Host Specificity and Risk Assessment of Releasing the Decapitating Fly *Pseudacteon curvatus* as a Classical Biocontrol Agent for Imported Fire Ants

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Host specificity of the decapitating fly *Pseudacteon curvatus* was studied to determine whether this species is suitable for release as a classical biocontrol agent of imported fire ants in the United States. A series of no-choice tests with 19 species of ants from 12 genera showed that *P. curvatus* will not develop in ants outside the genus *Solenopsis. P. curvatus* successfully parasitized the native fire ants *Solenopsis geminata* and *Solenopsis xyloni* in no-choice tests, but rates of parasitism were considerably less than those with the imported fire ant *Solenopsis invicta* (6 and 35% of the rate for *S. invicta,* respectively). Paired preference tests showed that *P. curvatus* has a three- to fourfold preference for *S. invicta* over either of the native fire ants. Furthermore, flies reared from native fire ants still strongly preferred imported fire ants. *P. curvatus* was not attracted to vegetables, fruits, meat, prepared foods, carrion, or dung. This study indicates that release of *P. curvatus* poses only a small risk to native fire ants. The argument is made that this risk needs to be balanced against potential benefits to numerous other native organisms and a high probability that release of this fly will actually benefit native fire ants because impacts on imported fire ants will almost certainly be much greater than those on native fire ants.

Key Words: Phoridae; *Pseudacteon curvatus; P. onyx; P. spatulatus;* Formicidae; *Solenopsis invicta; S. geminata; S. xyloni;* Argentina; United States; *Apocephalus* spp.; parasitoid; classical biological control; host preference.

INTRODUCTION

When the red fire ant, *Solenopsis invicta* Buren, and the black fire ant, *Solenopsis richteri* Forel, were accidently introduced into the United States 60–80 years ago, almost all of their natural enemies were left behind in South America (Jouvenaz, 1990). Recent stud-

ies show that fire ant densities in the United States are 5–10 times higher than they are in South America (Porter *et al.,* 1992, 1997). Escape from natural enemies is a likely cause for this intercontinental difference because careful examination of factors such as precipitation, temperature, habitat, land use, polygyny, and plant cover do not help explain why we have so many imported fire ants in the United States (Porter *et al.,* 1997).

Today, the red imported fire ant, *S. invicta,* is distributed throughout the entire southeastern United States (Callcott and Collins, 1996). The black imported fire ant, *S. richteri,* is largely restricted to a small region around the northern border of Alabama and Mississippi. Throughout its range, *S. invicta* is virtually ubiquitous in pastures, parks, yards, cultivated fields, and roadsides (Porter, 1992; Porter *et al.,* 1997). In fact, *S. invicta* is one of the most abundant insect pests in the southeastern quarter of the United States, with average densities of 80–200 mounds/ha and 1500–3500 ants/m^2 (Macom and Porter, 1996). Strict quarantine procedures have limited the spread of this pest (Lockley and Collins, 1990), but eventually populations will expand westward into Arizona and California (Anonymous, 1999), southward into Mexico and the Caribbean, and northward along a front from Oklahoma to Virginia.

Imported fire ants cause a wide variety of problems in the United States. They are responsible for hundreds of millions if not billions of dollars in economic losses every year (Lofgren, 1986; Barr and Drees, 1996; Thompson and Jones, 1996). They damage citrus trees (Banks *et al.,* 1991), soybeans (Adams *et al.,* 1983; Banks *et al.,* 1990), potatoes (Adams *et al.,* 1988), corn (Drees *et al.,* 1991), and other crops (Adams, 1986; Drees, 1988). They are a major medical concern to approximately half a million people who are severely allergic to even a single fire ant sting (~1% of the population; Adams and Lofgren, 1981; Stafford *et al.,* 1989; Baluga *et al.,* 1996) and to many more young

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children who are repeatedly stung by hundreds of fire ants when they accidently step onto the mounds. Fire ants are also a major nuisance to millions of additional people who are stung while gardening, hiking, working, golfing, or simply standing outside. Fire ants commonly damage outdoor electrical equipment such as air conditioners and power transformers (MacKay and Vinson, 1990; Schulz, 1991). Fire ants can be a significant problem for livestock and poultry operations (Barr et al., 1994; Barr and Drees, 1996). They are also a major environmental concern because they substantially reduce the biodiversity of ants and ground-dwelling arthropods as, well as populations of many vertebrates (Lofgren, 1986; Porter and Savignano, 1990; Vinson, 1994). Imported fire ants are occasionally beneficial; for example, they have been reported to reduce losses from sugarcane borers and to reduce tick populations (Reagan, 1986).

Currently, poison baits are the best option that we have for controlling fire ants. These baits provide 80–90% control for periods of 3–12 months (Collins et al., 1992). They work well in concentrated areas of high activity, such as school yards, parks, feed lots, and around homes. The problem with poison baits is that they must be used one to three times a year indefinitely, or the fire ants will return. The need for repeated applications makes poison baits too expensive for grazing lands and natural areas (Barr and Drees, 1996). Another problem is that baits are not specific enough to be used in natural areas without killing native ants (Williams, 1986) and many arthropod scavengers. Baits are also not registered for most agricultural uses.

Classical biocontrol agents offer a possibility for permanent large-scale control of imported fire ants. The major advantages of classical biocontrol is that it could be very cost effective (Bellows, 1993) and it should work well in pastures and natural areas that currently lack practical treatment options. A concern is that no one has ever successfully used classical biocontrol agents against any social insect—but only a few attempts have been made (Beggs et al., 1996). Nevertheless, social insects should be susceptible to biocontrol agents, as witnessed by the impacts of tracheal mites, foulbrood, and other natural enemies on honey bee colonies (Morse and Nowogrodzki, 1990).

Imported fire ants in the United States have escaped most of their natural enemies (Porter et al., 1997). Consequently, we may be able reduce fire ant populations in the United States by importing and releasing some of these natural enemies. Phorid flies in the genus Pseudacteon show promise as classical biocontrol agents because (1) they are widely distributed across seasons and habitats (Borgmeier and Prado, 1975; Fowler et al., 1995), (2) they have had evolutionary impacts on fire ant populations (Orr et al., 1995; Porter

et al., 1995c), and (3) they are very host specific (Porter, 1998a).

Flies in the genus Pseudacteon have the unusual habit of decapitating host ants and then pupating inside the empty head capsule of their host (Porter et al., 1995b). Pseudacteon flies do not kill fire ant colonies directly; rather, they stress colonies by parasitizing workers and limiting colony access to food resources (Feener and Brown, 1992). It is hoped that these effects combined with those of other natural enemies will tip the ecological balance in favor of native ants (Porter, 1998a). If this happens, increased competition with native ants may cause imported fire ant populations in many areas to drop to levels similar to those found in South America (Porter et al., 1997).

Host specificity is important for potential biocontrol agents because it greatly reduces possibilities of unintended consequences associated with their introduction (Simberloff and Stiling, 1996). Flies in the genus Pseudacteon are likely to be very host specific for several reasons. First, Pseudacteon flies have only been collected attacking ants and virtually all phylogenetically related phorid genera are also parasitoids of ants (Brown, 1993; Disney, 1994). Second, their elaborate ovipositors (Borgmeier and Prado, 1975) and adaptations for pupation in the head capsules of worker ants (Porter et al., 1995b) are highly evolved physical specializations that will dramatically limit their ability to parasitize other kinds of organisms. Third, the Pseudacteon species that attack Solenopsis fire ants appear to be specific to Solenopsis fire ants, as demonstrated by field collections (Disney, 1994) and a series of field tests in Brazil (Porter et al., 1995a; Porter, 1998b). Several species of Pseudacteon flies in the United States are parasites of ants in other genera (e.g., Crematogaster, Dorymyrmex, Linepithema), but they also do not attack ants outside of their host genus (Disney, 1994). Fourth, laboratory no-choice tests have demonstrated that several Pseudacteon species from Brazil (P. tricuspis, P. litoralis, P. obtusus) are specific to imported fire ants (Gilbert and Morrison, 1997; Morrison and Gilbert, 1999; Porter and Alonso, 1999); these species did not parasitize ants in other genera and rarely or never parasitized Solenopsis fire ants native to North America.

Several Pseudacteon species will attack both imported and native fire ants. A few Pseudacteon wasmanni and Pseudacteon pradei flies were attracted to S. geminata fire ants in Brazil (Porter et al., 1995a; Porter, 1998b), but low attack rates in the laboratory (Gilbert and Morrison, 1997) indicate that P. wasmanni is unlikely to do well with S. geminata. P. pradei has not been tested in the laboratory. Laboratory tests conducted by Gilbert and Morrison (1997) showed that P. curvatus flies from Brazil can successfully attack and parasitize S. geminata fire ants from Texas.

The objective of this study was to thoroughly examine the host specificity of *P. curvatus* flies from Las Flores, Argentina. I was particularly interested in quantifying parasitism rates resulting from no-choice tests with native fire ants and ants from other genera. I also examined host preferences of this fly in paired trials with native and imported fire ants. Further tests were conducted to determine whether host preferences were fixed or facultatively adjusted to the host from which the flies emerged. A series of tests was also conducted to determine whether *P. curvatus* was attracted to food items that might make it a nuisance or a vector of disease.

Based on the findings of this and other studies, *P. curvatus* was approved for field release in the fall of 1999. Field release trials began in the spring of 2000. This makes *P. curvatus* the second *Pseudacteon* species released in the United States as a fire ant biocontrol agent. *Pseudacteon tricuspis,* the first species, is permanently established at several sites around Gainesville, Florida (Porter *et al.,* 1999). A dozen or so additional releases of *P. tricuspis* have been made with cooperators in other states (Porter *et al.,* 1999; unpublished data) and by researchers in Texas (L. E. Gilbert, pers. comm.)

MATERIALS AND METHODS

The flies were collected from the El Toro ranch east of Las Flores, Buenos Aires Province, Argentina, March 1997. Flies were collected by setting out nine trays (40 × 30 × 10 cm) each with several thousand fire ants (*S. richteri*). These trays were set out in shady places in a large cow pasture where they each attracted a dozen or so *P. curvatus* flies, as well as a few individuals of several other *Pseudacteon* species (*P. tricuspis, P. borgmeieri, P. nudicornis,* and *P. obtusus*). These flies were allowed to attack the workers for about 5 h while the workers ran from one side of the tray to the other trying to hide under a small inverted box which was switched back and forth to keep the workers moving and exposed to the flies. These workers were airfreighted to our quarantine facility in Gainesville, Florida. About 1000 fly pupae were eventually recovered from these ants. One year and about 10 generations later, our laboratory colony of *P. curvatus* flies had grown sufficiently large to begin testing their host specificity. Rearing procedures were similar to those described by Porter and Briano (2000).

Host Specificity with Ants from non-Solenopsis Genera

To determine whether *P. curvatus* flies can attack and develop in ants from non-*Solenopsis* genera, we collected 19 species of ants from 12 nonhost genera. These species had workers that were in the same ap-

proximate size range as those normally parasitized by *P. curvatus* in fire ant colonies (see Table 1). Head widths of test ants were determined to the nearest 0.01 mm using a wedge micrometer (Porter, 1983). Tests were conducted in three white plastic trays (42 × 28 × 15 cm; Panel Controls Corp., Detroit, MI) with screened vents and tight-fitting glass lids, as described by Porter and Alonso (1999). In the bottom of each tray, I cut two long side-by-side holes under which I glued two smaller plastic trays (7 × 30 × 5 cm, 1 × w × h). This configuration produced two parallel chambers in the bottom of the big tray that allowed us to test two species of ants at the same time. Ants were contained in the two bottom trays by coating their sides with Fluon (ICI, Wilmington, DE).

A 10-cm bunch of plastic flowers on which the flies could rest was placed in one side of the three big trays. To maintain high humidity, we placed four moistened 3 × 3 × 4-cm sponges in the corners of the test trays and poured a 1-cm-thick layer of hard plaster (Castone; Dentsply, York, PA) in the bottoms of the two bottom trays. The plaster was moistened before each test run. Small 20-cm desk fans were directed toward the vents of the test boxes so that humidity did not condense on the glass lid or the sides of the trays. Flies were introduced into the trays via an injection port and removed via an aspirator arm, as described by Porter and Alonso (1999).

A small opaque inverted cup (4 cm diameter) with a large wire loop glued to the top was placed on the plaster in each of the two bottom trays. These cups were moved back and forth from one end of a tray to the other with the aspirator arm each time most of the ants had crawled under a cup to hide. This procedure kept the ants trailing continuously from one end of a bottom tray to the other so that the flies always had an opportunity to attack the ants.

Each test run lasted 3–4 h and used 10–15 female flies and an equivalent number of males. Groups of test ants contained several dozen to several hundred workers (usually 0.3–0.5 g). About 30% of tests included brood. The trays were inspected every 10 min for attacking flies. An estimate of "fly hours" was calculated by multiplying the length of the test by the average of the number of flies put in and the number taken out (Table 1). At the end of each test, worker ants were retained in small boxes (20 × 12 × 5 cm) with tight-fitting vented (2 × 3 cm) lids. Inside each box was a small 3-cm block of moist plaster and a nest tube with water held in the end by a cotton ball (16 × 125 mm). Ants were fed fresh sugar water every 3–4 days. We inspected the head capsules of dead workers for fly larvae or pupae every 1–2 days for a period of 30–40 days so that virtually all larvae had time to complete development in their host (unpublished data).

No-Choice Tests with Native Fire Ants

To determine whether *P. curvatus* flies can attack and develop in native *Solenopsis* fire ants, we conducted no-choice tests with *S. geminata* and *S. xyloni* MacCook. Two additional native species, *Solenopsis aurea* Wheeler and *Solenopsis amblychila* Wheeler, were not tested because colonies of these species were prohibitively difficult to obtain. Six trays used in these tests contained a single solid bottom covered with a 2- to 3-cm layer of moistened plaster; otherwise, they were the same as the trays described above. Timer motors were used to automatically raise an inverted cup in one end of each tray while lowering a cup at the other end of each tray. This caused the test ants to continuously trail back and forth between the two cups. Timer motors were set to run for 8 h a day (10:00 to 18:00 h). A moistened sponge (5 × 4 × 3 cm), a strip of blotter paper soaked in honey water, and a bunch of artificial flowers were placed on a sheet of plastic film in the center of each tray. The cup holding the flowers was coated on the outside with Fluon to exclude the ants.

We conducted nine trials with *S. geminata* and three control trials with *S. invicta;* all colonies were collected around Gainesville, Florida (April–May 1998). Each test group contained 0.3 g of workers and 1.0 g of brood. We conducted an additional four trials with *S. geminata* collected from Lampasas Co., Texas and two trials with *S. invicta* from Gainesville (June 1998). These tests contained 0.5 g of workers and 1.0 g of brood. Different colonies were used for each trial to assure that results were not due solely to differences in the attractiveness of individual colonies.

We conducted two trials with *S. xyloni* fire ants from Maricopa Co., Arizona (July 1998), five trials with *S. xyloni* from Bryan Co., Oklahoma (October 1998), and two trials with *S. xyloni* from Ventura Co., California (October 1998). These trials were conducted in conjunction with four trials of *S. invicta* from Gainesville. Each test used 0.4 g of workers plus 0.4–0.8 g of brood collected from a different colony.

Fifteen to 24 female flies and an equivalent number of males were added to all no-choice trials over a period of 2 days. The number of active flies was recorded periodically for all trials (except those with *S. geminata* from Texas). Tests lasted 3–4 days. *P. curvatus* flies usually live only 1 or 2 days; consequently, almost all of the flies were dead by the end of the trials. After test ants were removed from the trays, they were held and inspected for parasitism as described above. When test trays were reused, native fire ants were not used in trays that had been used by imported fire ants (and vice versa) unless the plaster bottoms were replaced. This procedure avoided confounding results with odors deposited on the plaster bottoms.

To determine whether *P. curvatus* flies would attack more *S. geminata* workers if they were in close association with *S. invicta* workers, we conducted three trials using *S. geminata* workers (0.3 g workers and 1.0 g brood) mixed together with fresh freeze-killed *S. invicta* workers (0.3 g).

To determine whether *P. curvatus* females reared from *S. geminata* workers would do better at parasitizing *S. geminata* workers, we set up a no-choice test colony and released 23 females and 22 males reared from *S. geminata* together with an additional 22 males reared from *S. invicta.* These flies were released over a 10-day period. More tests were not done because rearing flies from *S. geminata* was very difficult and additional flies were not available.

Paired Preference Tests

Host preferences of *P. curvatus* were examined in six paired trials with *S. invicta* and *S. geminata* (July 1998) and seven paired trials with *S. invicta* and *S. xyloni* (October 1998). We used 0.25 g of workers and 0.50 g of brood for each test group. Seven additional paired trials were conducted with *S. invicta* and *S. xyloni* (November 1998) using flies reared from *S. xyloni* to determine whether they would have a higher preference for *S. xyloni* than flies reared from *S. invicta.* These test groups had 0.25 g of workers and 0.05–0.10 g of brood. (Brood was limited in these tests because of the difficulty of obtaining *S. xyloni* brood late in the fall.)

Tests were conducted using the three test boxes that were constructed for use with ants in different genera (see above). Each test used ants from a different colony and received 11–16 female flies and an equivalent number of males. Trials lasted 3–4 h during which time we recorded the number of active females over each species every 10 min. Whenever possible, we also recorded the number of oviposition attempts per minute for flies hovering over each group of ants. At the end of these trials, workers were retained and checked for parasitism as described above. When the test boxes were reused, workers from one species of fire ant were not placed in a side that had been used by another species.

Attraction to Food

The following tests were conducted to determine whether *P. curvatus* is attracted to food items that might make it a pest. Tests were conducted in a large vented tray (55 × 40 × 13 cm) with a glass top similar to the test trays described above. Two bunches of plastic flowers were placed in opposite corners of the tray along with four moistened sponges. In the center of the tray, we placed a 5 × 5 matrix of shallow plastic cups (3 × 1.5 cm). Food items were placed in about 20 of these cups and moist lab tissues were placed in the

remaining cups. We then introduced 50 unfed flies, most of which were 1–2 days old. A small fan was aimed at one side of the tray to give air circulation. Occurrences of flies on food items were noted every 10 min for 1–2 h.

The following items were tested in one or more of five test runs: raw vegetables—cabbage, cauliflower, tomato, potato, corn, onion, green pepper, green bean, garlic, kale, lettuce, mushroom; fresh fruit—kiwi, red grape, green seedless grape, apple, apricot, strawberry, cantaloupe, banana, orange, grapefruit, peach, pear, plum; raw meat—beef, pork, chicken, shrimp, squid, scallop, smelt; prepared foods—egg salad, tuna salad, ham salad, cole slaw, barbecue beans, hot dog, cookie, macaroni salad, brownie, macaroni and cheese, cooked chicken, honey water; carrion—opossum, rotten chicken; dung—cow, dog, chicken, pig, human, horse.

Statistics

A one-way ANOVA was used to evaluate differences in the no-choice tests. Numbers of parasitized workers were log-transformed to equalize variance. One-tailed, paired t tests were used to compare fly activity and parasitized workers in the preference tests. A one-way ANOVA was used to compare attack rates. Attack rate data for the *S. invicta/S. geminata* tests were log-transformed to equalize variance. A three-way ANOVA was used to compare preference data for flies reared on *S. invicta* with flies reared from *S. xyloni*. "Preferred host" and "host source" were fixed factors and "test box" was used as a random factor nested in "host source."

Voucher specimens of the flies have been deposited in the Florida Collection of Arthropods, Gainesville, Florida; the Departamento Científico de Entomología, Museo de la Plata, Universidad Nacional de la Plata, Argentina; and the insect collection of the Laboratório de Quarentena "Costa Lima" EMBRAPA Meio Ambiente, Jaguariúna, SP, Brazil.

RESULTS

Host Specificity with Ants from non-Solenopsis Genera

P. curvatus females were observed hovering in attack mode over 17 of the 19 species of ants tested in genera other than *Solenopsis* (Table 1). In most cases, we also saw at least a few oviposition strikes or attacks. However, hovering activity and attack rates were always considerably lower than those observed under similar circumstances with *S. invicta.* No *P. curvatus* larvae or pupae resulted in any ants from genera other than *Solenopsis* (Table 1). In contrast, similar tests with *S. invicta* resulted in an average of 105 parasitized workers per test. We did, however, recover several native parasitic phorids from *Crematogaster pilosa* and *Pheidole morrisi* workers (Table 1).

No-Choice Tests with Native Fire Ants

In no-choice tests, *P. curvatus* flies attacked and developed successfully in the native fire ant *S. geminata* (Fig. 1). However, the number of active flies hovering over *S. geminata* was almost nine times less than that in *S. invicta* tests (Fig. 1A; 0.26 versus 2.3, $F =$ 146.9, $df = 1,10$, $P < 0.0001$). Similarly, the number of parasitized workers produced per female fly with *S. geminata* was 1/17 of the number produced with *S. invicta* (Fig. 1B; 0.42 versus 7.1, $F = 101.6$, $df = 1,16$, $P < 0.0001$). A conservative estimate is that female flies would need to produce a minimum of three offspring to replace themselves, produce males, and offset an estimated 33% mortality from larvae to adult flies. Parasitism rates with *S. geminata* were only 14% of this estimated minimum (one-sample t test, mean ≥ 3, $t = -20.1$, $P < 0.0001$). The percentage of larvae actually completing development to adult flies (50%) and the sex ratio ($\sim$1:1) did not differ between *S. invicta* and *S. geminata.* Fly activity and worker parasitism rates did not differ significantly between *S. geminata* collected in Florida and those in Texas ($P > 0.05$).

The 23 female flies that we reared from *S. geminata* were all unsuccessful at parasitizing *S. geminata* workers in a test colony probably because they were not attracted to the workers. Several other tests with *S. geminata* also did not produce parasitized workers, but this was never the case with *S. invicta* tests.

Scattering freeze-killed *S. invicta* workers on the bottom of three trays with *S. geminata* workers significantly increased the number of hovering flies for the first 2 h compared with nine tests with *S. geminata* workers alone (2.17 $\pm$ 0.75 versus 0.26 $\pm$ 0.07 flies, Scheffe test, $P = 0.0002$). However, the numbers of hovering flies in tests with *S. geminata* and freeze-killed *S. invicta* workers was not significantly different from the numbers observed in three tests with live *S. invicta* (2.17 $\pm$ 0.75 versus 2.29 $\pm$ 0.21, Scheffe test, $P > 0.05$). The next day there was no apparent effect of the freeze-killed workers on fly activity.

The number of parasitized *S. geminata* workers/female fly from tests with freeze-killed *S. invicta* was significantly less than the number resulting from live *S. invicta* (1.8 $\pm$ 1.4 versus 7.1 $\pm$ 1.3, Scheffe test, $P = 0.003$) and not different from the number resulting from tests with only live *S. geminata* workers (1.8 $\pm$ 1.4 versus 0.42 $\pm$ 0.13, $P > 0.05$). In other words, the increased hovering activity caused by the dead *S. invicta* did not clearly increase parasitism rates, although the parasitism rate in one colony (4.55 offspring/female fly) was 10 times the average in regular *S. geminata* colonies (0.42, Fig. 1).

P. curvatus also successfully attacked and developed in the *S. xyloni* workers used in no-choice tests (Fig. 1). This was true with *S. xyloni* from Arizona, California,

TABLE 1

Absence of Successful Parasitism in Nonhost Ant Genera When Exposed to the Decapitating Fly,
Pseudacteon curvatus in No-Choice Tests

Ant species	Head width (mm)[1]	Colonies tested	Est. fly h	Active flies/ observation[2]	Parasitized workers
Solenopsis invicta[3]	0.78 ± 0.10, 0.64–1.08[5]	6	35 ± 4	1.37 ± 0.19	105 ± 16
Aphaenogaster miamiana	0.80–0.95 ± 0.06	3	92	0.28 ± 0.05	0
Camponotus impressus[4]	0.76–0.88 ± 0.05 & 1.05–1.09 ± 0.04	3	93	0.09 ± 0.0	0
Crematogaster ashmeadi	0.74 ± 0.09	1	29	0.22	0
C. pilosa	0.72–0.92 ± 0.06	3	108	0.30 ± 0.06	0[6]
C. minutissima	0.63 ± 0.03	1	29	0.06	0
Dorymyrmex bureni	0.73–0.91 ± 0.05	3	109	0.15 ± 0.13	0
D. smithii	0.92 ± 0.04	1	35	0	0
Forelius pruinosus	0.56 ± 0.03	1	36	0.59	0
Lasius neoniger	0.76 ± 0.06	1	43	0.05	0
Leptothorax pergandei	0.68 ± 0.03	1	33	0.40	0
Linepithema humile	0.63 ± 0.05	1	30	0.16	0
Pheidole dentata[4]	0.62 ± 0.02 & 1.20 ± 0.08	2	65	0.16 ± 0.08	0
P. morrisi[4]	0.67 ± 0.03 & 1.26 ± 0.04	3	84	0.40 ± 0.20	0[7]
P. crassicornis[4]	0.65 ± 0.02 & 1.22 ± 0.03	1	31	0.19	0
P. diversipilosa[4]	0.66 ± 0.02 & 1.30 ± 0.02	1	47	0.14	0
P. megacephala[4]	0.52 ± 0.05 & 1.14 ± 0.05	1	23	0	0
Pseudomyrmex ejectus	0.71 ± 0.05	1	32	0.06	0
Tetramorium simillimum	0.58 ± 0.02	1	36	0.13	0
Trachymyrmex septentrionalis	0.89–1.02 ± 0.07	2	61	0.26 ± 0.02	0
Nonhost ants		31	1016	0.19 ± 0.04	0

[1] Mean worker head widths are reported ± SD for each species. A range is given when colonies had different-sized minor workers.

[2] The average number of active flies hovering close over ants during an observation. Data are shown ± SE when means are averaged from several colonies.

[3] Shown for comparison. Data are *S. invicta* averages from preference tests with *Solenopsis geminata*.

[4] Workers of these species are dimorphic; so two sizes are reported.

[5] Mean, standard deviation, and range for monogyne fire ant workers successfully parasitized by *P. curvatus* (unpublished data). Morrison and Gilbert (1998) reported that the mean head width of polygyne fire ant workers attacked by *P. curvatus* was 0.66 ± 0.11 mm.

[6] Three pupae of a native decapitating fly (probably *Pseudacteon onyx*) were found in two colonies. One male emerged and a female was dissected out of an aborted pupa.

[7] A maggot emerged from a major worker and pupated outside of the head capsule. Unlike *Pseudacteon* pupae, this pupa was fully sclerotized. A male fly in the genus *Apocephalus* emerged.

and Oklahoma. The two Arizona trials were dropped from the following analyses because large numbers of workers died in the 1st week after the tests were conducted. Four native *Pseudacteon* pupae (*P. spatulatus*) were found in the two Arizona colonies. Three flies emerged from these pupae, including two males and one female. The number of active flies hovering over *S. xyloni* workers was not significantly less than the number over *S. invicta* workers (Fig. 1A; 0.90 versus 1.26, $F = 2.10$, $df = 1,9$, $P > 0.05$). The number of parasitized *S. xyloni* workers per female fly, however, was only 35% of the number for *S. invicta* workers (Fig. 1B; 3.33 versus 9.45, $F = 6.68$, $df = 1,9$, $P = 0.029$). Nevertheless, the number of offspring per female did approach the minimum level at which a population might be able to be maintained. The percentage of pupating larvae successfully completing development to adult flies was 50% in *S. xyloni* and 64% in *S. invicta*.

Paired Preference Tests

The preference tests showed that *P. curvatus* flies strongly preferred the red imported fire ant over either native fire ant (Fig. 2). Approximately 80% of flies preferred to hover over *S. invicta* rather than *S. geminata* (Fig. 2A; 1.37 versus 0.39 flies/observation, $t = 3.44$, $df = 5$, $P = 0.009$, one-tailed test). Approximately 75% of flies preferred *S. invicta* over *S. xyloni* (Fig. 2A; 1.35 versus 0.48 flies/observation, $t = 2.87$, $df = 6$, $P = 0.014$, one-tailed test). Furthermore, the attack rate was 9 times higher for flies hovering over *S. invicta* than for flies hovering over *S. geminata* (Fig. 2B; 10.0 versus 1.4 strikes/min, $F = 37.5$, $df = 1,8$, $P = 0.0003$). No difference was found between the attack rates for flies hovering over *S. invicta* and *S. xyloni* (Fig. 2B; 6.0 versus 5.9 attacks/min, $F = 0.002$, $df = 1,9$, $P > 0.05$). Parasitism rates were much higher for *S. invicta* than for either native species in
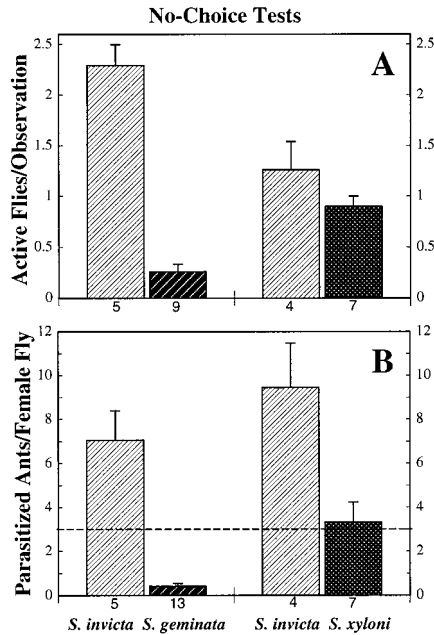
FIG. 1. No-choice host-specificity tests of the decapitating fly *P. curvatus* with the imported fire ant *S. invicta* and two native fire ants *S. geminata* and *S. xyloni.* (A) The mean number of active flies hovering over test ants in attack mode during each observation. (B) The mean number of parasitized fire ant workers produced per female fly. The dashed line indicates a conservative estimate of the minimum number of offspring/female necessary to produce a self-sustaining population. This number was calculated assuming 33% mortality from egg to adult and a 1:1 sex ratio (unpublished data). Actual values in the field should be higher because not every female would be successful in finding hosts to parasitize. Error bars show SE calculated from test means. The number of test colonies is indicated below each bar.

tion between preference and host origin was not ($F = 1.97$, $df = 1,12$, $P = 0.186$).

Attraction to Food

When 50 unfed flies were released into each of the five test chambers, almost all of them flew to the sides and corners of the trays. Little or no interest was shown in the food items. At any one observation, $4.6 \pm 1.0\%$ (SE, $n = 5$ tests) of the flies were on the food items or moist tissues. Over the course of the observations, at least 75% of the flies never visited the food items or moistened tissues. The frequency distributions of flies visiting food items and the moist tissues were not statistically different ($\chi^2 = 1.8$, $df = 3$, $P = 0.62$). Overall, 69% of the food items were never visited, 19% were visited once, 9% were visited twice, and 3% were visited three or more times ($n = 94$); this compares to 62, 27, 16, and 0% ($n = 26$) for the moist tissues. Two food items were visited five times, but
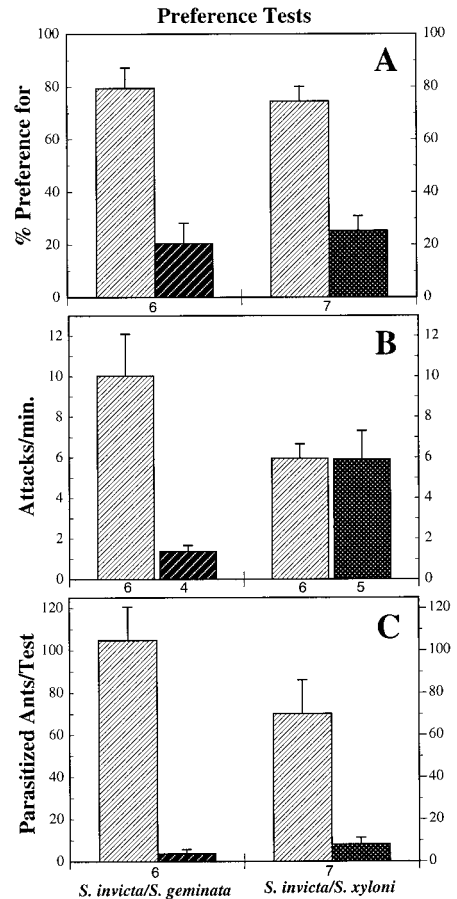
the preference tests (Fig. 2C). In the *S. invicta/S. geminata* tests, we found 28 times as many parasitized workers in *S. invicta* as in *S. geminata* (Fig. 2C; 104.8 versus 3.7 workers per test, $t = 5.85$, $df = 5$, $P = 0.001$, one-tailed test). This difference is close to the 32-fold difference that is predicted by multiplying hovering preferences (Fig. 2A) by the attack rates (Fig. 2B). In the *S. invicta/S. xyloni* tests, we found 8.6 times as many parasitized workers in *S. invicta* as in *S. xyloni* (Fig. 2C; 70.1 versus 8.1 workers per test, $t = 5.85$, $df = 6$, $P = 0.0025$, one-tailed test). This difference is more than twice that expected by multiplying differences in hovering preferences by attack rates, indicating that either oviposition attempts or development in *S. invicta* may be more successful than in *S. xyloni.*

We found that *P. curvatus* flies reared from *S. xyloni* ants retained their strong preference for *S. invicta* (Fig. 3). Almost 75% of hovering flies reared from *S. invicta* preferred *S. invicta* compared with 86% of flies reared from *S. xyloni* ($F = 0.191$, $df = 1,12$, $P = 0.670$). Preference for *S. invicta* was highly significant ($F = 64.6$, $df = 1,12$, $P < 0.0001$), but the interac-

FIG. 2. Paired host-preference tests for the decapitating fly, *P. curvatus.* (A) Percentage of active flies preferring to hover over either *S. invicta* or one of the two native species. (B) The attack rate of hovering flies. (C) The mean number of parasitized workers collected from each species of ant. Error bars show SE calculated from test means. The number of test pairs (A, C) or test colonies (B) are shown below bars.
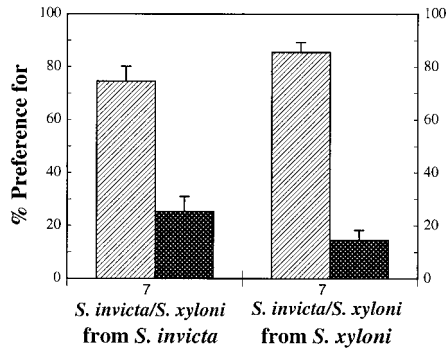
FIG. 3. Host-preferences of *P. curvatus* flies reared from *S. invicta* and from *S. xyloni.* Error bars are SE. The number of test pairs is shown below bars.

additional cups (five each) with the same food item in subsequent tests did not show unusual rates of visitation.

Large numbers of *P. curvatus* flies were present in the field when they were collected, but none of these flies were attracted to humans during the collection efforts. In fact, they appeared to avoid landing on our hands and never flew around our faces. My experiences in the field have always been the same at numerous sites with *P. curvatus* and other *Pseudacteon* flies.

DISCUSSION

Non-Solenopsis Genera

P. curvatus was not successful in parasitizing ants from any genera other than *Solenopsis* (Table 1). *P. curvatus* hovered in attack mode over most of the test ants and usually made at least a few oviposition attempts. Attacks on ants from nonhost genera are not known to occur in nature (Borgmeier, 1925; Borgmeier and Prado, 1975; Porter *et al.,* 1995a) and were likely a result of visual stimulation together with close confinement in the test box. The fact that all oviposition attempts failed indicates either that female flies could not successfully inject their eggs into the ants or that the larvae were not capable of developing in ants outside the genus *Solenopsis.* The low attack rates (Table 1) indicate that hovering flies recognized that these ants were not proper hosts. Laboratory specificity tests with *P. tricuspis, P. litoralis,* and *P. wasmanni* (Porter and Alonso, 1999) also failed to produce parasitized workers in other genera of ants, although attack activity was extremely low with these ants (Porter and Alonso, 1999).

Native Fire Ants

P. curvatus attacked and developed successfully in two species of native fire ants: *S. geminata* and *S. xyloni* (Fig. 1). Gilbert and Morrison (1997) also reported larval development of *P. curvatus* from Brazil in

S. geminata from Texas, although they did not rear the flies to adults. *P. tricuspis* from Brazil can also develop successfully in *S. geminata,* but this only happened once when freeze-killed *S. invicta* were mixed in with live *S. geminata* (Porter and Alonso, 1999). Several other imported *Pseudacteon* species (*P. litoralis, P. wasmanni, P. obtusus*) have been tested with *S. geminata,* but attack rates were too low to determine whether development is possible (Gilbert and Morrison, 1997; Morrison and Gilbert, 1999; Porter and Alonso, 1999). *P. borgmeieri,* a large sister species of *P. curvatus,* readily attacks *S. geminata* (Morrison and Gilbert, 1999), but the success of these attacks is not known.

While *P. curvatus* will attack and develop in *S. geminata,* our results indicate that this ant would not be a good host for *P. curvatus* because parasitism rates were only 1/7th of an estimated minimum necessary to maintain a population (Fig. 1B). Furthermore, *P. curvatus* had a strong preference for *S. invicta* over *S. geminata* (80%, Fig. 2A) and a very low rate of attack when hovering over *S. geminata* (Fig. 2B). This strong preference for *S. invicta* is apparently genetic because flies reared from *S. geminata* were no more successful attacking *S. geminata* workers than flies reared from *S. invicta.* Gilbert and Morrison (1997) reported that Brazilian *P. curvatus* had twice the attack rate on *S. invicta* as on *S. geminata* (1.53 versus 0.75 attacks/min). We found a sevenfold difference and considerably higher rates of attack (10.0 versus 1.38 attacks/min), probably because we used recently emerged flies and terminated our timing when flies stopped hovering.

The addition of freeze-killed *S. invicta* significantly increased hovering activity over *S. geminata.* These data indicate that airborne chemical cues are probably involved in attraction. Similar results were reported for *P. tricuspis* when attacking *S. geminata* mixed with freeze-killed *S. invicta* (Porter and Alonso, 1999). However, poor parasitism rates indicate that *S. invicta* odors alone are not enough to guarantee success.

Parasitism rates in no-choice tests with *S. xyloni* reached levels where *P. curvatus* might be able to sustain a population (Fig. 1B). However, these rates were only 35% of that produced from *S. invicta.* Furthermore, in preference tests, 75% of flies chose to attack *S. invicta* over *S. xyloni* (Fig. 2A). Attack rates were essentially the same (Fig. 2B), but production (Fig. 2C) was only 1/2 of that expected from multiplying preference by attack rates, suggesting that problems may have occurred during oviposition or early larval development. Flies reared from *S. xyloni* were no more likely to hover over *S. xyloni* than flies which emerged from *S. invicta* (Fig. 3). Furthermore, our laboratory colony of *P. curvatus* maintained a strong preference for *S. richteri* workers even after having been reared on *S. invicta* workers for over 2 years and 20 or more generations (Porter and Briano, 2000). In other words, host

preferences in *P. curvatus* are apparently "hardwired" in the genome rather than facultatively adjusted to the host. Overall, these tests indicate that *P. curvatus* would do three to four times better with *S. invicta* than it would with *S. xyloni,* assuming that it is even capable of finding *S. xyloni* in the field.

Risk Assessment of Field Release

P. curvatus was not attracted to a variety of vegetables, fruits, raw meat, carrion, excrement, and prepared foods. They were also not attracted to people in the field. Furthermore, no reports exist in the literature of flies in the genus *Pseudacteon* or any other related genera of parasitic phorid flies being a pest of any kind in either North America or in South America. This information strongly indicates that *P. curvatus* will not be a nuisance or a vector of diseases. In fact, the only time people are likely to see these miniature flies is over disturbed fire ant mounds.

Our host specificity tests (Table 1) together with field collection data of *P. curvatus* and related species (Borgmeier, 1925; Borgmeier and Prado, 1975; Porter *et al.,* 1995a) indicate that the possibility of host switching to ants in other genera is virtually nonexistent on a historical time scale. Furthermore, based on the evolutionary stability and specificity of flies in the genus *Pseudacteon* and related genera (Brown, 1993), there is no realistic possibility that *P. curvatus* would ever become a generalist parasite attacking ants in many genera.

P. curvatus clearly poses some risk to the native fire ants since it can successfully complete development in them. However, the risks for *S. geminata* appear to be very low because *P. curvatus* fell far short of being able to parasitize sufficient *S. geminata* workers in the no-choice tests (Fig. 1) to sustain a population. The fact that *P. curvatus* reared from *S. geminata* did not switch host preference to *S. geminata* indicates that host preference is genetically rather than facultatively controlled.

A preference to attack *S. geminata* is unlikely to evolve in sympatry with *S. invicta* because of (1) the poor success of flies attacking *S. geminata,* (2) the relatively low abundance of *S. geminata,* and most importantly (3) the lack of a mating barrier with relatively huge populations of flies that would be produced from *S. invicta* hosts. In short, the inclination to attack *S. geminata* workers should be strongly selected against.

A preference to attack *S. geminata* in allopatry is also unlikely to evolve because there are few allopatric populations of *S. geminata* left in the United States. Furthermore, *P. curvatus* would be unlikely to compete well against the native species of *Pseudacteon* that already attack *S. geminata* and presumably do not suffer from poor rates of parasitism and low rates of

attraction to their natural host. Additionally, if *P. curvatus* did manage to disperse into an allopatric population of *S. geminata* and survive, the likelihood is that expanding populations of *S. invicta* would shortly convert the area into sympatry and any preliminary adaptations for attacking *S. geminata* would be quickly lost because of a lack of a mating barrier with *P. curvatus* flies adapted to *S. invicta.*

For the reasons discussed above, the evolution of *P. curvatus* populations capable of surviving on *S. geminata* seems remote. While the remoteness of these evolutionary scenarios cannot be proven, it is supported by the fact that none of the *Pseudacteon* species that attack *S. invicta* and *S. saevissima* complex ants have been collected attacking *S. geminata* complex ants, even though there are broad regions of overlap in northern South America. Similarly, none of the *Pseudacteon* species that attack *S. geminata* complex ants in the United States have switched to attacking *S. invicta* workers, even though there would have been strong selective advantages to do so because of diminishing populations of native fire ants and the lack of competing *Pseudacteon* species on *S. invicta.* Native *Pseudacteon* species are simply not attracted to imported fire ants in the field (Morrison, 1999).

Similar arguments can be made for *S. xyloni,* except that parasitism rates with *S. xyloni* approached minimal levels at which *P. curvatus* might be able survive on this ant. Nevertheless, parasitism rates with *S. xyloni* were only 1/3 of what they were with *S. invicta.* Furthermore, *P. curvatus* had a strong preference for *S. invicta* workers that was maintained even in flies reared from *S. xyloni.* Before the invasion of *S. invicta,* *S. xyloni* was distributed throughout most of the southern United States from South Carolina to California (Creighton, 1950). Today it has been eradicated from virtually the entire southeastern United States except northern parts of Oklahoma and Arkansas. *S. xyloni* does not offer much ecological resistance to the continued expansion of *S. invicta* in Arkansas, Oklahoma, and west Texas because existing populations of *S. xyloni* are sporadic at best in these states (unpublished observations). In another 25 years, *S. invicta* may have virtually eradicated *S. xyloni* from the entire southeastern United States and may be well on its way to doing so on the west coast as well (Anonymous, 1999).

Concern has also been expressed that *P. curvatus* might disrupt the foraging efforts of *S. geminata* or *S. xyloni* in areas where they cooccur with *S. invicta.* Indeed, this is likely to occur on a limited scale because *S. geminata* and *S. xyloni* workers did exhibit defensive responses to *P. curvatus* flies in our lab tests. However, inhibition of foraging of native fire ants should occur much less frequently in the field than inhibition of *S. invicta* foraging because of the strong preference for *S. invicta* workers (Fig. 2). In the field, it seems likely that this preference would be even stron-

ger, because most *P. curvatus* flies would either never start attacking the native fire ants or would move on to find *S. invicta* workers.

P. curvatus will clearly pose a much greater threat to *S. invicta* than it will to either of the native species that were tested (Figs. 1–3). This being the case, the chances are much greater that *P. curvatus* will actually **benefit** *S. geminata* and *S. xyloni* rather than harm them—this is because whenever *S. invicta* invades a region it severely reduces populations of *S. geminata* and eliminates populations of *S. xyloni* (Hung and Vinson, 1978; Porter and Savignano, 1990; Porter *et al.,* 1991; Porter, 1992; Wojcik, 1994). Consequently, almost any parasite or pathogen that does much better with imported fire ants than native fire ants should provide a net benefit to the native fire ants.

Two other *Solenopsis* fire ant species occur in North America: *S. amblychila* and *S. aurea* (Moody *et al.,* 1981; Francke *et al.,* 1983; Trager, 1991). These fire ants are limited to arid and semiarid habitats from west Texas to California. Neither species is common compared to *S. geminata* or *S. xyloni;* however, they are not considered rare either. Their suitability as a host for *P. curvatus* is untested; consequently, we must assume that these two species would be at least as susceptible as the two native species that were tested (Figs. 1 and 2). Arid conditions, however, might be a problem for *P. curvatus* which, like other *Pseudacteon* species, requires moist or humid conditions in which to pupate. As discussed above, both of these ant species are much more likely to be threatened by *S. invicta* than they are by *P. curvatus.* It is important to note that *P. curvatus* and other *Pseudacteon* species will, at best, stress imported fire ant populations, thus reducing their ability to compete with native ants (Porter, 1998a). If this happens, imported fire ant populations may be reduced severalfold in certain habitats, but there is no realistic chance that these flies will eradicate imported fire ants and even less chance that they would eradicate native fire ants.

We also need to be concerned with how the release of *P. curvatus* might affect the survival of native *Pseudacteon* species (Porter, 1998a). The fact that *P. curvatus* might be able to sustain a population on *S. xyloni* suggests that there is some risk to native *Pseudacteon* species; nevertheless, this risk again needs to be balanced against possible benefits. The greatest threat to the survival of the native *Pseudacteon* flies is continued expansion of the imported fire ants. As explained above, invading imported fire ants seriously reduce or eliminate the native fire ants that these flies require as hosts (Morrison *et al.,* 1997). This being the case, the chances are much better that release of *P. curvatus* will actually benefit the native flies than harm them. Furthermore, *P. curvatus,* a species that strongly prefers *S. invicta* (Fig. 2) and develops poorly on the native fire ants (Fig. 1), would need to compete with native decap-

itating flies that have already coevolved to parasitize the native fire ants.

Risks to native fire ants need to balanced against the possible benefits to dozens if not hundreds of other native species. *S. invicta* poses a substantial and serious ecological threat to a wide variety of ants and ground-dwelling arthropods (Camilo and Phillips, 1990; Hook and Porter, 1990; Porter and Savignano, 1990; Vinson, 1991; Jusino Atresino and Phillips, 1994; Stoker *et al.,* 1995). Fire ants even appear to affect populations and distributions of vertebrates such as deer (Allen *et al.,* 1997), quail (Allen *et al.,* 1995), waterbirds (Drees, 1994), and mice (Ferris *et al.,* 1998). A number of rare and endangered animals, such as gopher tortoises, sea turtles, horned lizards, alligators, the Schaus swallowtail butterfly, the Stock Island tree snail, the Florida grasshopper sparrow, and the least tern, may also be negatively affected by fire ants (Lockley, 1993; Wojcik *et al.,* 2000). Classical biocontrol agents like *P. curvatus* are the only likely option for mitigating fire ant impacts on most of these native species.

Several species of *Pseudacteon* flies will almost certainly need to be released to achieve maximum levels of impact on fire ant populations. This is because different species of flies attack different sizes of fire ants (Campiolo *et al.,* 1994; Morrison *et al.,* 1997) at different times of the day (Pesquero *et al.,* 1996) using different attack strategies (Orr *et al.,* 1997). Furthermore, some species of flies do better in different geographic regions (Borgmeier and Prado, 1975), whereas other species or biotypes may be more effective against red fire ants or black fire ants (Porter and Briano, 2000; Porter, unpublished data). In short, imported fire ants in the United States occur in a large variety of habitats, are distributed across a wide range of climatic conditions, and include two species and their hybrid. It is unrealistic to expect that a single *Pseudacteon* species would provide effective control across this very heterogeneous mosaic. The problem is further complicated by the fact that *Pseudacteon* flies are expected to impact fire ant populations indirectly, primarily through inhibition of foraging rather than direct parasitism (Porter, 1998a). Consequently, the actual elimination of fire ant colonies, if biocontrol efforts are successful, is most likely to occur through competition with native ants rather than *Pseudacteon* parasitism itself (Feener and Brown, 1992). Most theoretical models of multiple predator/parasitoid systems do not consider this type of system or this degree of complexity (e.g., Sih *et al.,* 1998; Briggs, 1993).

While release of a single species is unlikely to be the best strategy, it is still wise to select species that are complimentary. *P. curvatus* clearly fits this requirement. It is the smallest of the common *Pseudacteon* flies that attack *S. invicta* (Porter, 1998a; Morrison *et al.,* 1997) and as such it attacks only small and medi-

um-small fire ant workers (Morrison and Gilbert, 1998). This makes *P. curvatus* an important complement for *P. tricuspis,* which attacks only medium and medium-large fire ants (Morrison and Gilbert, 1998; Morrison *et al.,* 1999). Furthermore, the biotype that we used from Las Flores Argentina is likely to be better adapted to cooler climatic conditions and may be especially effective against black and hybrid fire ants in the United States because it prefers them when given a choice (Porter and Briano, 2000). *P. tricuspis,* the first species released, has been established at several sites around Gainesville, Florida for 2–3 years (as of summer 2000). A systematic study of the impact of this fly on fire ant populations is just beginning, but it is fairly clear from preliminary observations that *P. tricuspis* alone will not solve the imported fire ant problem.

No other likely *Pseudacteon* species are available to fill the niche that *P. curvatus* could fill in the United States. *P. obtusus* has been suggested as a possibility; however, this species is not as small, has a different attack strategy (Orr *et al.,* 1997; S.D.P., personal observations), and has not yet been found in sufficient densities (see Morrison and Gilbert, 1999) to attempt serious rearing efforts. Furthermore, the variety of *P. obtusus* that attacks *S. richteri* workers is medium or even medium-large in size (unpublished data).

Several additional considerations are also important in regard to the field release of *P. curvatus.* (1) Native fire ants already have several species of native *Pseudacteon* phorids that parasitize them (Disney, 1994); therefore, *P. curvatus* would not be a completely novel parasite for which these ants have no defense. (2) *S. geminata* and *S. xyloni* are still common species outside the range of *S. invicta.* In fact, both are often considered pests in those areas (Smith, 1936, 1965; Thompson, 1990). *S. geminata* still persists in numerous sites in Florida and parts of Texas (Porter *et al.,* 1991; Porter, 1992). It is also a pantropical pest, having been introduced from South and Central America into Africa, India, Australia, and most of the island groups of the Pacific (Trager, 1991); in other words, it is a robust species that is unlikely to be seriously impacted by small perturbations. *S. xyloni* is still found along the northern fringe of the imported fire ant range in the United States (Porter *et al.,* 1991) and is common from west Texas through to California and south into Mexico (Creighton, 1950). (3) Native fire ants, which have their own set of pathogens and parasites (Wojcik, 1990; Morrison *et al.,* 1997; Jouvenaz *et al.,* 1977), were never as abundant as the imported species (Porter *et al.,* 1988; Porter, 1992; Vinson, 1994), so there is little or no likelihood that they would simply replace each other as community-dominating pests.

In summary, releasing *P. curvatus* into the United States poses no danger to people, livestock, plants, or arthropods other than ants. These flies will pose a real risk only to native fire ants. This study indicates that the negative impacts on imported fire ants will almost certainly be much greater than their impacts on native fire ants. This being the case, field release of *P. curvatus* is much more likely to **benefit** native fire ants than harm them. In short, I feel the limited risks to native fire ants are clearly outweighed by potential benefits to people, numerous native organisms, and even the native fire ants themselves.

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