BIOLOGY AND BEHAVIOR OF *PSEUDACTEON* DECAPITATING FLIES (DIPTERA: PHORIDAE) THAT PARASITIZE *SOLENOPSIS* FIRE ANTS (HYMENOPTERA: FORMICIDAE)

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ABSTRACT

Larvae of phorid flies in the genus *Pseudacteon* have the unusual habit of decapitating fire ant workers and pupating inside the empty head capsule which they use as a pupal case. Flies in this genus are the subject of considerable interest because they have the potential of being used as classical biological control agents against imported fire ants in North America. This paper details what is known and not known about their interesting life history, attack behavior, mating behavior, host specificity, and impacts on fire ant behavior. The biogeography, community structure, and possible impacts on fire ant populations are also considered.

Key Words: biological control, classical biocontrol, parasitoid, larvae, pupae, host specificity

RESUMEN

Moscas forídeas do gênero *Pseudacteon* produzem larvas que apresentam um habito não usual de decapitar as formigas operarias e pupas dentro da capsula cefalica vazia, a qual elas utilizam como câmara pupal. Estas moscas são asunto de considerável interesse porque elas têm potencial de serem utilizadas como agentes de controle biológico classico contra as formigas lava-pé importadas na América do Norte. Este trabalho detalha o que é conhecido e desconhecido sobre seu ciclo de vida, com-

portamento de ataque, comportamento de reprodução, especificidade hospedeira e impactos do comportamento da formiga lava-pé. A biogeografia, a estrutura comunitaria e os possíveis impactos sobre as populações da formiga lava-pé são também relatadas.

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Phorid flies in the genus *Pseudacteon* (Coquillett 1907) and several related genera (Pergande 1901) produce larvae that decapitate worker ants and pupate inside their empty heads. Not surprisingly, these miniature flies (Fig. 1) are about the size of the heads of their hosts. The attack behavior of *Pseudacteon* flies was first described in detail by Wasmann (1918) in Holland, Borgmeier (1922) in Brazil, and Smith (1928) in

Fig. 1. Lateral view of female *Pseudacteon nocens*. Length is about 1.4 mm.

the United States. Over a period of 50 years, Borgmeier gradually named most of the known species in this genus (Borgmeier 1925, 1962, 1963, Borgmeier & Prado 1975). The possibility of using these flies as fire ant biocontrol agents lead Williams (1980) to make extensive collections and observations in Brazil. Feener and Brown (1992) reported that *Pseudacteon* flies disrupted foraging of native fire ants in Central America and proposed that flies from South America might make good biocontrol agents for imported fire ants in the United States. Orr et al. (1995) and Porter et al. (1995c) documented substantial impacts of *Pseudacteon* flies on fire ant foraging in South America. The unusual life history of immature *Pseudacteon* flies was first described by Pesquero et al. (1995) and Porter et al. (1995b). Research groups at the University of Texas (Gilbert 1996) and the USDA-ARS laboratory in Gainesville, Florida are currently examining the potential use of *Pseudacteon* flies for classical biocontrol of imported fire ants in the United States.

<center>LIFE HISTORY</center>

The life cycle for *Pseudacteon* flies begins when a torpedo-shaped egg (Fig. 2A; Wasmann 1918) is injected into the body of a worker ant. The duration and morphology of the first instar is unknown, but the second instar is found in the ant's head by day four (Fig. 2B; Porter et al. 1995b). During this instar and most of the third instar (Fig. 2C), the maggot apparently relies on ant hemolymph for nutrition, because little
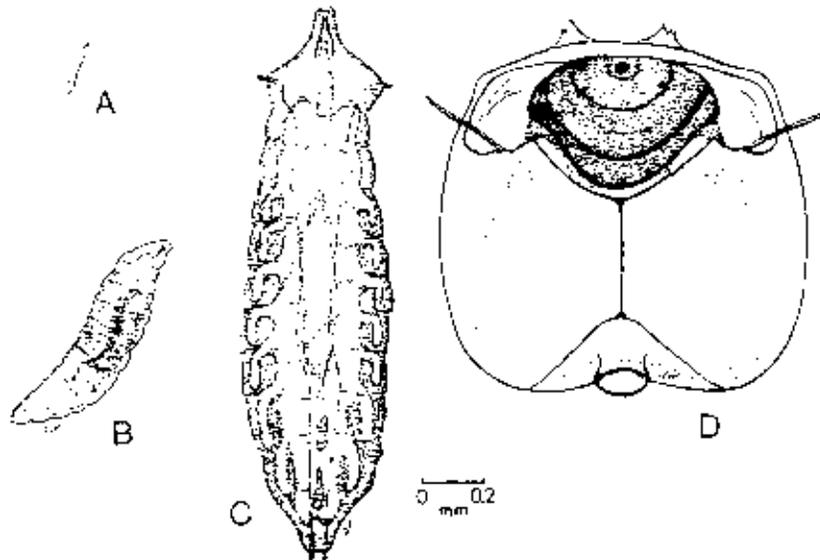

Fig. 2. Developmental stages of *Pseudacteon litoralis*. A) Egg, B) Second instar, C) Third instar. Note the two anterior spiracles projecting laterally behind the head region and the two paired posterior spiracles. D) Puparium inside head capsule of fire ant worker. The head capsule is shown in ventral view with the sclerotized cap of the fly puparium filling the mouth opening of its host. The remainder of the puparium is indicated by a dotted outline. Two respiratory horns extend diagonally out of the ant head capsule. (modified from Porter et al. 1995b)

if any tissue is consumed. Parasitized ant workers appear normal and healthy until a few hours before the maggot is ready to pupariate. It is not yet known what effects developing larvae may have on the behavior of their hosts; however, suppressing foraging would extend the longevity of their host (Mirenda & Vinson 1981, Porter & Jorgensen 1981) thus giving the larvae a better chance to complete development.

The decapitation process begins when parasitized workers crumple on their sides unable to walk (Fig. 3.1). The third instar maggot seems to release an enzyme or hormone that causes the intercuticular membranes of its host to degenerate (Porter et al. 1995b). This process usually loosens the head and first pair of legs; sometimes the other legs and gaster are also affected. The maggot then proceeds to consume the entire contents of the ant head, a 6-12 h process that usually results in decapitation of its living host (Fig. 3.2). The legs and sting of the headless body are often still twitching. In laboratory colonies, most decapitated and dying workers are rapidly carried out of the nest chambers onto the refuse pile. Using a series of hydraulic extensions (Fig. 4A), the maggot then pushes the ant's mandibles and tongue apparatus aside (Fig. 3.3). Eventually the maggot maneuvers itself under the tentorial arms inside the head capsule (Fig. 5). The first three segments then compress and harden to form a distinctive plate that precisely fills the oral cavity (Fig. 2D, Fig. 3.4). The remainder of the puparium remains unsclerotized and is protected by the ant head capsule (Fig. 5). Three to four days later, during actual pupation, two whisker-like respiratory horns emerge diagonally out of the puparium, positioned so that they extend out of the corners of the oral cavity of their host's head capsule (Fig. 2D and 5; Porter et al. 1997). This unusual type of puparium is shared by all 10 of the *Pseudacteon* species that have been reared to this stage (Porter et al. 1995b, Morrison et al. 1997, Porter et al. 1997; unpublished data).

The fate of *Pseudacteon* puparia in the field is not known, but based on laboratory observations, puparia are probably initially deposited with dead fire ant workers in refuse piles on the surface of the ground (Howard & Tschinkel 1976). Eventually the puparia are probably scattered by rain, wind and/or other species of scavenging ants. Pupal development requires 2-6 weeks, depending on temperature (Morrison et al.
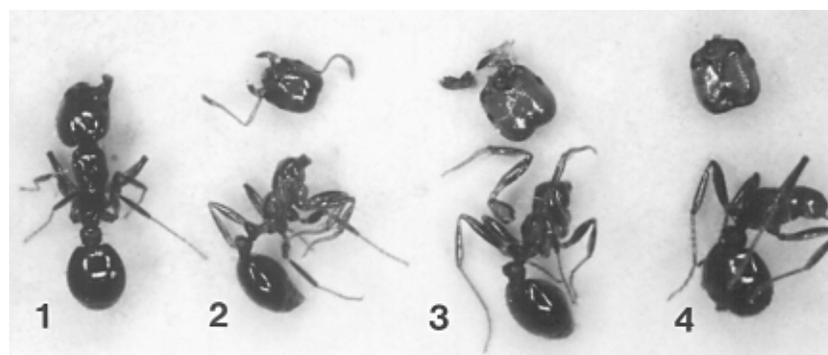

Fig. 3. Four stages in the decapitation of fire ant workers parasitized by *Pseudacteon* flies. 1) Crippled worker with degenerating intersegmental membranes and relaxed mandibles. 2) Decapitated worker with maggot consuming tissues in the head. 3) Ant head with mandibles and tongue apparatus pushed aside in preparation for pupariation. 4) Decapitated worker with fly puparium inside head.
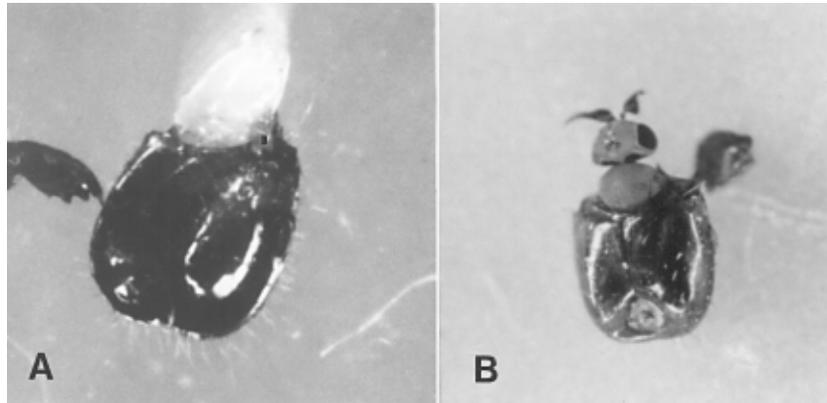
Fig. 4. A) Maggot pushing away ant mouth parts with a series of hydraulic extensions just prior to pupariation. B) Adult male fly in the process of emerging from puparium.

1997, Porter et al. 1997; unpublished data). The total developmental period from egg to adult is 5-12 weeks, again depending on temperature.

Emergence of adult flies generally requires only a few seconds (Fig. 4B). The sclerotized cap pops open and the adult fly slips out of the ant head capsule. Emergence only occurs in the first few hours after sunrise (Porter et al. 1997), as is the case for many kinds of flies. Newly emerged flies are ready to mate and lay new eggs within several hours of eclosion. Adult *Pseudacteon* flies are 0.9-1.5 mm in length (Borgmeier & Prado 1975), depending on the sex and species of fly. Adult flies can live 3-7 days in
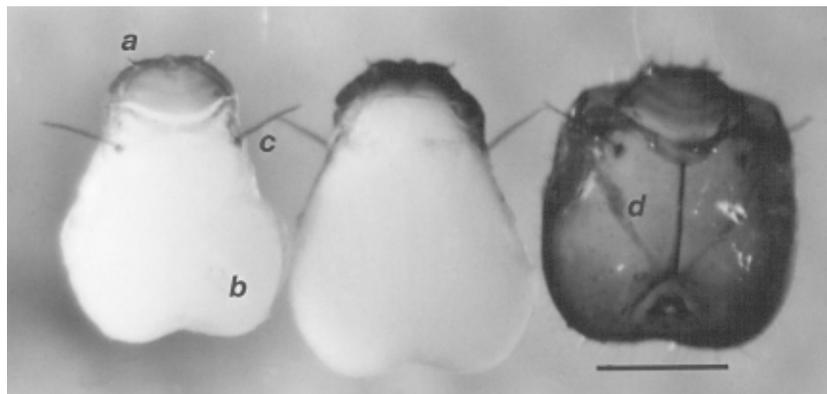

Fig. 5. Two *Pseudacteon* puparia removed from ant head capsules (dorsal and ventral views) together with puparium still in ant head capsule. Note the large white unsclerotized portion of the puparium that is normally protected by the head capsule of its host. a) Left anterior larval spiracle (compare Fig. 2c), b) Posterior larval spiracles (compare Fig. 2c), c) Pupal respiratory horns, d) Tentorial arms of ant extending diagonally across dorsum of fly puparium. Bar indicates 0.5 mm.

the laboratory if they are relatively inactive (Pesquero et al. 1995, Gilbert 1996, Porter et al. 1997). However, the life span of flies that are attacking ants is probably much shorter (Porter et al. 1997). Virtually nothing is known about what adult flies do or where they spend their time when they are not attacking fire ants. Adults will stop and drink water or lap up sugary substances if they contact them, but they do not appear to be attracted to them. *Pseudacteon* flies are not attracted to various kinds of fruits, flowers, human food products, or human feces (Porter et al. 1997; unpublished data). They are also not attracted to people. Data from Austin, TX indicates that adult flies commonly disperse several hundred meters from host colonies (Morrison et al. unpublished manuscript, University of Texas at Austin).

Interestingly, the sex of most *Pseudacteon* species seems to be facultatively determined by the size of the host (Fig. 6; Porter et al. 1997, Morrison et al. in press). This is probably because fire ant workers are highly variable in size (2-6 mm in length) and female flies are more fit if they emerge from larger hosts. The exact mechanisms of sex determination in *Pseudacteon* flies is unknown. Maternal sex determination via haplodiploidy occurs in many parasitic hymenoptera, but haplodiploidy is not known to occur in the family Phoridae or other related families of flies. Karyotypes should help resolve this question, as would transferring developing eggs or larvae from small hosts to large hosts and vice versa.

<div align="center">ATTACK BEHAVIOR</div>

Female *Pseudacteon* flies hover 3-5 mm above their hosts while orienting for an attack (Fig. 7; Borgmeier 1922, Smith 1928, Williams 1980, Porter et al. 1995c). Once properly aligned, they dive in and inject an egg into the thorax of a worker ant using a hypodermic-shaped internal ovipositor (Wasmann 1918, Zacaro & Porter unpublished data). Each species of fly parasitizes a characteristic size range of ants (Morri-
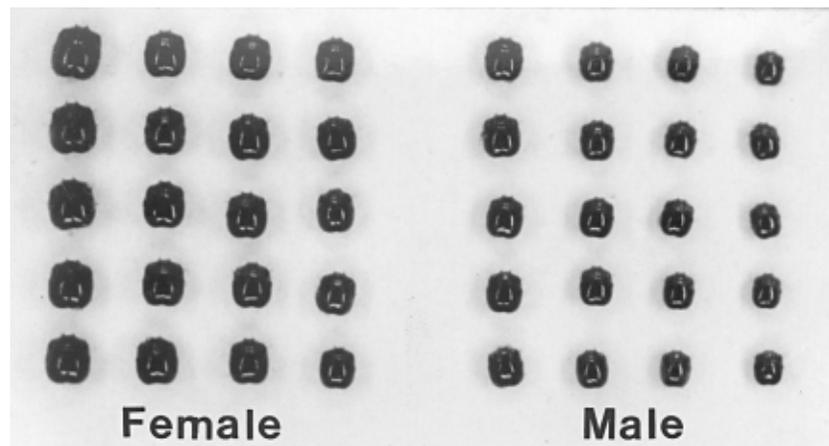

Fig. 6. Sex in most *Pseudacteon* flies appears to be determined by the size of their host. Female flies generally emerge from host head capsules that are distinctly larger than males. With *Pseudacteon tricuspis*, the lower quartile of female-producing head capsules overlaps with the upper quartile of male-producing head capsules. The width of head capsules ranges from about 1.3 mm (left) to 0.7 mm (right).

Fig. 7. Female *Pseudacteon* flies generally hover a few millimeters above their hosts prior to diving in and rapidly injecting an egg into the thorax.

son et al. 1997). This size range is usually consistent even across different ant species and colonies having different size ranges of workers (Morrison et al. in press, Morrison and Gilbert 1998). Male and female alates in the ant colony are ignored by most flies (Smith 1928, Williams & Banks 1987) and are never successfully parasitized (unpublished data). Egg laying bouts for *Pseudacteon tricuspis* Borgmeier and *Pseudacteon litoralis* Borgmeier generally last about an hour, during which time they attempt to oviposit 30-120 times (Morrison et al. 1997). Oviposition attempts result in parasitism 8-35% of the time depending on the species of fly and conditions (Porter et al. 1995b, Gilbert & Morrison 1997, Morrison et al. 1997, Porter et al. 1997). Female flies have 100-200 mature eggs in their ovaries upon emergence (Zacaro & Porter unpublished data).

Oviposition strikes are fast to very fast, requiring only 0.1-1.0 sec depending on the species (Borgmeier 1922, Porter et al. 1995a, unpublished observations). Each species of fly has a distinctively shaped external ovipositor (Fig. 8) which is presumably used in a lock-and-key fashion to align the internal ovipositor with a particular part of the host's body. The form of the external ovipositor varies greatly from species to species suggesting that each is used quite differently (Feener 1987). Unfortunately, the small size of the fly and the rapid speed of the attack has so far precluded any studies concerning the relationship between ovipositor form and function. The exact sites for egg injection are also not known, but the coxal region seems likely for most species.

Workers frequently appear stunned after an oviposition strike and often stilt up on their legs (Fig. 9A) for a few seconds to a minute before running away. The flies are generally too agile to be captured by fire ant workers; nevertheless, attacking fire ants is a dangerous activity. Only about 30% of female flies survive after 4 h of attacks in the laboratory (unpublished data). Many flies are apparently captured and killed when they accidently fall into clusters of ants. Other flies simply appear to run out of energy, stop flying, and are eventually chased down and killed by the ants.

How do flies locate fire ants? The answer is probably by cuing in on chemical odors (Borgmeier 1922, Donisthorpe 1927). When fire ant mounds are disturbed in South America, *Pseudacteon* flies usually begin appearing within 20 min if conditions are appropriate. Presumably, they are able to detect fire ant odors over long distances. Ex-
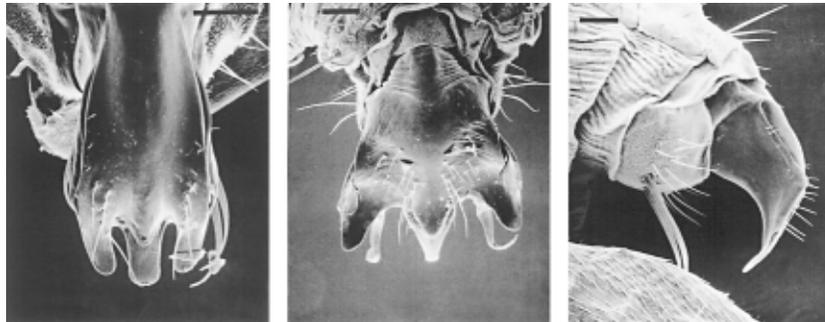
Fig. 8. Different species of *Pseudacteon* flies have very distinctive external ovipositors which are apparently used in a lock-and-key fashion to position the hypodermic-like internal ovipositor for injecting a single egg into their hosts. *Pseudacteon affinis* (left), *Pseudacteon tricuspis* from Argentina (center), *Pseudacteon borgmeieri* (right). Black bars indicate 50 μm.

actly how far is unknown; however, the fact that flies often require some time to appear suggests that they might be attracted from 10-20 m or more. However, studies of fly dispersal around Austin, TX suggest that flies are attracted at distances of less than 50 m (Morrison et al. unpublished manuscript). Chemical cues also seem important in the short-range recognition (10-40 cm) of fire ant workers. In the field in Brazil, several species of flies are capable of discriminating effectively and rapidly between *S. geminata* and *saevissima* complex fire ants (Trager 1991) at distances of 40 cm or more, even though workers are almost certainly visually indistinguishable at that distance (Porter et al. 1995a). It is not known whether long-range attraction cues are the same as the short-range recognition cues, but it seems likely. At distances
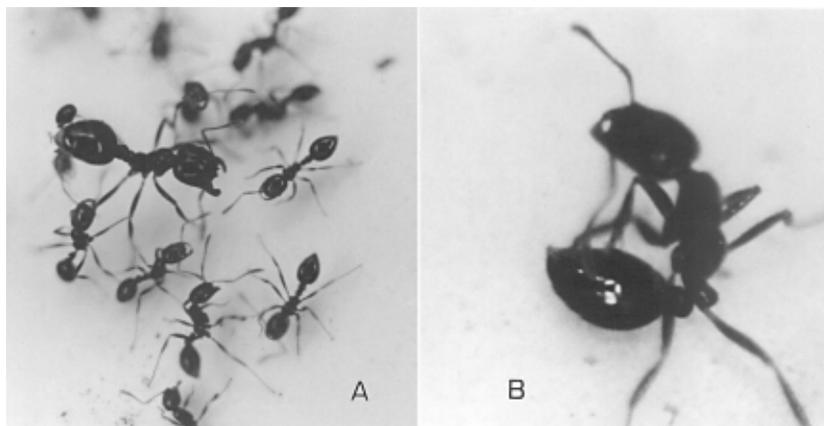

Fig. 9. A) After being attacked by decapitating flies, workers will often stilt up on their legs and remain immobile for several seconds to a minute as if they are stunned. B) When fire ant workers are being attacked, they often assume a stereotypical c-shaped defense posture.

of less than 10 cm, visual cues are probably very important. *Pseudacteon* flies have eyes with hundreds of ommatidia; presumably these afford them the necessary visual acuity to track, orient and attack fire ant workers. Nevertheless, even at 10 cm, odor cues appear to be necessary to initiate and maintain attack behavior (Porter & Alonso unpublished manuscript). The flies might also be able to use contact odors to assess the age and quality of fire ant workers. The source and nature of chemical cues are unknown, but alarm pheromones, recruitment pheromones, cuticular hydrocarbons, and aerosolized ant venom are all likely possibilities worth investigating (Orr et al. 1997).

MATING BEHAVIOR

In several *Pseudacteon* species (*P. tricuspis, P.crawfordi* Coquillett*, and P. browni* Disney) both sexes are attracted to fire ants and mating occurs while females are looking for workers to attack (Feener 1987, Feener & Brown 1992, Porter et al. 1997). Males can usually be distinguished from females because they are slightly smaller and because they do not track the movement of fire ant workers. Rather they hover in the air spinning around looking for females. Mating in *P. tricuspis* is initiated in the air when the male grabs hold of the female (Fig. 10). Copulation generally requires only a fraction of a second during which time the pair fall briefly to the ground before breaking up and flying away (Porter et al. 1997). Both sexes mate multiple times. The sex ratios of *P. tricuspis* adults collected in the field are often highly male-biased (e.g., 5:1, Pesquero et al. 1993; 2:1, Fowler et al. 1995, assuming all males were *P. tricuspis*). Males of most other species of *Pseudacteon* flies are not attracted to fire ants and their mating behaviors are currently unknown.

PSEUDACTEON BIOGEOGRAPHY

Pseudacteon flies have been collected in Europe, Asia, North America, and South America (Disney 1994, Michailovskaya 1995). At least 18 species of *Pseudacteon* flies have been found attacking *Solenopsis* fire ants in South America (Table 1). Another

Fig. 10. Male *Pseudacteon tricuspis* approaching female to mate while the female is searching for fire ant workers to attack. During mating, the pair generally fall to the ground where they remain in copula a few tenths of a second before breaking up and flying away. Black bar indicates 0.5 mm.

TABLE 1. *PSEUDACTEON* FLIES THAT ATTACK FIRE ANTS IN NORTH AND SOUTH AMERICA.

Species[1]	Known Range[1]	Ovipositor[1]	Abundance[2]
South America—*saevissima* complex ants			
P. borgmeieri	South America	unlobed	uncommon
P. convexicauda	Brazil	unlobed	rare
P. curvatus	South America	unlobed	common
P. solenopsidis	Brazil	unlobed	local
P. nudicornis	South America	bilobed	uncommon
P. affinis	Brazil	trilobed	rare
P. comatus	Brazil	trilobed	rare
P. cultellatus	South America	trilobed	rare
P. dentiger	Brazil	trilobed	rare
P. lenkoi	Brazil	trilobed	rare
P. litoralis	South America	trilobed	very common
P. nocens	South America	trilobed	uncommon
P. obtusus	South America	trilobed	common
P. pradei	Brazil	trilobed	common
P. near pradei	Brazil	trilobed	rare
P. species A	Brazil	trilobed	rare
P. tricuspis	South America	trilobed	very common
P. wasmanni	Brazil	trilobed	very common
Americas (Northern Hemisphere)—*geminata* complex ants			
P. crawfordi	U.S.A.	unlobed	
P. species B	U.S.A.	unlobed	
P. longicauda	Central America	unlobed	
P. antiguensis	Caribbean	bilobed	
P. browni	U.S.A., Central Amer.	bilobed	
P. grandis	Caribbean	bilobed	
P. spatulatus	U.S.A.	bilobed	
P. arcuatus	Caribbean, Costa Rica	trilobed	
P. bispinosus	Honduras	trilobed	

[1]Determined from Borgmeier & Prado 1975, Disney 1991, Disney 1994, specimens collected by and M. A. Pesquero and L. W. Morrison, and B. V. Brown's "scrapbook".
[2]Approximations from personal collecting efforts and (Williams 1980).

eight species attack fire ants in North America, Central America, and northern South America. Additional species will likely be discovered as collecting efforts are intensified and expanded into new areas. Also, several other species might need to be split if distinctive populations are determined to be separate species. (e.g., *Pseudacteon obtusus* Borgmeier and *P. tricuspis*). In contrast to the large number of *Pseudacteon* species that attack fire ants, only seven species (Disney 1994) are known to attack other

genera of ants in the New World (*Crematogaster, Linepithema, Dorymyrmex, Liometopum, Neivamyrmex*).

Most *Pseudacteon* species in South America are broadly distributed (Borgmeier & Prado 1975; unpublished data) across a wide range of habitats and climates. For example, *P. litoralis*, *P. tricuspis*, *P. obtusus*, and *Pseudacteon curvatus* Borgmeier have all been collected from São Paulo, Brazil in the north to Cuiaba, Brazil in the west, and south to Buenos Aires, Argentina. Even some of the less common *Pseudacteon* species (e.g., *P. borgmeieri, P. nudicornis* Borgmeier, *P. cultellatus* Borgmeier, *P. nocens* Borgmeier) have been collected from São Paulo south to Buenos Aires. These ranges encompass climates from tropical to temperate and habitats from tropical rain forests and swamps to temperate rangelands and seasonally dry "cerrado" forests. Several *Pseudacteon* species in North and Central America are also fairly widely distributed (Disney 1991).

Pseudacteon flies that attack fire ants appear to be associated with species in either the *saevissima* or the *geminata* complexes (Table 1; Borgmeier & Prado 1975, Gilbert & Morrison 1997, Porter 1998). Within both complexes, *Pseudacteon* species usually attack several species of fire ants (Disney 1994, Porter et al. 1997). However, phorid flies in South America have never been reported to attack the largest species of *Solenopsis* fire ants: *S. macdonaghi* Santschi, *S. megergates* Trager, *S. interrupta* Santschi, or *S. quinquecuspis* Forel. It will be interesting to determine whether these large fire ants lack *Pseudacteon* parasitoids, share them with their slightly smaller but more abundant relations (*Solenopsis invicta* Buren, *S. saevissima, Solenopsis richteri* Forel), or have their own, as yet undiscovered, communities of *Pseudacteon* flies.

Little is known about physical factors that limit the distribution of *Pseudacteon* species, but presumably there are thermal and moisture limits, as well as, limits associated with plant cover. Most decapitating flies do not seem restricted to specific habitats or narrow vegetational types. The abundance of *Pseudacteon* flies at particular sites can be quite variable from month to month, or even from week to week. The activity *Pseudacteon* flies around Austin, TX was limited by strong winds and stopped when air temperatures fell below 20°C (Morrison et al. unpublished data). Fowler et al. (1995) reported that *Pseudacteon* flies were active throughout the year in Rio Claro near São Paulo, Brazil with peak populations occurring in the spring. Populations in the fall can also be quite high (personal observations). There is no clear evidence for diapause or discrete generations in these flies, although species in Austin, TX do not appear to emerge during the winter months (Morrison et al. unpublished manuscript).

COMMUNITY STRUCTURE

In South America, 5-8 species of *Pseudacteon* flies are often found at the same site (Porter et al. 1995a, Pesquero et al. 1996, Fowler 1997, Orr et al. 1997). At least three behaviors help explain how so many closely related species partition niche space while using the same host. First and perhaps most importantly, species in sympatric communities attack different sizes of fire ant workers (Fig. 11A; Campiolo et al. 1994, Fowler 1997, Morrison et al. 1997). When sympatric flies are viewed as a community, almost all sizes of fire ant workers are subject to attack from one *Pseudacteon* species or another (Morrison et al. 1997).

A second way that some phorid flies divide niche space is by selecting different periods of diurnal activity. In Brazil, *P. litoralis* is crepuscular, whereas the medium-sized *P. tricuspis* is most active from late morning until late afternoon (Pesquero et al. 1996).

A third way sympatric *Pseudacteon* species limit competition is that they attack fire ants engaged in different activities (Orr et al. 1997). For instance, some flies (i.e.,
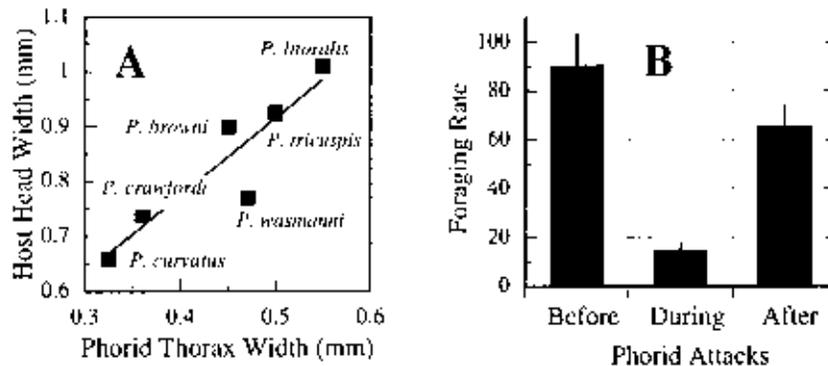
Fig. 11. A) Different species of *Pseudacteon* flies attack different sizes of fire ant workers. Often 5-8 species of flies occur at a single site. Taken together, species will attack >90% of fire ant workers (from Morrison et al. 1997). B) In South America, fire ant foraging generally terminates or is greatly reduced 2-3 minutes after decapitating flies begin attacking foraging workers. (modified from Porter et al. 1995c).

Pseudacteon solenopsidis (Schmitz), *P. borgmeieri, P. obtusus, P. nudicornis*) appear to specialize on fire ants along foraging trails (Orr et al. 1997) while other species appear to specialize on ants at mound disturbances or during fire ant mating flights (Smith 1928, Williams 1980, Pesquero et al. 1993). *Pseudacteon solenopsidis* has the interesting habit of chasing fire ant workers 10-20 cm off foraging trails before attacking them (Borgmeier 1922, Orr et al. 1995, Orr et al. 1997). This mode of attack is time-consuming; however, it may avoid shutting the foraging trail down (see below).

IMPACTS ON FIRE ANT BEHAVIOR

Fire ant workers are keenly aware of the presence of phorid flies (Borgmeier 1922). A single attacking fly usually stops or greatly inhibits the foraging efforts of hundreds of workers within 2-3 minutes (Fig. 11B; Feener & Brown 1992, Orr et al. 1995, Porter et al. 1995c). Orr et al. (1997) reported that the degree of response was related to the number of attacks. As soon as fire ant workers recognize the flies, they retreat into exit holes or find cover. Other workers will curl into a stereotypical c-shaped defensive posture (Fig. 9B; Feener & Brown 1992) that has only been reported when the ants are under attack by phorids. The c-shaped posture seems to be more common among *S. geminata* workers than *saevissima* complex workers (Feener & Brown 1992, Porter et al. 1995a, 1995c). Foraging rates usually remain suppressed as long as the flies are active and often for 15-60 minutes after the flies leave (Feener & Brown 1992, Porter et al. 1995c).

The flies inhibit fire ant foraging as long as they are present, often for periods of several hours (Orr et al. 1995). At any one time, phorid flies in South America can inhibit foraging at 10-20% of baits with fire ants (Porter et al. 1995c). Reduced foraging appears to facilitate competition from ant species that might otherwise be excluded from food sources in fire ant territories (Feener 1981, Orr et al. 1995). Several flies are also sufficient to stop nest construction or "freeze" the activity of entire colonies in laboratory nest trays (Fig. 12; Porter et al. 1995c). In Brazil, the "freezing" response varies from colony to colony (Porter et al. 1995c). Some colonies always show strong

responses while others show little or no response. Strangely, this variability was not related to collection location or species morphotypes.

The cessation of foraging, the c-shaped defense posture, and the freezing response are all specific fire ant behavioral defenses against phorid flies. Another probable defense is the foraging tunnel system (Disney 1994, Porter et al. 1995c). This system is a series of tunnels 2-7 cm below the ground surface that radiate out from the mound like branches on a tree (Markin et al. 1975). Even though a colony's territory may be 10 m across, foragers usually do not travel more than 0.5 m above ground from an exit hole. It would be difficult for fire ants to maintain large territories and therefore large colonies, if all foragers emerged from a central nest and traveled above ground for many meters with phorid flies attacking them. The tunnel system also allows colonies to shut down those portions of their territory under phorid attack while allowing them to maintain activity in the remainder.

The cues that fire ants use to recognize phorid flies are unknown. The ants can apparently see attacking flies and will clearly twist and turn to avoid their attacks. Olfactory and auditory cues might also be perceived by the ants at close range. Observations in the field indicate that hovering male flies can suppress foraging (Feener & Brown 1992, Porter et al. 1995c), but attacking females might be necessary to initiate defensive responses (Orr et al. 1997). If this is true, then fire ants may be releasing pheromones to trigger the group defensive responses.

HOST SPECIFICITY

All *Pseudacteon* flies are almost certainly parasitoids of ants. They have never been reported to attack any other kind of organism, and virtually all phylogenetically related phorid genera are also ant parasitoids (Brown 1993, Disney 1994). Their elaborate ovipositors and the adaptations of at least 11 species for pupation in the head capsules of worker ants (Fig. 2D) further supports the conclusion that they are very specialized parasitoids. Most *Pseudacteon* species are probably specific to ants in a specific genus (Disney 1994). A possible exception is *P. formicarum* in Europe. Donisthorpe (1927) reported that this fly attacks ants in several genera (*Lasius, Formica, Myrmica, Tapinoma*), but Wasmann (1918) held that it was probably specific to ants in the genus *Lasius*. Hosts of this fly have never been verified by rearing tests.
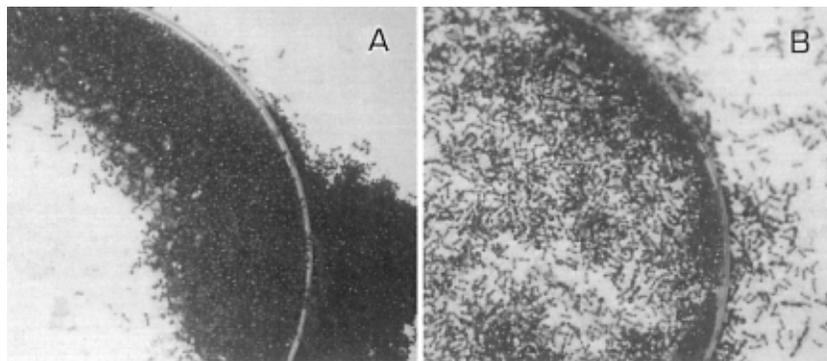

Fig. 12. A) If fire ants are unable to flee during attacks of decapitating flies, they will often "freeze" and refuse to move even when prodded. B) Normal colony activity with no flies present.

The *Pseudacteon* species that attack fire ants appear to be specific to fire ants. Of more than 20 New World species, only one unconfirmed report exists of a rare species being collected over another genus of ants (Borgmeier 1962). Some *Pseudacteon* species are apparently specific to individual fire ant species or species groups. For instance, at least three species of *Pseudacteon* phorid flies attack native *Solenopsis* fire ants in the U.S. (Table 1), but they have never been reported to attack imported fire ants even when they clearly have had the opportunity (Morrison et al. 1997). The host specificity of several parasitic *Pseudacteon* flies in South America was tested in the field with 23 species of ants from 13 genera (Porter et al. 1995a). As expected, these flies were attracted only to *Solenopsis* fire ants. A second field study showed that *Pseudacteon* flies are specific to ants in the genus *Solenopsis* (Porter 1998). Furthermore, several series of no-choice tests conducted in quarantine showed, that four species of *Pseudacteon* flies (*P. litoralis, P. tricuspis, P. wasmanni* (Schmitz), and *P. obtusus*) readily attack imported fire ants, but they virtually do not attack native fire ants (Gilbert & Morrison 1997, Porter & Alonso unpublished manuscript, Morrison & Gilbert unpublished manuscript). A fourth species (*P. curvatus*) does attack both native and imported fire ants, although it still has not been reared to the adult stage in native fire ants (Gilbert & Morrison 1997).

IMPACTS ON FIRE ANT POPULATIONS

The overall impact of phorid flies on fire ant populations is unknown; however, it is clearly sufficient to have caused the evolution of a number of phorid-specific defensive behaviors (Fig. 9B, 11B, and 12). These behaviors could only have evolved if *Pseudacteon* flies had exerted population-level impacts on the survival of fire ant colonies and/or their rates of sexual production (Porter et al. 1995c).

The introduction of exotic species usually occurs without natural enemies (DeBach 1974). This was certainly true for *S. invicta*. Over 30 natural enemies have been identified in South America (Williams 1980, Jouvenaz 1986, Porter et al. 1992) compared to only four in the United States (Collins & Markin 1971, Jouvenaz et al. 1977, Neece & Bartell 1981, Wojcik 1990, Kathirithamby & Johnston 1992, Williams et al. 1998).

The absence of natural enemies can allow exotic species to reach much higher population densities in newly invaded regions than in their native habitats (van den Bosch et al. 1973, Huffaker & Messenger 1976). Not surprisingly, fire ant populations in the United States are generally five times higher than in South America (Porter et al. 1992, Porter et al. 1997). Imported fire ants are one of the most abundant insects in the southeastern United States with average densities of 80-200 mounds/ha and 2,000-4,000 ants/m^2 (Macom & Porter 1996). Escape from natural enemies is a likely explanation for these unusually high densities, because analyses of factors such as climate, habitat, population structure, and cultural practices have not been useful in explaining intercontinental population differences (Porter et al. 1997).

Consequently, it is hoped that the introduction of phorid flies and other natural enemies from South America will be able to sufficiently tilt the ecological balance in the United States so that our native ants can compete with the imported fire ant on an "level playing field" (Fig. 13; Feener 1981, Feener & Brown 1992). If this happens, imported fire ant populations in the United States could be reduced to levels similar to those in South America. Phorid flies in North and Central America also have the possibility of being exported as biocontrol agents of exotic *S. geminata* populations in Africa, India and the Pacific region.

Ants are among the most important of all terrestrial arthropod groups in terms of both biomass and impacts on community structure (Hölldobler & Wilson 1990). Con-
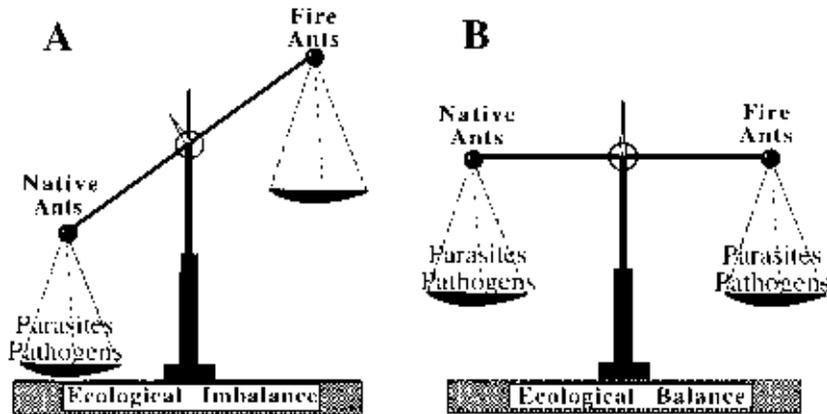
Fig. 13. A) One likely explanation for the unusually high densities of fire ants in the United States is that native ants are weighed down by their natural enemies while imported fire ants have escaped almost all of their natural enemies. B) Importing fire ant enemies that were left behind in South America may reestablish a more natural ecological balance. If this happens, fire ants will loose their competitive advantage and populations should drop.

sequently, there has been considerable interest in the structure and diversity of ant communities, most focused on competition among different species of ants (Wilson 1971). Relatively little, however, is known about the effects of pathogens and parasites on ant community structure (Feener 1981, Orr 1992, Briano et al. 1995, Orr et al. 1995), perhaps because experimental manipulations at the community level are usually very difficult or impossible to conduct. Fire ant biocontrol efforts offer a unique opportunity to experimentally test the hypothesis that parasitoids, specifically phorid flies, are important in structuring the diversity and composition of ant communities.

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