Host Specificity of Fire Ant Decapitating Flies (Diptera: Phoridae) in Laboratory Oviposition Tests

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ABSTRACT Host specificities of 3 species of *Pseudacteon* decapitating flies (*P. litoralis* Borgmeier, *P. tricuspis* Borgmeier, *P. wasmanni* Schmitz) were tested in quarantine facilities in Gainesville, FL. Female flies from Brazil were placed into test trays containing either red imported fire ants, *Solenopsis invicta* Buren; tropical fire ants, *Solenopsis geminata* Forel; or native ants from 6 other genera (*Crematogaster, Pheidole, Aphaenogaster, Neivamyrmex, Forelius, Camponotus*). Tests lasted 60–90 min. The 3 species of flies tested were all at least 15 times more likely to attack their natural host, *S. invicta,* than they were to attack the native fire ant, *S. geminata.* More than 200 larvae resulted from numerous attacks on *S. invicta* workers. No larvae resulted from the few possible attacks on *S. geminata* or the other species of ants that were tested. We induced several *P. tricuspis* to attack a few *S. geminata* workers by mixing these workers in with freeze-killed *S. invicta* workers. One adult fly emerged from these attacks, demonstrating that *P. tricuspis* can develop in *S. geminata* workers. This indicates that the field release of *P. tricuspis* poses some risk to native fire ants; however, the extremely low rates of attack on *S. geminata* in the laboratory and in the field indicate that this risk would be minimal. The argument is made that this small risk is acceptable because, among other things, native fire ants are under much more risk from expanding populations of imported fire ants than they would be from imported *Pseudacteon* flies.

KEY WORDS *Solenopsis, Pseudacteon,* biocontrol, classical biological control, parasitoid, Brazil

ALMOST 20 SPECIES of *Pseudacteon* flies are known to attack *Solenopsis* fire ants in South America (Porter 1998a). Most of these flies are promising candidates for use as fire ant biological control agents for the following 3 reasons: (1) they are widely distributed across seasons and habitats (Borgmeier and Prado 1975, Fowler et al. 1995, Porter et al. 1995a), (2) they have had evolutionary impacts on fire ant populations (Orr et al. 1995, Porter et al. 1995c), and (3) they are highly host specific. The host specificity of potential biological control agents is important because it greatly reduces possibilities of unintended economic and environmental consequences (Simberloff and Stiling 1996) associated with their introduction.

Several lines of evidence indicate that *Pseudacteon* flies are specific in their host preferences. First, all *Pseudacteon* flies are almost certainly parasites of ants. They have never been reported to attack any other kind of organism, and virtually all phylogenetically related phorid genera also are ant parasites (Brown 1993, Disney 1994). Their elaborate ovipositors (Borgmeier and Prado 1975) and adaptations for pupation in the head capsules of worker ants (Porter et al. 1995b) demonstrate extensive physical specializations for parasitism of ants. Furthermore, *Pseudacteon* species that attack fire ants appear to be specific to fire ants (Disney 1994). Of >24 New World species which attack fire ants, only 1 unconfirmed report exists of an uncommon species, *Pseudacteon convexicauda* Borgmeier, being collected while hovering above another genus of ants (Borgmeier 1962). Several species of *Pseudacteon* flies are specific parasites of ants in other genera (e.g., *Crematogaster, Dorymyrmex, Linepithema*), but all species of *Pseudacteon* flies with lobed ovipositors, including *P. litoralis* Borgmeier, *P. tricuspis* Borgmeier, and *P. wasmanni* Schmitz, have been collected attacking ants only in the genus *Solenopsis* (Disney 1994, Porter et al. 1995a). Several *Pseudacteon* flies apparently are specific to species complexes within the genus *Solenopsis.* For instance, at least 3 species are known to parasitize *Solenopsis geminata* in the United States, but they have never been collected attacking the 2 imported fire ants, *Solenopsis invicta* Buren and *Solenopsis richteri* Forel, even though they clearly have had the opportunity (Feener 1987, Morrison et al. 1997).

The host specificity of *Pseudacteon* flies was tested in the field in South America with 23 species of ants from 13 genera (Porter et al. 1995a). *Pseudacteon* flies in these tests were attracted only to *Solenopsis* fire ants. A 2nd set of field tests near São Paulo, Brazil demonstrated that the *Pseudacteon* flies in this region showed a very strong preference for fire ants in the *saevissima* complex (including *S. invicta*) over *S. geminata,* a fire ant in the closely related *geminata* complex (Porter 1998b). A recent laboratory study (Gilbert and Morrison 1997) in Texas showed that 3 of 4 species

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of *Pseudacteon* flies from Brazil were at least an order of magnitude less likely to attack native *S. geminata* fire ants than they were to attack the imported *S. invicta* fire ants. The objective of our study was to determine if several common species of *Pseudacteon* flies from Brazil would attack and develop in native ants from Florida. We concentrated on the native fire ant *S. geminata,* but also included ants from 6 other genera.

Materials and Methods

This study was conducted in quarantine facilities at the Center for Medical, Agricultural and Veterinary Entomology (CMAVE) in Gainesville, FL. Flies for these tests were collected while attacking *S. invicta* and *Solenopsis saevissima* (F. Smith) fire ants. Collections were made around the cities of Jaguariuna (December 1995 and June 1996) and Rio Claro (December 1995 and March 1996) in the state of São Paulo, Brazil, using techniques described by Porter et al. (1995a, 1995c). We were able to collect and transport sufficient numbers of flies from Brazil to test the host specificity of 3 *Pseudacteon* species—*P. litoralis, P. tricuspis,* and *P. wasmanni.* All flies were collected 6–36 h before air transport to the United States because of their short life span. Tests were conducted within 2–3 d of their arrival in quarantine.

The flies in December were transported in polypropylene vials (17 by 100 mm) containing groups of 3 flies (Porter et al. 1997). The flies in March and June were transported individually in clear polystyrene vials (12 by 75 mm). All vials contained a wet cotton plug in the bottom and a piece of laboratory tissue (5 by 7 mm) (Kimwipes, Kimberly Clark, Roswell, GA) that had been moistened in 50% honey water and plastered on the inside of the vial. To avoid condensation that might entrap the flies, each vial was vented with a plastic cap constructed by cutting out the center and fusing a square of hot screen (80 mesh per inch, 0.2 mm openings) over the hole. During transport to quarantine facilities, vials were placed inside several small plastic boxes that were each covered by several self-sealing plastic bags, all of which were placed inside a sealed Styrofoam container.

Oviposition tests were conducted inside 6 white plastic trays (8 by 28 by 42 cm) (Panel Controls, Detroit, MI) each with 4 screen vents (1.5 by 14 cm, 80 mesh). On one end of the tray, we cut a small injection port the same diameter as the transport vials. On the other end of the tray we constructed a rubber sleeve gasket for a 45-cm aspirator arm. The arm was designed so it could slide in and out the length of the tray and twist around as necessary for extraction of test flies. The outside end of the aspirator arm was connected to an Allen-type double chamber aspirator (Porter et al. 1995a) that had been modified to use the 12 by 75-mm transport vials as the inner chamber. The top of each tray was covered by a piece of glass that rested on a layer of silicon caulk. This silicon seal was initially constructed by coating the glass lid with petroleum jelly and gently laying it down on a thick bead of slightly tacky caulk.

Inside each tray, we placed a moist piece of paper towel to keep the humidity high. We also placed the bottom halves of 2 petri dishes (150 by 25 mm) in each tray. These dishes were lined with Fluon and contained several hundred test ants from 2 separate colonies. Most test trays contained workers from either 2 *S. invicta* or from 2 *S. geminata* colonies. We included workers from 2 colonies in each tray to minimize possible variance resulting from differences in colony attractiveness. We setup no-choice tests with only *S. invicta* or *S. geminata* in the same tray because we were not interested in assessing which species of ant the flies preferred (Porter 1998b). Rather, we wanted to determine if test flies would switch to *S. geminata* as a secondary host in the absence of *S. invicta.* All test trays with *S. invicta* that were run in March and June contained 1 petri dish with polygyne workers and 1 with monogyne workers.

Tests with *S. geminata* and *S. invicta* were conducted with paired sets of trays to avoid confounding our results with temporal variation. Most test runs began with 3 healthy female flies per tray and lasted 60–90 min. At the end of tests, flies were aspirated individually back into the transport vials. Whenever survival and health permitted, flies from tests with *S. invicta* were swapped into trays with *S. geminata* and vice versa so that most flies were tested with both species.

Additional tests also were conducted with ants from several other genera. In these tests, procedures were the same except 2 species of ants were placed together in the same tray. Most of the flies used in these tests had previously been used in attacks on *S. invicta* and *S. geminata.*

Workers from trays with ovipositing flies for the March and June tests were transferred into small nest boxes with water tube nests and checked daily for decapitated workers with pupating larvae (Porter et al. 1995b) beginning about day 12.

To determine whether *Pseudacteon* flies would attack *S. geminata* workers when they were surrounded by *S. invicta* colony odors, we set up 2 test trays. Each test tray contained 2 petri dish arenas with 1 g of fresh, freeze-killed *S. invicta* workers resting on a plaster pad (Castone) that was removed recently from an old *S. invicta* laboratory colony. We then placed several hundred live *S. geminata* workers in each petri dish and released 5 females of *P. tricuspis* into each tray.

Voucher specimens of flies and ants have been deposited in the Museu de Zoologia, Universidade de São Paulo, Brazil; the EMBRAPA-CNPMA quarantine laboratory in Jaguariuna; and the Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Service, Division of Plant Industry, Gainesville, FL.

Results

Results showed that all 3 *Pseudacteon* species were highly host specific in no-choice laboratory tests (Fig. 1). Sixty percent of *P. tricuspis* flies (50/84) attempted to oviposit on *S. invicta* fire ants compared with only 2.9% (2/72) on the native fire ant *S. geminata* (Fisher

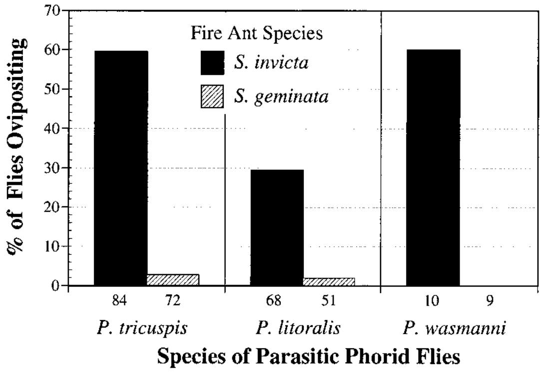

Fig. 1. Percentage of 3 parasitic *Pseudacteon* phorid flies that attacked the imported fire ant *S. invicta* and the native fire ant *S. geminata* in no-choice laboratory tests. The number of flies tested is indicated below each bar. These tests were conducted sequentially for 60–90 min with each species of fire ant using groups of 2–3 female flies. Results were pooled after chi-square tests showed no evidence of group effects.

exact $P < 0.0001$). Twenty-nine percent of *P. litoralis* (20/68) attempted to oviposit on *S. invicta* compared with only 1.9% (1/51) on *S. geminata* (Fisher exact $P < 0.0001$). Sixty percent of *P. wasmanni* (6/10) attempted to oviposit on *S. invicta* compared with none (0/9) on *S. geminata* (Fisher Exact $P = 0.011$). Not only did far fewer flies attack *S. geminata* workers, but the frequencies of their oviposition attempts were much lower. We observed hundreds of attacks on *S. invicta* workers for *P. litoralis* flies (4.1 ± 2.1 attacks per minute [mean ± SE] SD, $n = 23$) and *P. tricuspis* flies (2.6 ± 1.7 attacks per minute, $n = 17$), but only a single attempt was observed with *P. litoralis* on *S. geminata* and only 3 and 5 attacks total were observed for 2 *P. tricuspis* on *S. geminata*.

Most of the tests with *P. tricuspis* (18 tests) and *P. litoralis* (20 tests) attacking *S. invicta* were done with groups of 3 flies. There was no evidence for group synergism or group suppression of activity in these tests. The frequency of having 0, 1, 2, or 3 ovipositing flies of the 3 present did not differ significantly (chi-squared tests, df = 3, $P > 0.05$) from frequencies predicted by the overall percentage of ovipositing individuals (see Fig. 1). The frequencies of *P. tricuspis* and *P. litoralis* attacking *S. invicta* were not significantly different for flies tested originally with *S. invicta* and for flies that were swapped into *S. invicta* trays after being tested with *S. geminata* (Table 1; χ^2 tests, $P > 0.05$). The same was true for flies originally tested with *S. geminata* and those that were swapped into *S. geminata* trays after being tested with *S. invicta* (Table 1; χ^2 tests, $P > 0.05$); however, the 2 *P. tricuspis* females and the 1 *P. litoralis* female that attacked workers of *S. geminata* (Table 1) did so shortly after being transferred from a tray where they had been attacking *S. invicta* workers. Both polygyne and monogyne *S. invicta* workers were attacked in ≈85% of trials in which attacking flies had a choice of both forms (*P. tricuspis*-33/38; *P. litoralis*-17/20).

Table 1. Percentages of 2 species of *Pseudacteon* flies attacking *Solenopsis* fire ants, first in no-choice tests with one ant species and then in no-choice tests with the other ant species

Fly species	% flies attacking	
	S. invicta	*S. geminata*
Pseudacteon tricuspis		
Initial tests	56% (24/43)	0% (0/43)
After swap	55% (11/20)	11% (2/18)[a]
Pseudacteon litoralis		
Initial tests	26% (9/35)	0% (0/36)
After swap	33% (9/27)	6% (1/18)[a]

[a] Note that flies attacked *S. geminata* workers only after being swapped in from tests with *S. invicta* workers. This trend, although interesting, was not significant (χ^2 tests, $P > 0.05$).

We reared 183 *P. tricuspis* larvae and 108 adults from the 45 ovipositing females in the March and June tests using *S. invicta* workers. No parasitoids were produced from the 2 *P. tricuspis* flies that attempted to attack *S. geminata* workers. We reared 30 *P. litoralis* larvae and 15 adults from the 13 ovipositing females in the March and June tests with *S. invicta* workers. No parasitoid was produced from the single *P. litoralis* attack on an *S. geminata* worker. The number of parasitized workers are not available for *P. wasmanni* because this information was not collected in December when this species was tested.

When *P. tricuspis* females were placed in the 2 trays containing *S. geminata* workers and freeze-killed *S. invicta* workers, several flies in each tray immediately showed interest and shortly began hovering 5–10 mm above the ants. Most of the hovering activity, however, was directed toward small clusters of dead *S. invicta* workers. Nevertheless, several attacks were directed at *S. geminata* workers in 1 tray and a dozen or so in the 2nd tray. Hovering activity of 1 or 2 flies continued intermittently in both trays for ≈1 h. From these attacks, we found 1 parasitized *S. geminata* worker which eventually yielded a female fly.

The *Pseudacteon* flies showed very little interest in ants from other genera. The results for *P. tricuspis* are as follows: *Crematogaster ashmeadi* Mayr, 1/20 flies attempted to oviposit; *Pheidole dentata* Mayr, 0/11; *Aphaenogaster fulva* Roger, 1/15; *Aphaenogaster miamiana* Wheeler, 1/3; *Camponotus floridanus* (Buckley), 0/6; *Neivamyrmex opacithorax* (Emery), 0/6. The results for *P. litoralis* were: *C. ashmeadi*, 1/12; *P. dentata*, 0/12; *A. fulva*, 0/12; *A. miamiana*, 0/9; *Forelius pruinosa* Wheeler, 0/6. The results for *P. wasmanni* were: *C. ashmeadi*, 0/3; and *A. fulva*, 0/3. The 4 cases where flies attempted oviposition were all limited to no more than several attempts, most of which did not appear to be effective, either because the ant did not react as if it had been oviposited in or the position of the fly did not appear appropriate. No parasites were produced by any of the attacks on ants from other genera.

Discussion

The small percentages of *Pseudacteon* flies that attacked *S. geminata* fire ants in the no-choice laboratory tests (Fig. 1) demonstrate that *P. tricuspis, P. litoralis,* and *P. wasmanni* are all very host specific to *S. invicta.* Those few flies that did attack *S. geminata* generally attacked only several times in an hour compared with dozens of times per hour for attacks on *S. invicta* workers. Gilbert and Morrison (1997) conducted similar no-choice tests with these 3 *Pseudacteon* species using polygyne *S. invicta* and polygyne *S. geminata* from Austin, TX. They found that individual flies were 10–20 times more likely to attack *S. invicta* workers than they were to attack *S. geminata* workers, and that overall attack rates were 1 or 2 orders of magnitude higher with *S. invicta* than with *S. geminata.* Furthermore, the absence of larval development in the *S. geminata* used in this study and those used by Gilbert and Morrison (1997) demonstrated that the few attacks we observed were not successful, a situation that is not surprising considering only 10–30% of attacks result in successful parasitism, even with highly motivated flies attacking their usual hosts (Porter et al. 1995b, Morrison et al. 1997, Porter et al. 1997).

Tests with freeze-killed *S. invicta* workers showed that *P. tricuspis* females can be induced to attack *S. geminata* workers successfully and that these flies can complete development in *S. geminata.* However, tests with *S. geminata* in Brazil demonstrated that *P. tricuspis* and *P. litoralis* are not attracted to *S. geminata* under field conditions (Porter 1998b). Even when trays of both kinds of ants were placed side by side and then exchanged with each other, neither *P. tricuspis* nor *P. litoralis* attacked any *S. geminata;* whereas >500 parasitized workers were removed from the *S. invicta* and *S. saevissima* colonies (Porter 1998b). A few *P. wasmanni* have been attracted to *S. geminata* fire ant colonies in the field in Brazil (Porter et al. 1995a) and they are probably capable of completing development in this species (Porter 1998b). Nevertheless, the no-choice laboratory tests (Gilbert and Morrison 1997, Fig. 1) suggest that *P. wasmanni* is much less likely to attack *S. geminata* than *S. invicta.* Not all *Pseudacteon* species, however, may be this specific. Gilbert and Morrison (1997) reported that *Pseudacteon curvatus* Borgmeier, a small fly with a simple hooked ovipositor, readily attacked both *S. invicta* and *S. geminata* workers in no-choice laboratory tests and that many of these attacks resulted in parasitism. It is currently unknown, however, if this species can successfully locate *S. geminata* workers in the field and whether it is a parasitoid of *geminata* complex ants in regions of Brazil where they overlap with *saevissima* complex ants.

Overall, the field attraction studies (Porter et al. 1995a, Porter 1998b) and no-choice oviposition studies (Gilbert and Morrison 1997, Fig. 1) discussed above indicate that *P. tricuspis, P. litoralis,* and *P. wasmanni* are highly specific parasitoids of *saevissima* complex fire ants. Nevertheless, the fact that these flies occasionally will attack *S. geminata* and 1 or 2 *Pseudacteon* species (*P. tricuspis* and *P. wasmanni*) can complete development in *S. geminata* indicates that field release of these flies in the United States as biocontrol agents for imported fire ants would pose a small risk for native populations of *S. geminata* and probably *S. xyloni.* A small risk to *S. geminata* probably is acceptable for 4 reasons as follows: (1) This ant and its sister species *S. xyloni* already have at least 3 species of *Pseudacteon* phorids that attack them in the United States but do not attack the imported fire ants (Feener 1987, Morrison et al. 1997). Consequently, it seems very unlikely that imported *Pseudacteon* species that are rarely or never attracted to *S. geminata* could switch to a new host and out-compete the phorid parasites that have already coevolved with *S. geminata.* (2) The range of *saevissima* complex fire ants in South America is broadly jointed with that of *S. geminata* (Trager 1991); therefore, most of the phorid parasites of *saevissima* complex ants probably have had millions of years to make the jump to *S. geminata* without success. (3) *S. geminata* is neither rare nor endangered. In fact, this species is a pantropical pest of disturbed areas (Smith 1965, Trager 1991, Williams 1994). Fortunately, densities of *S. geminata* in the United States have never approached those achieved by imported fire ants (Porter 1992) so there is little danger that *S. geminata* would simply replace imported fire ants should the imported species be controlled by biocontrol agents. (4) *S. invicta* is slowly displacing *S. geminata* from most of its range in the United States (Porter et al. 1991, Porter 1992, Wojcik 1994). In other words, the clear and present danger that *S. invicta* poses to *S. geminata* almost certainly is much greater than the small risk that introduced *Pseudacteon* flies might have (Gilbert and Morrison 1997). This final argument is especially applicable to *S. xyloni* because the red imported fire ant, *S. invicta,* has eradicated *S. xyloni* from almost all of its former range in the southeastern United States (Porter et al. 1991). Nevertheless, *S. xyloni* is not a threatened species because it is still abundant around the margins of the imported fire ant range and in the southwestern United States where it often is considered a pest (Smith 1965). In short, the choice is to do nothing and permit *S. invicta* to continue displacing *S. geminata* and replacing *S. xyloni* in the United States, or to take a small risk with importing several parasitic flies that might help reverse this trend.

Our laboratory tests with *P. tricuspis, P. litoralis,* and *P. wasmanni* indicate that these flies do not parasitize ants in other genera (i.e., *Crematogaster, Pheidole, Aphaenogaster, Neivamyrmex, Forelius, Camponotus*). Most of the flies tested simply rested on the sides of the test trays and showed no interest in the ants from other genera. A small portion of the flies, however, did hover for a few minutes over *Aphaenogaster* and *Crematogaster* ants and several possible attacks were observed, but no parasites developed from any of these attacks. Field tests in Brazil with 23 species of ants from 13 genera failed to attract any *Pseudacteon* phorids to any species of ants except fire ants (Porter et al. 1995a). These data strongly suggest that *P. tricuspis, P. litoralis,* and probably all other *Pseudacteon* phorids that attack fire ants would present only a negligible risk to non-*Solenopsis* ants if they were introduced into the United States. *Pseudacteon* phorids can switch to ant hosts in different genera because several species have done that during the process of evolution (Disney 1994). However, these host shifts have been extremely rare and are only likely to occur over evolutionary time scales of tens of thousands or millions of years. Even then such shifts would probably be limited to a small subset of ants of similar size and morphology (Morrison et al. 1997, 1999). Furthermore, none of the 25 or more species of *Pseudacteon* flies with lobed ovipositors (including all 3 species tested in this study) have ever been collected in the field attacking anything except *Solenopsis* fire ants (Disney 1994), suggesting that they may be too specialized to make the switch to another ant genus under any conditions.

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