Pseudacteon* species of different sizes are present.

This study shows that developmental periods of some *Pseudacteon* species are a small fraction of those of other species, indicating that, other factors being equal, these species should have more rapid intrinsic rates of population growth, and might complement slower developing species in terms of adult population dynamics. Interestingly, even among larger phorids, some species can develop in one-half or one-third of the time of others of similar size, and several large species have developmental rates similar to those observed in small phorid species (Fig. 1).

Four *Pseudacteon* species studied (*P. borgmeieri*, *P. cultellatus*, *P. nocens*, and *P. obtusus*) attacked and successfully developed in both *S. invicta* and *S. richteri*. However, they varied in details of their developmental responses to these and other *saevissima* group ants. *P. borgmeieri* and *P. obtusus* tended to take longer to develop in *S. invicta* than in *S. richteri*, whereas *P. cultellatus* and *P. nocens* showed a tendency for developing faster in *S. invicta*. In the case of *P. nocens*, its faster development on *S. invicta* is consistent with the fact that this phorid species never encounters *S. richteri* in its geographic range (P.J.F., unpublished data; Ross and Trager 1991). However, the other three phorid species have broader distributions and are found at Corrientes (where *S. invicta*, but not *S. richteri* occurs) as well as in Buenos Aires (where *S. richteri*, but not *S. invicta* are found) (P.J.F. and O.A.B., unpublished data). Surprisingly, while all *P. cultellatus* individuals came from *S. richerti* hosts around Buenos Aires, this species seemed to develop faster in its novel host (*S. invicta*). For these four species that were reared on both hosts, in all cases lower pupal mortality occurred in *S. invicta*, and especially so for *P. nocens* and *P. obtusus*, for which the rearing success was >75%. *P. nocens* not only developed faster, but had higher early stage survivorship when reared on *S. invicta* compared with *S. richteri*.

All phorid species tested on *saevissima* group *Solenopsis*, other than *S. invicta* and *S. richteri*, attempted

to oviposit (Table 3). Although host specificity tests will have to be made on United States native *S. geminata* for many of the species we reared, other examples of *saevissima* group generalists that strongly discriminate against *S. geminata* are known. For instance, Brazilian *P. obtusus* did not attack *S. geminata* in host specificity trials (Morrison and Gilbert 1999), whereas *P. tricuspis, P. litoralis,* and Argentinean *P. borgmeieri* attacked *S. geminata* weakly and did not successfully complete development (Gilbert and Morrison 1997, Porter 1998b, Porter and Alonso 1999, Morrison and Gilbert 1999). *P. curvatus* is the only known South American *Pseudacteon* capable of developing in *S. geminata,* although the performance of Argentinean *P. curvatus* is worse on *S. geminata* compared with *saevissima* group hosts (Porter 2000, and see Porter and Alonso 1999 for *P. tricuspis*).

This study provides, for the first time, evidence that fire ant-specialized *Pseudacteon* species can attack many host species within the *saevissima* complex from their native range. In a recent review, Porter (1998a) called attention to the lack of information in this regard. This information is vital from a biological control perspective for the following reasons:

1) To control exotic fire ants in theUnited States, it is preferable that the candidate *Pseudacteon* species originating from *S. richteri* attack and develop well on *S. invicta.*

2) It is important to locate *Pseudacteon* species from areas with climates that best match the wide range of conditions found in the distributional ranges of *S. invicta* and *S. richteri* in North America. Only when the geographic range of *S. invicta* and other *saevissima* group species in Argentina (P.J.F., unpublished data) is combined, would one find the variety of climates characteristic of *S. invicta*'s introduced range in North America.

3) It is relevant to acknowledge, as a prima faciae precaution, that the host flexibility by different *Pseudacteon* species within their native *Solenopsis* hosts may raise potential concerns about possible host switches onto species within the *S. geminata* complex in the United States. Our host specificity results largely agree with, and extend, those published by Gilbert and Morrison (1997) and Porter and Briano (2000). *P. curvatus,* for instance, is a very flexible and efficient parasitoid within the *Solenopsis* genus, as adults were reared from several hosts (Table 3). Other *Pseudacteon* species, while motivated to attack nonpest *Solenopsis* species, varied in their developmental performances on these hosts, and never fully completed their life cycles. We also found high fidelity by the Argentinean *P. obtusus* toward fire ant hosts, as was found previously for the smaller Brazilian *P. obtusus* (Morrison and Gilbert 1999).

In general, the data presented in this study will help to prioritize *Pseudacteon* species with respect to potential for biological control of *S. invicta* and *S. richteri* ants only after host specificity tests with native United States ants are performed. However, results with *P. borgmeieri,* a species already tested for oviposition specificity (Morrison and Gilbert 1999), suggest several reasons to reconsider this phorid as a potential candidate for introduction into the United States. First, *P. borgmeieri* never developed successfully in *S. macdonaghi* or *S. quinquecuspis* despite oviposition attempts. Hence, although this species will attempt to oviposit on many host species, internal attributes of some *Solenopsis* hosts apparently prevent its successful development. In this study, we showed that it develops well on *S. invicta* and *S. richteri,* both imported into the United States. Second, in laboratory experiments comparing the relative effects of eight *Pseudacteon* species on fire ant foragers, *P. borgmeieri* was the species whose attacks on workers incapacitated attacked ants for the longest periods of time and showed the greatest disturbing effect on secondary ants (ants attracted to the victim) (Wuellner et al. 2002). Third, because *P. borgmeieri* is the only species present and active during the winter in Buenos Aires, it may have physiological capacities not present in other *Pseudacteon* that might attack imported fire ants. Therefore, it may be the only *Pseudacteon* species that could impose biological control on exotic fire ants in the United States during cold months of the year (P.J.F., unpublished data). In Texas, *S. invicta* continues conspicuous foraging throughout the winter on warm days. In contrast, *S. geminata* and its phorids are rarely observed from November to March (Wuellner and Saunders 2003). Thus, although it attacks *S. geminata* in a laboratory setting, *P. borgmerieri*'s winter flight period should minimize its access to the native fire ant while providing phorid pressure on imported fire ants when they become active on mild winter days.

All seven *Pseudacteon* species tested were reared successfully on both *S. invicta* and *S. richteri.* These results are encouraging, as both ant species are the focus of biocontrol efforts in the United States. Furthermore, our findings support the incorporation of several complementary species of *Pseudacteon* in the biological control of *S. invicta* and *S. richteri,* as has been previously suggested (Morrison et al. 1997, Orr et al. 1997, Porter 2000). This concept now has more general support (Mills 1994) in the literature of biological control.

Acknowledgments

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