Patterns of Host Specificity in *Pseudacteon* Parasitoid Flies (Diptera: Phoridae) that Attack *Solenopsis* Fire Ants (Hymenoptera: Formicidae)

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**ABSTRACT** *Pseudacteon* phorids that parasitize the red imported fire ant, *Solenopsis invicta* Buren, in South America are not present in the introduced range of this pest species in the United States. Sequential host specificity tests were conducted with 4 South American *Pseudacteon* species, *P. litoralis* Borgmeier, *P. wasmannii* (Schmitz), *P. tricuspid Borgmeier*, and *P. curvatus* Borgmeier, to investigate the degree to which these species attack the native North American fire ant, *Solenopsis geminata* (F.). Three species, *P. litoralis*, *P. wasmannii*, and *P. tricuspid*, showed little interest in ovipositing on *S. geminata*, even when highly motivated to oviposit on *S. invicta*. By comparison, *P. curvatus* oviposited on *S. geminata* readily. Larval development of *P. curvatus* did occur in *S. geminata*, but no adult flies emerged. Methods for assaying host specificity and the biocontrol potential of these unique insects are discussed.

**KEY WORDS** *Pseudacteon*, *Solenopsis*, biocontrol, host specificity, parasitism, parasitoid

The possibility of using phorid flies of the genus *Pseudacteon* in the biological control of pest ants of the genus *Solenopsis* (Feener and Brown 1992) has recently stimulated a broad front of research on *Pseudacteon* life history and interactions with *Solenopsis* ants (Orr et al. 1995; Porter et al. 1995a, b, c; Morrison et al. 1997). One crucial component of assessing their biocontrol potential is elucidation of the degree of host specificity, because it is desirable to minimize impact on native ant species.

Field tests in South America have indicated that *Pseudacteon* spp. are not attracted to ants in genera other than *Solenopsis* (Porter 1995b). Moreover, *Solenopsis* in the *saevisissima* complex were observed to attract large numbers of *Pseudacteon* individuals, whereas *S. geminata* (F.) (in the *geminata* complex) attracted relatively few (Porter 1995b). Both imported fire ant species in the United States, *S. invicta* Buren and *S. richteri* Forel, are in the *saevisissima* complex, whereas all native North American fire ants are in the *geminata* complex (Trager 1991).

We studied the relative tendencies of 4 *Pseudacteon* species (that attack *Solenopsis* species in the *saevisissima* complex in South America) to attack *S. geminata* and *S. invicta* populations from Texas. Our experiments addressed the following 3 questions: (1) Are *Pseudacteon* spp. that attack workers in the *saevisissima* complex confined to that species complex by oviposition choice? (2) If not, which *Pseudacteon* species are relatively more restricted to the *saevisissima* complex? (3) Does apparent oviposition into *Solenopsis* species outside the *saevisissima* complex lead to larval development?

**Materials and Methods**

Four species of *Pseudacteon* flies were imported from Brazil: *P. litoralis* Borgmeier, *P. tricuspid Borgmeier*, and *P. curvatus* Borgmeier were collected from a residential area near the University of Campinas (UNICAMP), Sao Paulo State, Brazil. *P. wasmannii* (Schmitz) was collected along roadsides in the foothills near Jundiai, Sao Paulo State, Brazil. Female age and reproductive condition at capture were unknown, although all individuals were collected during oviposition attacks on *saevisissima* complex species (*S. invicta* or *S. saevissima*). Vitality of phorids on arrival varied among individuals, and only females that showed typical attack behavior during an initial exposure to *S. invicta* were used in the trials.

Polygyne (multiple queen) colonies of the red imported fire ant, *S. invicta*, were obtained from Brackenridge Field Laboratory and Circle C Ranch, Travis County, Texas. Polygyne colonies of the native fire ant, *S. geminata*, were obtained from Circle C Ranch and along Barton Hills Drive in Austin, TX. Host preference tests were conducted at intervals from April 1995 to July 1996.

All tests were conducted in the paraquarantine containment facility at The University of Texas Brackenridge Field Laboratory. *Pseudacteon* females were kept in dark, cool, and humid conditions (≈15°C, 70% RH) when not exposed to ants. To test host specificity, *Pseudacteon* females were introduced into flight boxes constructed of white plastic trays (51 by 39 by 15 cm, Panel Controls Corporation, Detroit, MI) covered with clear glass. Foam
weather-stripping (20 by 5 mm; Frost King, Los Angeles, CA) was adhered to the glass where it met the top of the tray to prevent escapes. In each trial, \( \approx500 \) worker ants representing the natural range of size variation found in these polymorphic species were placed in a flight box along with a single *Pseudacteon* female whose oviposition attacks were observed continuously. Different trays of ants were used for each species of *Pseudacteon* tested. The bottom of the trays were covered with a light colored, fine-grained sand to provide a nonslippery substrate for the workers to walk across and a light colored surface for easy observation of phorids and ants. The sides of the trays were covered with Fluon (polytetrafluoroethylene; ICI Fluoropolymers, Exton, PA), which prevented workers from scaling the walls but still allowed the phorids to perch on the vertical sides. In each tray, water and sugar water (in test tubes plugged with cotton) were provided ad libitum. Four freeze-killed crickets were also offered as food. *Pseudacteon* females occasionally visited crickets and sugar water and appeared to feed. Fluorescent lights placed \( \approx30 \) cm above the top of each tray provided illumination. All trials were conducted at \( 25^\circ C \).

*Pseudacteon* females were tested as individuals by exposing them sequentially to alternative hosts. We used sequential choice tests, rather than the often employed simultaneous choice tests (in which female parasitoids would have access to 2 or more host species at the same time in a common container [e.g., Calvert 1973, Lajeunesse and Johnson 1992]), because *Pseudacteon* spp. are apparently attracted to the vicinity of their host ant species by olfactory cues and then attack by visual cues (Feener and Brown 1992, Disney 1994, Orr et al. 1997). The buildup of odors resulting from 2 ant species in the same closed container might result in attacks on inappropriate hosts, or even potential hosts not normally located or approached.

To begin each trial, a single *Pseudacteon* female was introduced into a small cup (with Fluon on its outer sides to exclude ants) within a tray of the red imported fire ant, *S. invicta*, its South American host. The cup provided a refuge for the phorid, which often hesitated a few minutes before it took flight. If, after taking flight, a phorid did not attack within 20 min of exposure to *S. invicta*, the trial was aborted. If a female began to attack *S. invicta*, all attacks within a 5-min period were recorded. Five minutes was judged to be adequate to establish motivational state and measure attack rate (yet it was well short of typical oviposition bout durations observed in females given unlimited opportunity to attack). After 5 min, each *Pseudacteon* female was transferred immediately to a tray containing only the native fire ant, *S. geminata*, to which it was exposed for 20 min. In most, but not all trials, the phorid was returned immediately to the original *S. invicta* tray to determine whether it was still motivated to attack *S. invicta.*

To handle and transfer phorids, we used simple aspirators consisting of a transparent screw cap microcentrifuge tube (the end of which was cut off and covered with fine mesh netting) plugged end first into a length of Tygon tubing. Flying phorids were captured by gently aspirating them against the mesh end of the tube until the tube was capped or the phorid was released into a new tray. Tubes were numbered and served as housing for individual phorids from the time of collection in the field until the termination of the experiments. *Pseudacteon* spp. were identified within these tubes using a 10 power hand lens in the field, and a dissecting microscope was used to verify identifications in the laboratory before tests.

Some phorids apparently became exhausted or disoriented at various times during the trials and were in danger of being captured, or were actually captured, by ants. When this happened before the full 20-min exposure to *S. geminata*, the trial was ended prematurely and was not included in the analysis.

Attack rates are based on the time between the 1st attack and the removal of the phorid. Usually, when a phorid began to attack it did not stop until it was removed from the tray or placed in a tray with an unacceptable host. Indeed, in another experiment, we observed that many females were capable of attacking almost continuously for >1 h (Morrison et al. 1997).

To determine whether larval development occurred, attacked workers were monitored for 60 d after exposure to phorids. In the *Pseudacteon* species tested, pupariation usually occurs in 14–19 d (at 30°C), depending on the species (Morrison et al. 1997). At pupariation, the host worker is killed, the mouthparts of the worker are cut and pushed away, and the puparium is visible in the mouth cavity of the worker ant (Porter et al. 1995c). Three instars preceded the pupal stage (Porter et al. 1995c), and workers that were still alive after 30 d were dissected and examined for the presence of larvae which did not survive to the pupal stage.

Reference specimens of the 4 *Pseudacteon* species tested have been deposited in the Natural History Museum of Los Angeles County.

**Results**

Most *Pseudacteon* females readily attacked *S. invicta* workers in our experimental flight boxes, and oviposition behavior observed in the context of our laboratory experiments was not qualitatively different from that observed in the field. Females of *P. litoralis*, *P. wasmanni*, and *P. tricuspis* revealed high degrees of specificity for *S. invicta*, attacking *S. geminata* only rarely. Of the females that demonstrated a motivation to attack *S. invicta*, only 8.7% of the *P. litoralis*, 11.1% of *P. wasmanni*, and 4% of *P. tricuspis* females attacked *S. geminata*. Of the females that were exposed to *S. invicta* a 2nd time, 95.2% of the *P. litoralis*, 61.5% of the *P. wasmanni*, and 71.4% of
the *P. tricuspis* resumed attacking *S. invicta*. These differences in proportions of females attacking *S. geminata* compared with *S. invicta* (in the 2nd exposure) are significant at *P* < 0.0001 (binomial test) for all 3 *Pseudacteon* species (Table 1). In contrast, 65% of the *P. curvatus* females which attacked *S. invicta* also attacked *S. geminata*. There were no significant differences in attack rates (*H* = 5.50, df = 3, *P* = 0.1388; Kruskal-Wallis test) among females of the 4 *Pseudacteon* species on initial exposure to *S. invicta*. Too few attacks were observed on exposure to *S. geminata* to make similar statistical comparisons.

The number of attacks per female per minute were higher for females of *P. litoralis*, *P. tricuspis*, and *P. curvatus* that attacked *S. invicta* than for the subset of females attacking *S. geminata*, and similar for the females of *P. wasmanni* that attacked *S. invicta* and the subset of those that also attacked *S. geminata* (Table 1). Females of *P. curvatus* that chose to oviposit into both *Solenopsis* species attacked *S. invicta* at a significantly faster rate than *S. geminata* (*Z* = 2.10, *P* = 0.035; Wilcoxon matched-pairs signed-ranks tests, *n* = 13) (Table 1). Not enough attacks were observed on *S. geminata* to make similar statistical comparisons.

*Pseudacteon* *litoralis*, *P. wasmanni*, and *P. tricuspis*, when placed in the flight box with *S. geminata*, usually flew low over the workers and closely inspected them for the first few minutes of exposure, but rarely attempted to oviposit. Most individuals quickly lost interest and spent the majority of the 20-min period perching high on the walls or attempting to escape from the flight box. The fact that most phorids resumed attacking when transferred back to *S. invicta* indicates that the absence of attacks on *S. geminata* was not caused by fatigue or lack of eggs, but rather was a response to an inappropriate host.

Because *P. curvatus* readily attacked *S. geminata*, it was not exposed to *S. invicta* a 2nd time. In 4 additional trials in which *P. curvatus* females were introduced to a tray of *S. geminata* 1st and *S. invicta* 2nd, 2 of the females attacked *S. geminata* (without previous exposure to *S. invicta*) and *S. invicta*, and 2 females only attacked *S. invicta*.

Consideration of all females of each *Pseudacteon* species collectively reveals additional information on species-level host specificity (Table 2). Rates of attack on *S. geminata* relative to initial exposure to *S. invicta* were an order of magnitude less for *P. wasmanni* and *P. curvatus*, 2 orders of magnitude less for *P. litoralis*, and 3 orders of magnitude less for *P. tricuspis*. Rates of attack on *S. invicta* in the 2nd exposure were 1–2 orders of magnitude higher than on *S. geminata* in the 3 species exposed to *S. invicta* a 2nd time.

*Pseudacteon* females, when initially placed in the flight box, often required several minutes to orient to their new surroundings and begin attacking workers. This initial orientation time was significantly longer for *P. wasmanni* than for *P. litoralis*, but no significant differences were observed among any other species (*H* = 8.13, df = 3, *P* = 0.0434, multiple comparison procedure based on the Kruskal-Wallis test).

### Table 1. Number of individuals attacking, and attack rates for each of *Pseudacteon* spp. on *S. invicta* and *S. geminata*

<table>
<thead>
<tr>
<th>Attacks</th>
<th><em>P. litoralis</em></th>
<th><em>P. wasmanni</em></th>
<th><em>P. tricuspis</em></th>
<th><em>P. curvatus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of individuals attacking</td>
<td>23</td>
<td>18</td>
<td>25</td>
<td>20</td>
</tr>
<tr>
<td>Attack rate per individual (attacks per min)</td>
<td>2.33 ± 1.77</td>
<td>3.21 ± 2.83</td>
<td>1.91 ± 1.30</td>
<td>1.53 ± 1.44</td>
</tr>
<tr>
<td>Total no. attacks</td>
<td>345</td>
<td>354</td>
<td>275</td>
<td>244</td>
</tr>
<tr>
<td>Attack rate per individual (attacks per min)</td>
<td>2.04</td>
<td>2.50</td>
<td>1.58</td>
<td>1.00</td>
</tr>
</tbody>
</table>

### Table 2. Total time exposed, attack number, and attack rate for all individuals of each *Pseudacteon* species considered collectively

<table>
<thead>
<tr>
<th>Attacks</th>
<th><em>P. litoralis</em></th>
<th><em>P. wasmanni</em></th>
<th><em>P. tricuspis</em></th>
<th><em>P. curvatus</em></th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial exposure to <em>S. invicta</em></td>
<td>163.1</td>
<td>141.7</td>
<td>174.5</td>
<td>243.2</td>
</tr>
<tr>
<td>Total no. attacks</td>
<td>332</td>
<td>354</td>
<td>275</td>
<td>244</td>
</tr>
<tr>
<td>Attack rate (attacks per min)</td>
<td>2.94</td>
<td>2.50</td>
<td>1.58</td>
<td>1.00</td>
</tr>
<tr>
<td>Exposure to <em>S. geminata</em></td>
<td>345</td>
<td>303.9</td>
<td>424.1</td>
<td>284.4</td>
</tr>
<tr>
<td>Total no. attacks</td>
<td>9</td>
<td>50</td>
<td>1</td>
<td>8</td>
</tr>
<tr>
<td>Attack rate (attacks per min)</td>
<td>0.926</td>
<td>0.164</td>
<td>0.002</td>
<td>0.30</td>
</tr>
<tr>
<td>Subsequent exposure to <em>S. invicta</em></td>
<td>239.6</td>
<td>114.5</td>
<td>471.7</td>
<td>471.7</td>
</tr>
<tr>
<td>Total no. attacks</td>
<td>219</td>
<td>135</td>
<td>317</td>
<td>317</td>
</tr>
<tr>
<td>Attack rate (attacks per min)</td>
<td>0.91</td>
<td>1.18</td>
<td>0.67</td>
<td>0.67</td>
</tr>
</tbody>
</table>
Table 3. Orientation time (time elapsed before 1st attack) for initial and subsequent exposure to S. invicta for each of 4 Pseudacteon species

<table>
<thead>
<tr>
<th>Exposure</th>
<th>P. litoralis</th>
<th>P. wasmanni</th>
<th>P. tricuspis</th>
<th>P. curvatus</th>
</tr>
</thead>
<tbody>
<tr>
<td>Initial exposure to S. invicta, s</td>
<td>221.8 ± 231.7</td>
<td>441.5 ± 270.7</td>
<td>341.7 ± 214.8</td>
<td>367.9 ± 297.3</td>
</tr>
<tr>
<td>Subsequent exposure to S. invicta, s</td>
<td>148.4 ± 153.3</td>
<td>154.6 ± 213.9</td>
<td>245.8 ± 202.7</td>
<td>232.8 ± 158.2</td>
</tr>
<tr>
<td><em>P</em> (Wilcoxon matched-pairs signed-rank tests)</td>
<td>0.50</td>
<td>0.09</td>
<td>0.97</td>
<td>0.15</td>
</tr>
</tbody>
</table>

Numbers represent mean ± SD.

* Exposure to S. geminata.

Orientation time was shorter for all 4 species in the 2nd exposure to S. invicta (but not significantly). No significant differences in orientation time were observed among Pseudacteon species in the 2nd exposure to S. invicta (*H* = 5.47, df = 3, *P* = 0.14; Kruskal-Wallis test). Once a phorid began orienting to and attacking workers, capturing the phorid and moving it to another flight box did not cause it to lose interest in the ants or dramatically change its behavior. Because average orientation times ranged from 3.7 to 7.5 min on 1st exposure to S. invicta and 2.5–4.1 min on 2nd exposure, and females were exposed to S. geminata for 20 min, this orientation time should not have precluded our observation of attacks.

No signs of larval development were observed in S. geminata workers attacked by *P. litoralis*, *P. wasmanni* or *P. tricuspis*. Relatively few workers were attacked by *P. litoralis* and *P. tricuspis* however (*n* = 9 and 1, respectively). In another study we determined that successful parasitism rates (number of workers displaying larval development of phorids per number of workers attacked) of these Pseudacteon species on S. invicta were relatively low (11.8–18.5%; Morrison et al. 1997), however, and larval development in S. geminata cannot be ruled out on the basis of such small sample sizes.

Larval development of *P. curvatus* did occur in S. geminata, but complete development to the adult stage did not. Our attempts to rear *P. curvatus* in S. invicta were also largely unsuccessful, however, and failure of *P. curvatus* to develop completely in S. geminata may simply reflect inappropriate rearing conditions, rather than the inability of *P. curvatus* to complete development in S. geminata.

Rates of successful parasitism (evidence of larval development) for *P. curvatus* on S. invicta and S. geminata were similar (8.38% [n = 167 attacked workers] versus 8.45% [n = 142 attacked workers], respectively). These success rates were slightly lower than those for *P. litoralis*, *P. wasmanni*, or *P. tricuspis* on S. invicta reported previously (Morrison et al. 1997).

Discussion

If no information existed on the life history and host specificity of Pseudacteon spp., a number of ant genera would have required consideration as potential hosts. Pseudacteon, however, has undergone a major radiation on the host genus Solenopsis: 22 of 34 Pseudacteon species are known only from the saevisisima or geminata complexes of Solenopsis (Disney 1994). (Disney's [1994] records of *P. borgmeierii* Schmitz on 2 Camponotus spp. are spurious [Porter et al. 1995b]). One powerful constraint on host shifts by Pseudacteon to ant genera other than the polymorphic Solenopsis (aside from the use of host-specific chemical cues) may result from the fact that sex in Pseudacteon spp. appears to be determined environmentally, with larger worker ants producing female phorids (L.W.M, S. D. Porter, and L.E.G., unpublished data). Many ant species are monomorphic and would give rise to only 1 sex, even if Pseudacteon chose to oviposit and could develop in the novel host.

Some Pseudacteon spp., such as *P. crawfordii* Coquillett and *P. browni* Disney, are confined to the geminata species complex in North America and have failed to shift to the imported fire ants, S. invicta or S. richteri (both in the saevisisima complex), during the 6–7 decades of exposure and despite growing populations of the introduced species. Many of the 16 or more Pseudacteon species associated with the saevisisima complex in South America (Disney 1994) may also be restricted to a single species complex. Such specialization would be reflected in a strong preference for S. invicta over S. geminata, as we have reported for three of the Brazilian species in this study. We suggest that such specialized behavior, in light of the reliance of these Pseudacteon species on worker size variation for sex determination, would virtually preclude any possibility of host shifts beyond the genus Solenopsis. Pseudacteon has frequently been observed in the field in both North and South America hovering around natural or experimental encounters between Solenopsis and numerous other ant genera, yet no apparent attempt to oviposit on novel hosts has been observed (Orr et al. 1995, Porter et al. 1995b, L.W.M and L.E.G. unpublished data).

Testing host specificity in Pseudacteon spp. could potentially be accomplished in a number of ways: One could expose whole groups of females to a number of potential host ant species, following a common practice in insect host range or host choice studies (e.g., Calvert 1973, Lajeunesse and Johnson 1992). We decided against using groups of females, however, because we wished to avoid difficulties associated with interpreting results based on testing multiple females per arena (Horton 1995), to obtain
as much individual attack rate data as possible, and to produce ants infected by known phorid females.

Exposing individual Pseudacteon females to potential hosts sequentially, rather than simultaneously, decreases the likelihood that females will be confused by multiple olfactory stimuli and attack species not normally attacked. This phenomenon is known for hymenopteran parasitoids of herbivorous insects. After an initial attraction to odors of the host food plant, nonhosts placed on the same plant are attacked (examples in Vinson 1976). In other cases, host odors themselves probably create similar confusion. In tests of aphelinid parasitoids of aphids, Lajuennesse and Johnson (1992) found that an aphid species that was attacked as frequently as the natural host in simultaneous choice experiments was 20 times less likely to be attacked than the natural host in sequential tests. The Pseudacteon–Solenopsis system presents similar problems in host specificity studies. If long-range cues are predominantly chemical and short-range cues are visually primary, morphologically similar nonhosts might be mistakenly attacked by Pseudacteon females motivated by host odor.

It is possible that the few attacks we observed on S. geminata by a small subset of P. littoralis, P. wasmanni, and P. tricuspis females were simply artifacts of our experimental set-up: after becoming stimulated to attack by strong olfactory cues from S. invicta, females continued to attack the morphologically similar S. geminata after transfer to the tray of that species. If so, either initial exposure to S. geminata or subsequent exposures to first S. invicta and then S. geminata with an intervening time period might result in fewer attacks on S. geminata. We decided against exposing phorids to S. geminata first, because in that case we would not know if the individual was motivated to attack its normal host. (Many flies were not motivated to attack in the initial exposure to S. invicta.) In the additional tests in which P. curvatus was exposed to S. geminata first, its willingness to oviposit demonstrated that this species did not require any prior motivational cues from S. invicta.

We chose to transfer Pseudacteon females immediately between trays of Solenopsis species, completely testing each phorid within a <1-h period (when it was obviously motivated to attack) because it allowed us to avoid confounding effects of testing females on different Solenopsis spp. at different times or on different days. Although some phorids were motivated to attack at the 1st exposure to S. invicta, others demonstrated no motivation to attack until a 2nd or 3rd exposure 2 or 3 d later. Individuals that showed no motivation to attack in initial tests were later retested and often did attack. Conversely, some phorids that attacked on one day demonstrated no motivation to attack on subsequent days. Pseudacteon females lived only a few days in the laboratory, and in general appeared less vigorous over time despite efforts to feed them and slow down their metabolism by keeping them cool. By compressing the sequential tests into a brief period when each Pseudacteon female was obviously motivated to attack, and transferring females directly from S. invicta to S. geminata, our approach may have generated more attacks on S. geminata than would occur by other exposure regimes, or in nature, and thus represents a conservative approach.

Implications for Biological Control. Our results suggest that, in nature, P. curvatus will almost certainly attack S. geminata, whereas P. littoralis, P. wasmanni, and P. tricuspis may attack only infrequently if at all. It is important, however, to consider the biological, as well as statistical, significance of our results. Some individuals of P. littoralis, P. tricuspis, and P. wasmanni did attack S. geminata, although all exhibited a statistically significant preference for S. invicta. Assuming that these attacks were not simply artifacts of our experimental set-up and that these species may occasionally attack S. geminata in nature, the crucial question is how much parasitism pressure on S. geminata is acceptable as a by-product of controlling S. invicta?

We argue that P. littoralis, P. tricuspis, and P. wasmanni are good biocontrol candidates even if they do occasionally attack S. geminata because S. geminata already has its own Pseudacteon spp. that parasitize S. geminata to the exclusion of S. invicta, even though S. invicta is much more abundant. Also, S. geminata populations are declining dramatically, because this species is being competitively replaced by S. invicta over much of its range (Porter et al. 1988; L.E.G. and L.W.M., unpublished data). Finally, perhaps the best measure of parasitism pressure is the number of oviposition attempts rather than the number of individual phorids observed to attack. Thus, even in the few cases where P. littoralis, P. tricuspis, and P. wasmanni did attack S. geminata in our experiments, females appeared to lose interest after very few attacks on S. geminata. Using this measure, the parasitism pressure exerted on S. geminata by these 3 exotic phorid species pales in comparison to the pressure exerted on S. invicta, and in comparison to the pressure exerted on S. geminata by native Pseudacteon spp. (L.W.M., unpublished data). Thus, the effect on S. geminata populations of occasional attacks by these 3 exotic phorid species will probably not be biologically significant. In fact, any negative effects on S. geminata populations as a result of attack by introduced Pseudacteon spp. will almost certainly be vastly outweighed by the positive effects caused by competitive release from its close competitor, S. invicta.

It is possible that populations of these same Pseudacteon species from other South American localities may attack S. geminata with greater frequency. Yet complementary field studies of the host specificity of different populations of these same Pseudacteon species in Brazil have revealed similar preference patterns to those documented in this study, with many females attracted to S. saevissima complex colonies (including S. invicta) and few at-
tracted to S. geminata colonies (Porter et al. 1995b; S. D. Porter, USDA-ARS, CMAVE, unpublished data). Because of their species-specific functions, ant communication odors (e.g., Vander Meer et al. 1988) are less likely to vary geographically than are host plant and herbivore feeding odors used as oviposition and feeding cues by herbivorous insects or their parasitoids. Moreover, because Pseudacteon appear to orient to trail and alarm odors of their host ants (see Orr et al. 1997), we would not predict the high degree of geographical variation in host relationships of ant-attacking phorid species as is found within some species of herbivorous insects (for examples, see Fox and Morrow 1981). Thus, in contrast to more commonly studied parasites and parasitoids, the host preferences of Pseudacteon individuals from a single Pseudacteon population are likely to reflect those across the entire range of the species.

Although none of the Pseudacteon species tested were observed to complete larval development in S. geminata, this possibility cannot yet be ruled out. Pseudacteon spp. have been difficult to rear in the laboratory, and early, unsuccessful attempts by other investigators led to doubt whether Pseudacteon phorids were actually parasitoids on Solenopsis ants (Jouvenaz et al. 1981). Recent advances in rearing techniques, however, should eventually elucidate the question of whether complete development in S. geminata is possible for any or all of the South American Pseudacteon spp. tested. But, even assuming that development is possible for all 4 species, our tests revealed all but P. curvatius were strongly specific to S. invicta and not likely to attack S. geminata under circumstances that realistically simulate field encounters.

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