

Solenopsis (Hymenoptera: Formicidae) Fire Ant Reactions to Attacks of *Pseudacteon* Flies (Diptera: Phoridae) in Southeastern Brazil

SANFORD D. PORTER,¹ ROBERT K. VANDER MEER,¹ MARCOS A. PESQUERO,²
SOFIA CAMPIOLO,³ AND HAROLD G. FOWLER³

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ABSTRACT We studied the responses of *Solenopsis* fire ants to *Pseudacteon* phorid fly attacks in southeastern Brazil. The presence of these phorid parasites triggered a suite of phorid-specific defense responses including reduced foraging, bait guarding, a curled defensive posture, and general colony immobility. The existence of these phorid-specific defenses indicates that *Pseudacteon* phorids exert substantial evolutionary pressure on South American fire ant populations.

KEY WORDS *Solenopsis invicta*, *Solenopsis saevissima*, biological control, defense responses, parasitic flies, Brazil

Pseudacteon PHORID FLIES are among several dozen natural enemies of *Solenopsis* fire ants in South America (Jouvenaz 1983). Maggots of at least 1, and probably all, *Pseudacteon* species grow and pupate in the heads of their hosts (Porter et al. 1995a). The presence of phorid flies causes a number of responses in fire ant workers including gaster flagging, attempts to escape, and defensive displays (Williams et al. 1973, Williams and Banks 1987). Feener and Brown (1992) reported that the presence of *Pseudacteon* phorids around *Solenopsis geminata* (F.) ants in Costa Rica triggered stereotypical defensive postures and greatly reduced foraging rates. They also predicted "that the South American phorid parasitoids of [fire ants] are likely to have similar effects on their host." The objective of this article was to test this prediction with *Pseudacteon* phorid parasites of fire ants in southeastern Brazil.

Materials and Methods

Studies were conducted in February 1994 around the city of Rio Claro in the state of São Paulo, Brazil. To examine how phorids affect fire ant foraging, we set out sliced Vienna sausage baits on the ground near several field colonies. Within 5-10 min, large numbers of fire ants were recruited to many of the baits. At 7 baits, we were able to measure forager traffic before the arrival of

Pseudacteon phorids, during their attacks, and then after the phorids were removed with an aspirator. Foraging rates were calculated from the time required for predetermined number of ants (usually 20 or 30) to cross a set location on the foraging trail. Counts were terminated after ≈ 1 min when transit rates were slow. When transit rates were heavy, we counted incoming ants separately from outgoing ones. Counts were made at haphazard intervals depending on the number of baits being monitored and the presence of phorids. We also conducted several preliminary tests to see if foragers would respond to phorids flying inside a petri dish or glued to the heads of insect pins.

In another set of tests, 11 colonies were collected from 3 locations around Rio Claro and set up in laboratory trays each with several thousand workers (Porter et al. 1995b). These colonies were carried to the field in several groups of 2-6 colonies. Each group of colonies was set out together at 2-4 locations several kilometers apart. Before each test, we set out 1 colony and waited until several phorids arrived. The remaining colonies were then set out one at a time and observed for 5-10 min each. During tests, the lid of the nest chamber was removed so that the entire colony was exposed to phorid attacks.

Fire ant colonies were identified to species using the Trager (1991) key and independently separated into groups using cuticular hydrocarbon and venom alkaloid patterns. For these chemical analyses, samples of 5-25 workers were heat-killed ($\approx 60^\circ\text{C}$), air-dried, and soaked for 24 h in enough hexane to cover the ants. The hexane was transferred to another vial and analyzed by gas chromatography (GC) as previously reported (Vander Meer et al.

¹Medical and Veterinary Entomology Research Laboratory, USDA-ARS, P.O. Box 14565, Gainesville, FL 32604.

²Departamento de Zoologia, Instituto de Biociencias, Universidade Estadual Paulista, 13610, Botucatu, SP, Brazil.

³Departamento de Ecologia, Instituto de Biociencias, Universidade Estadual Paulista, 13500, Rio Claro, SP, Brazil.

1985, Ross et al. 1987). Basic alkaloid and hydrocarbon retention times were determined with separate *S. invicta* Buren and *S. geminata* standards. When contaminating peaks obscured venom alkaloid patterns, GC mass spectroscopy was used to identify and quantify fire ant piperidine alkaloids (MacConnell et al. 1971). Patterns of alkaloids and hydrocarbons were visually compared and categorized without knowledge of collection information or morphological identifications.

Voucher specimens of ants and flies have been deposited in the collection of Harold Fowler and with the Museu de Zoologia, Universidade de São Paulo, Brazil.

Results

General Observations. Attacking *Pseudacteon* flies looked like minute grey fuzz balls that alternately floated and darted a few millimeters above the worker ants. Oviposition attempts were extremely fast (0.1–0.8 s) and difficult to observe in any detail. Workers were frequently knocked off their feet by the attack, often curling briefly into a ball before righting themselves and running a few steps. Most of these workers then stopped and rose up on their legs as if they had been stunned. Generally, the legs were spread and the gaster was raised slightly. A sharp sideways tap from an insect pin elicited a similar stilted posture except that this reaction usually lasted only a few seconds. Ants attacked by phorids in nest trays usually remained motionless in this stilted position for several minutes; however, they were still capable of running if prodded or otherwise disturbed. In some colonies, other workers clustered around the attacked worker. The flies are generally much too agile and fast to be caught by the ants, although we observed at least 3 occasions, out of several thousand oviposition attempts, when flies fell into a group of workers and were killed before they could escape.

Effects on Foraging. The appearance of phorid parasites caused a dramatic drop in fire ant foraging to baits (Fig. 1). The mean transit rate fell 6-fold from 90 ± 14 workers per minute to 15 ± 3 workers per minute (\pm SEM; paired *t*-test, $t = 6.85$, $df = 6$, $P < 0.0005$, data were log transformed). The reduction in foraging activity usually occurred within several minutes of phorid arrival. Most of the remaining foragers moving along the trails did not appear to be transporting food. After removal of the phorids, foraging rates gradually increased over a period of 10–40 min until post-phorid rates were similar to prephorid rates (Fig. 1, inset). The average foraging rate after removal of phorids (Fig. 1, inset) was calculated from the final observation at each bait rather than means of sequential observations because most rates were still rising rapidly.

The following *Pseudacteon* phorids were captured and removed from tests A–G (Fig. 1): (A) 8 unidentified males, (B) 2 unidentified males, (C) 1

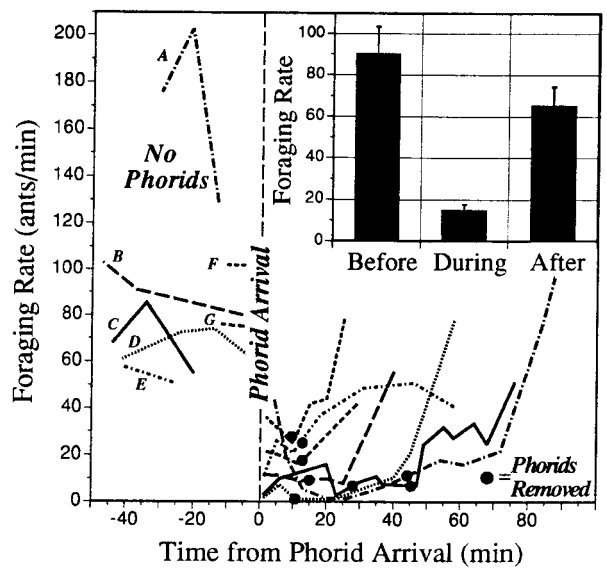


Fig. 1. Effect of parasitic phorid flies (*Pseudacteon*) on fire ant (*Solenopsis*) foraging. Data lines (A–G) show foraging rates to and from baits at separate field colonies before the arrival of the phorid flies, during their attacks, and after their removal. Note that flies were removed twice from the bait indicated by the solid black line. The inset graph shows mean foraging rates \pm SEM of fire ants before, during, and after attacks of the parasitic flies.

female near *P. tricuspis* Borgmeier and several unidentified males, (D) 1 *P. litoralis* Borgmeier female, (E) 1 *P. wasmanni* (Schmitz) female, (F) 1 *P. obtusus* Borgmeier female, and (G) 1 *P. litoralis* female. Male *Pseudacteon* flies are currently unidentifiable because keys are based on ovipositors. The species of fire ants at baits were not determined, but they probably included both *S. saevissima* (F. Smith) and *S. invicta*.

Upon sensing the phorids, some ants returned quickly into the tunnel system whereas others tried to hide under the bait or in surrounding plant detritus. However, 1 or 2 dozen ants (mostly minor workers) usually remained standing on the bait in a stilted alert posture spaced approximately a body length apart. This alert or guarding posture was similar to the posture assumed after being attacked by a phorid; the difference was that these ants often turned side-to-side, waved their antennae, and appeared to dispense venom by vibrating their gaster (Obin and Vander Meer 1985, Williams and Banks 1987). Enough guard ants usually remained, once a trail had fully formed, to defend the bait from other ants until the phorid(s) left and normal foraging resumed. At one bait, however, we saw a phorid fly attack fire ant workers shortly after recruitment was initiated. Recruitment stopped almost immediately and only 6 workers were left standing guard at the bait. Eventually, a large *Eciton* worker discovered the bait and proceeded to grab the remaining fire ant workers in its mandibles and drop them off the bait one by one. The end result was that *Camponotus* ants eventu-

ally dominated the bait rather than either fire ants or *Ectatomma*.

Fire ant foraging was inhibited as long as *Pseudacteon* flies remained active over the bait, a period that lasted anywhere from a few minutes to several hours (personal observations; Orr et al. 1995). After the phorids left or were removed (Fig. 1), foraging remained suppressed at 2 of the baits (A and B) for 20–30 min before resuming pre-phorid rates even though the trails were originally formed in only 5–10 min. At any particular time, ≈10–20% of the baits with fire ants had phorid activity. *Pseudacteon* phorid activity was limited to daylight hours.

Attempts to elicit fire ant defensive responses to phorids flying and walking around inside a petri dish failed. We also glued 8 live female phorids (7 *P. pradei* and 1 *P. wasmanni*) to the heads of insect pins and then waved these nonflying individuals a few millimeters over several baits with fire ants. Again no response was observed.

Reactions of Laboratory Colonies. During a companion study of phorid specificity (Porter et al. 1995b), we repeatedly set out 2 fire ant colonies in laboratory trays to attract phorids. The 1st colony showed little general reaction to the presence of the phorid parasites. Individual workers stilted up on their legs when hit, but colony activity was not visibly diminished. However, workers in the 2nd colony reacted very dramatically to the arrival of *Pseudacteon* phorid flies. Within 2–3 min after the 1st phorids arrived, all 10,000 or so workers stopped running around. Previously seething clusters of ants became torpid and matted, almost as if they were dying from heat stress. Many individual workers assumed the stereotypical c-shaped phorid defense posture (Feener and Brown 1992) with the gaster tucked up under the thorax so that both the sting and the head were directed upward. Apparently this posture puts workers in a position that makes phorid oviposition difficult. The mandibles and waving antennae may also help ward off attacks. A few minutes after the phorids were removed, the ants always resumed normal activity.

To study this phenomenon further, 9 additional colonies were set up in laboratory trays and tested along with the previous 2 colonies at different locations and times of day. The immobility response of colony workers was scored subjectively by the same observer (S.D.P.) according to the following 4 categories: (1) strong (almost all workers), (2) medium (most workers), (3) low (a few dozen workers), or (4) none (no workers). The same groups of colonies were tested at different locations, at different times of day, and with different species of phorids attacking them (that is, *P. wasmanni*, *P. pradei*, *P. litoralis*, and a species near *P. tricuspis*). Five of the 11 colonies (45%) consistently responded to phorid attacks with strong or medium levels of colony immobility and usually also with the curled c-shaped posture (Table 1). This consistency indicates that the colony immo-

Table 1. Immobility responses of fire ant colonies, *Solenopsis*, in laboratory trays to *Pseudacteon* phorid fly attacks

Colony	Morphology ^a	Chemistry group ^b	Immobility response ^c
I	<i>S. saevissima</i>	A ₁	None-none-none-none
II	<i>S. saevissima</i>	A ₁	Strong-medium-strong-strong
III	<i>S. saevissima</i>	A ₁	Low-none-none
IV	<i>S. saevissima</i>	A ₁	Strong-strong
V	<i>S. invicta</i>	B ₁	Low-none-none-none
VI	<i>S. invicta</i>	B ₂	Strong-strong-strong
VII	<i>S. invicta</i>	B ₂	Medium-low
VIII	Uncertain	B ₂	Low-low
IX	Uncertain	C ₁	Strong-medium-strong
X	Uncertain	C ₁	None-none
XI	Uncertain	C ₂	Strong-strong

^a Taxonomic determinations using the Trager (1991) key.

^b Groupings based on gas chromatograph analysis of cuticular hydrocarbon and venom alkaloid patterns; subscripts indicate alkaloid subgroupings (see text).

^c Sequential responses of fire ant colonies to phorid attacks at 2–4 separate locations.

bility response was not associated with time of day, location, or any particular *Pseudacteon* species. Also, we did not detect any association with the quantity of brood in the colony or experimental handling. Behavioral responses did not correspond to the 3 geographic sources of the colonies. Although responses of individual colonies were consistent in time and space, enough variability existed between colonies to suggest that the phenomenon may not be entirely a simple dichotomy. For example, some nonimmobilized colonies consistently had a few workers responding with the curled posture (5–20), whereas others had none at all.

Species differences among the ant colonies would have been the most obvious explanation for the different responses. Identifications using the Trager (1991) key indicated that 4 colonies were *S. saevissima*, 3 were *S. invicta*, and 4 had characters that made them difficult to assign to either species (Table 1). Independent examination of component peaks from gas chromatographs of cuticular hydrocarbons and venom alkaloids produced groups that were largely congruent with the morphological identifications (Table 1).

Hydrocarbon analysis segregated the colonies into 3 distinct groups. Group A was characterized by 5 major peaks and the absence of the *S. invicta* peak with the longest retention time (see Vander Meer et al. 1985). Group B hydrocarbons were characterized by 3 major peaks corresponding to the *S. invicta* pattern, including the longest retention time peak. Group C hydrocarbons were characterized by having 4 of 5 *S. invicta* peaks including the peak with the longest retention time plus a major peak of shorter retention time.

Analysis of the alkaloids was in general concordance with the results for the hydrocarbons and taxonomic determinations. Colonies in group A had identical alkaloid patterns, with the C_{13,1} sub-

stituted alkaloid dominant. Colonies VI, VII, and VIII clearly had the same alkaloid pattern in group B ($C_{11:0}$, $C_{13:1}$, $C_{13:0}$, $C_{15:1}$, and $C_{15:0}$ alkaloids all present in significant proportions, but with $C_{13:1}$ as the major alkaloid); however, colony V was unique and had a pattern that most closely resembled *S. invicta* in the United States ($C_{15:1}$ dominant). Colonies IX, X, and XI were grouped together in group C on the basis of their similar proportions of $C_{13:1}$, $C_{13:0}$, $C_{15:1}$, and $C_{15:0}$ alkaloids; however, colony XI had an unusually high proportion of *cis*-alkaloids. We found no evidence in the chemical patterns that any of the 11 colonies were hybrids of the others (Vander Meer et al. 1985).

Overall, the chemical and morphological identifications are quite congruent with each other; however, they were not useful in predicting which colonies responded to phorid attacks. Some colonies in each group responded strongly whereas others did not respond at all.

Discussion

Effects on Foraging. As expected, fire ants in Brazil responded strongly to the presence of *Pseudacteon* phorids. We observed an 83% reduction in fire ant foraging rates when phorids were present. This effect was almost the same as the 85% reduction reported by Feener and Brown (1992) for *S. geminata* in Costa Rica. Orr et al. (1995) recently reported that the arrival of *Pseudacteon* flies consistently reduced the number of *S. invicta* foragers found at baits at several sites in Brazil. They reported that fire ant foraging was inhibited by attacks of 4 *Pseudacteon* species: *P. solenopsidis*, *P. nocens*, *P. curvatus*, and *P. litoralis*. We found that foraging was inhibited by *P. litoralis* plus 3 additional species: *P. obtusus*, *P. wasmanni*, and an undescribed species near *P. tricuspis*. These observations indicate that fire ant foraging is probably inhibited by most if not all of the 17 species of *Pseudacteon* (Disney 1994) that attack fire ants.

After removal of the phorids, fire ant foraging rates gradually increased until they were almost the same as those before the phorids arrived (Fig. 1). At 2 of the baits, we observed a 20–30 min lag period between the time phorids were removed and the time that foraging traffic resumed. A similar lag was reported by Feener and Brown (1992). Both male and female flies were capable of inhibiting fire ant foraging (compare, Feener and Brown 1992), a situation that should improve their usefulness as biocontrol agents. Orr et al. (1995) demonstrated that the presence of phorid parasites affected the competitive balance between fire ants and other species of ants. When phorids were present, other ant genera dominated baits near fire ant mounds, but when these flies were removed, fire ants quickly displaced all of the competing ants. Parasitic phorid flies can also substantially affect foraging activity in other ant genera (Feener 1988, Orr 1992).

In contrast to Feener and Brown's (1992) observations, foragers in our studies usually did not become immobile or assume a curled defensive posture when phorids attacked. Instead, foragers generally returned rapidly to their nest entrances or temporarily hid in the leaf litter as described by Williams and Banks (1987) for *S. invicta* in south central Brazil. The stilted alert posture and spaced-out distribution of *Solenopsis* workers on baits under phorid attack has not been previously reported. This guarding behavior appears to be an adaptation that allows fire ant colonies to maintain control of large food resources while temporarily reducing their exposure to phorid parasitism.

Exactly how foraging ants perceive the phorids is unknown. The sound of the buzzing fly is one possible cue. Ants are sensitive to substrate vibrations (Spangler 1974, Roces et al. 1993) and may have sensory receptors in their antennae like those in honey bees (Dreller and Kirchner 1993). A phorid fly hovering a few millimeters above a worker is probably not a subtle auditory cue. The oviposition attacks themselves are another possible cue; however, males alone also caused defensive responses. The general odor of the fly is probably not a primary cue because waving several live nonflying phorids over foraging ants had no effect on their behavior. Similarly, the sight of phorids flying and crawling overhead inside a petri dish did not affect ant behavior.

The fire ant foraging tunnel system (Markin et al. 1975) has many benefits, but it seems likely that this system may have developed at least partially in response to evolutionary pressure from phorid parasites (p. 75, Disney 1994). Certainly, it would seem very difficult for fire ants to maintain large territories, and thus large colonies, if all forager traffic emerged from a central nest and traveled overland for many meters as is the case with other types of ants. The tunnel system reduces average above-ground forager transit distances to ≈ 30 cm (Markin et al. 1975), potentially allowing colonies under phorid attack to shut down portions of their foraging effort while maintaining activity in the remainder of their territories.

Reactions of Laboratory Colonies. In response to phorid attacks, we observed general immobility and curled defensive postures in about half of our test colonies. The general worker response in affected colonies indicates that most if not all worker sizes and age classes are capable of perceiving the presence of *Pseudacteon* phorids. Why only half of the colonies were affected is unknown. The immobility response was not associated with time, location, or several other possible factors. What was most puzzling is why variability in this response appeared to cut across fire ant species. The congruence between the morphological identifications and the chemical groupings (Table 1) suggests that the different responses were not the result of unrecognized cryptic species. These results seem to suggest a genetic polymorphism

maintained by bidirectional selection, but why the same polymorphism would occur in several fire ant species is unknown, especially without chemical evidence for hybridization in the GC analyses (Vander Meer et al. 1985). Perhaps natural variation for this trait is simply very large.

Our laboratory test colonies were unusual in that workers had no place to escape and they were not defending food resources. Also, the extent of the response in these colonies was clearly unusual because entire fire ant colonies are rarely, if ever, exposed to phorid attacks. Nevertheless, large numbers of workers can be exposed during mating flights (Pesquero et al. 1993), when a mound is kicked open by large animals, and occasionally when mass recruiting to large baits. Presumably, responses of workers under these conditions could be similar to responses observed with entire laboratory colonies. Nevertheless, we did not observe a colony level dichotomy of responses (for example, Table 1) among ants foraging to baits; however, additional observations on this point are still warranted.

Potential as Biocontrol Agents. The curled posture, the reduction in foraging, the bait-guarding behavior, and the general worker immobility all appear to be phorid-specific defense responses. These defensive responses are not seen under other circumstances and have not been reported from imported fire ant populations in North America. This suite of phorid-specific defense responses strongly indicates that *Pseudacteon* phorids are exerting substantial evolutionary pressure on fire ant populations in South America. The exact magnitude of this pressure is unknown, but it seems likely that it may be an important factor allowing other ants to compete and coexist with fire ant colonies (Orr et al. 1995).

The practical implications of these observations are that they provide important evidence that phorids might be able to help suppress fire ant populations in North America (Feener and Brown 1992). Additional information concerning the frequency of phorid parasitism and the net loss of foraging opportunities caused by defensive responses would be useful; nevertheless, predicting the effectiveness of biological control agents is very difficult even with the best information (Murdoch et al. 1985). For example, effects of phorids in North America could be amplified because fire ant populations in North America are 5- to 10-fold higher than they are in South America (unpublished data: Porter et al. 1992). Another consideration is that North American fire ant populations have had ≈ 15 generations without the selective effects of phorid parasitism; consequently, their defensive abilities may be somewhat diminished. Habitat, soil, climate, and many other factors can also positively or negatively affect the success of potential biological control agents (Stiling 1993). Ultimately, the only way to determine the effectiveness of using *Pseudacteon* flies as fire ant bio-

logical control agents in North America will be to actually release them and monitor the outcome.

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Current Contact Information (Oct. 2004)
Sanford D. Porter

Mailing Address:

USDA-ARS, CMAVE
P.O. Box 14565
Gainesville, FL 32604 USA

Street Address:

USDA-ARS, CMAVE
1600 S.W. 23rd Drive
Gainesville, FL 32608 USA

Office: 352 374-5914

Secretary: 374-5903

FAX: 374-5818

E-mail: sdp@nersp.nerdc.ufl.edu (preferred)

E-mail: sdporter@gainesville.usda.ufl.edu (alternate)

Official Web Site: <http://www.ars.usda.gov/pandp/people>

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