Biology of *Pseudacteon* (Diptera: Phoridae) ant parasitoids and their potential to control imported *Solenopsis* fire ants (Hymenoptera: Formicidae)

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**ABSTRACT**

Phorid flies in the genus *Pseudacteon* are parasitoids of ants. Many *Pseudacteon* species are specific to *Solenopsis* fire ants, which are important economic pests. *Pseudacteon* phorids have a relatively small direct effect of mortality on their host ants. The presence of *Pseudacteon* phorids causes behavioral changes in host workers, however, often putting the host species at a competitive disadvantage relative to other ant species in the community. Because of this relatively large indirect effect, *Pseudacteon* phorids are potential biocontrol agents of pest *Solenopsis* fire ants. Much recent research has focused on various aspects of *Pseudacteon* biology and the interactions of *Pseudacteon* species with their *Solenopsis* hosts.

**INTRODUCTION**

The Phoridae is one of the most biologically diverse insect families (22). It has been suggested that these minute sleepest makes up nearly 2% of the animal species on Earth (20). Because they are so small and inconspicuous, however, the ecological importance of phorids may be underestimated, and very little is known about most species (20, 22). It does appear that parasitoidism is the most common lifestyle, and ants are the most common hosts (20).

One group of phorids that has received a relatively large amount of attention are species in the genus *Pseudacteon* (17) that are parasitoids of *Solenopsis* fire ants (86). These *Pseudacteon* species are so small (0.9-1.5 mm in length [6]) and inconspicuous that they are virtually never observed in nature except in the vicinity of their host ants. They have been the subject of much recent research, however, because they are potential biocontrol agents of imported *Solenopsis* fire ants, *S. invicta* and *S. richteri*, in the U.S. (27, 64, 81).

The earliest accounts of *Pseudacteon* flies attacking their host ants date back over 70 years, and exist from Europe (89), South America (4), and the United States (84). It was not until the 1970's, however, that researchers began extensive observations of *Pseudacteon* species that attack *Solenopsis* workers in South America, in hope that such species would prove to be effective biocontrol agents for imported fire ants in the southeastern U.S. Although the behavior observed in this era suggested that *Pseudacteon* species were parasites of ants, all attempts to rear larvae from infected hosts failed (91, 92, 93). Moreover, it became obvious that *Pseudacteon* phorids attacked relatively few
workers and, even if parasitic, were considered of dubious value as biocontrol agents (45).

Subsequent studies, however, revealed that phorid flies may strongly affect the behavior of their ant hosts, and resulted in a resurgence of research on *Pseudacteon*. Feener (24) presented the first evidence that phorid flies (genus *Apocephalus*) were able to shift the competitive balance between two ant species, by reducing recruitment of the host ant species to interspecific interactions. Additional studies on other species of ants and phorids revealed a similar pattern. Whereas the direct effect of mortality from parasitism may be low, the presence of phorid flies can have a large indirect effect, altering the behavior of the host species, which may result in a competitive disadvantage at some aspect of interspecific competition (26, 29, 63).

The first evidence that *Pseudacteon* phorids could have relatively large indirect effects on *Solenopsis* workers came in 1992. Feener and Brown (27) demonstrated that food retrieval in *S. geminata* in Costa Rica was dramatically decreased in the presence of *Pseudacteon* phorids, and proposed that *Pseudacteon* species from South America could be effective biocontrol agents for imported fire ants in the United States. *Pseudacteon* flies were confirmed as parasitoids of ants in 1995 (68, 77), and the life histories of two South American species, *P. litoralis* and *P. tricuspis*, were soon described (77, 82). These studies set the stage for a large body of basic research on *Pseudacteon* biology and *Pseudacteon-Solenopsis* interactions.

**PSEUDACTEON BIOLOGY**

**Development**

*Pseudacteon* flies that attack *Solenopsis* ants are solitary parasitoids (i.e., only one larva is able to complete development in a host, although superparasitism may occur). Female phorids inject a single egg into the side of a worker ant's thorax (25, 56, 77). One early report described *P. obtusus* depositing an egg on the posterior end of a worker's head capsule (90). Such behavior has not been observed since, however, in any *Pseudacteon* including *P. obtusus* (56, 77, 82), and represents either a spurious observation or an abnormal oviposition attempt.

The developmental stages of *P. tricuspis* have been described in detail (77). As in most other phorids, there are three instars. The larva migrates to the head of the ant during the first or second instar. The larval stages apparently feed on ant hemolymph. Infected workers do not appear abnormal until just before pupariation.

At pupariation, the third instar apparently releases an enzyme that causes degeneration in the intercuticular membranes of its host, usually causing the ant's head to fall off. The maggot consumes the entire contents of the head capsule over a 6-12 hour period. The maggot pushes the ant's mandibles aside, and maneuvers itself so that the first three segments of the puparium fill the oral cavity. These three segments harden into a plate that is the same color as the ant head capsule. Several days after pupariation, two respiratory horns extend out of the puparium, one at each corner of the oral cavity of the head capsule (77, 82).

In the laboratory, ant head capsules containing phorid puparia are removed from the colony and discarded with other dead workers (82). In nature, head capsules with puparia are probably removed from the colony and placed on the surface of the ground, as are dead workers in general (44). The adult fly emerges by pushing open the sclerotized pupal plate and crawling out of the oral cavity of the ant head capsule. All *Pseudacteon* parasitizing *Solenopsis* workers that have been studied to date have a similar developmental life history (56, 70, 82).

The duration of the larval and pupal stages is dependent upon the species of *Pseudacteon* and temperature. A comparative study of 6 *Pseudacteon* species revealed that longer developmental times were associated with larger-bodied phorid species (56). Larval development times (defined as the time from
oviposition to pupariation) ranged from 13 to 18 days at 30°C, and pupal development times (defined as the time from pupariation to emergence) ranged from 15 to 19 days at 30°C. Larval development times were 25-37% longer at 25°C (56).

Emergence of the adult almost always occurs within a few hours of sunrise (70). The life span of the adult is unknown in nature; adults generally live a week or less in the laboratory (70, 77, 82). Very little is known of the natural history of the adult, as adult *Pseudacteon* in nature have only been observed when in the vicinity of their ant hosts.

In general, the adults of many Phoridae are thought to be somewhat generalist feeders on plant nectar, sap, or honeydew. Adult phorids, especially females, have also been commonly observed feeding on freshly-dead insects (22). Adult *Pseudacteon* phorids do not appear to be attracted to these potential food sources in great numbers. Of 498 specimens of Phoridae found at different types of food or dung baits in Cuba, only 8 were *Pseudacteon* (*P. antiquensis*) (39). In a laboratory test of *P. curvatus* with different types of food, carrion, or dung baits, >75% of 50 individuals tested never visited any of the food items (72). Adult phorids have been observed to apparently feed on sugar water or amino acid solutions in the laboratory, if they come into contact with them, although they do not appear to be attracted to them from a distance (70).

In the *Pseudacteon* species studied thus far, sex of the emerging adult is determined by the size of the ant worker, with larger workers producing more female phorids (57, 61, 82). The exact mechanism underlying this sex ratio variation has not yet been elucidated, although environmental sex determination is a likely possibility. Examination of *Pseudacteon* life history reveals several traits assumed to be important in models predicting conditions under which environmental sex determination is favored (61). Environmental sex determination in insects appears to be very rare (12), and there is evidence for it in only one other phorid: temperature appears to affect the sex ratio in *Megastelia scalaris* (22).

*Pseudacteon* species are apparently restricted to development in workers (70). No confirmed reports of parasitization of alates exist, although *Pseudacteon* species have the opportunity to attack alates during mating flights (66, 90). A report exists of an unidentified phorid puparium found in an alate queen of *S. invicta* in Brazil (94). The puparium has since been determined not to be that of a *Pseudacteon* phorid (S. Porter, personal communication).

**Population Ecology**

We still know relatively little about the population-level ecology of *Pseudacteon* phorids, primarily because they are so small and inconspicuous, and attracted in large numbers to apparently nothing except their host ants. These same characteristics, however, are desirable in a biological control agent of fire ants. A summary of what we do know is presented below:

**Phenology**

In tropical Brazil (São Paulo State), *Pseudacteon* phorids that parasitize *Solenopsis* workers are active all year, although species compositions and relative abundances vary seasonally (33, 65). In central Texas (near Austin), adult *Pseudacteon* were found to be active from April to December. Adult phorids were not observed hovering over their host ants when daily high temperatures were <20°C (59). Such cool temperatures commonly impose a lower physiological limit to flight activity in small insects (51).

*Pseudacteon* populations in central Texas revealed a large amount of variation in population abundance both spatially and temporally (59, 60). Populations were observed to peak either in the spring, summer, or fall, and some populations revealed two peaks separated by a trough (59, 60). A large amount of weekly variation in population abundance was observed, indicating that adults have short life-spans in nature as well as in the laboratory (60).
The factors affecting *Pseudacteon* population size and phenology are apparently diverse. There is some evidence that rainfall patterns may be an important factor under some conditions (59). A study of the proximate effects of air temperature, soil temperature, relative humidity, soil moisture, and wind speed revealed that no single variable accounted for more than 23% of the variation in *Pseudacteon* activity (on days when air temperatures were >20°C). In contrast, up to 73% of the variation in host ant activity could be explained by one of the variables (60). Such abiotic variables may affect *Pseudacteon* populations directly, or indirectly through the activity patterns of their ant hosts. Only weak positive correlations between phorid activity and host ant activity ($r = 0.15$ to 0.23) have been observed (60).

**Dispersal**

Studies of the dispersal abilities of *Pseudacteon* species in central Texas have revealed that adults are capable of dispersing at least 650 m away from the nearest host ant colony. Dispersal appeared to be in random directions and was not affected by the prevailing winds (59). Although males have been found to be more prone to dispersal in some phorid species (22), no evidence of variation in sex ratios as a function of distance were found in the *Pseudacteon* species studied. Some phorid species are known to disperse over long distances and are often a common component of the aerial plankton (7, 36, 95).

Passive dispersal may also occur, probably over relatively short distances, as the *Solenopsis* head capsule containing the *Pseudacteon* pupa is positively buoyant (59). Some species of Phoridae have been reared from pupae found in flood refuse (3, 47).

Host *Solenopsis* populations may be fragmented across the landscape because of habitat variation or the presence of competing ant species (59, 69, 74, 80, 87). In central Texas, it appears that the distances adult *Pseudacteon* are able to actively disperse by flight are relatively large compared to the interpatch distances separating host *S. geminata* populations (59). This scenario represents a type of metapopulation often referred to as a 'patchy population', in which dispersal takes place on a spatial scale greater than that of the local events causing metapopulation fluctuations (41, 42).

**Sex ratio**

It has been observed that sex ratios of adult *Pseudacteon* collected in the vicinity of their hosts are often male-biased (33, 59, 60, 66), although in some cases males are absent from collections (65). Males of some *Pseudacteon* species are attracted to host ants, apparently to find mates (25, 27, 81, 82), while in other species, mating apparently occurs elsewhere (10, 65).

It is not known why adult sex ratios are biased towards males. Basic sex allocation theory predicts that, in the absence of complicating factors, selection should favor a 50:50 sex ratio if sons and daughters are equally costly to produce (30, 40). The best documented studies of adult sex ratios have been conducted in central Texas, on *Pseudacteon* species parasitizing the polygyne (multiple queen) form of *S. geminata* (59, 60). Because polygyne *Solenopsis* workers are on average smaller than monogyne (single queen) workers (38, 49), and offspring sex in *Pseudacteon* is dependent upon worker ant size (61), it has been suggested that adult sex ratios may be dependent to some degree upon *Solenopsis* social form (57). Insufficient comparable data are available, however, to test this hypothesis.

Adult sex ratios are unknown in *Pseudacteon* species in which males are not attracted to host ants. Reports of sex ratios derived from collections made over host ants that group numerous phorid species together probably underestimate the true number of males in the population (59).

**Species Diversity**

This review focuses on New World
Pseudacteon, although members of this genus are also present in Europe and Asia (22, 52). At present, there are 28 Pseudacteon species that are known to attack Solenopsis workers in North, Central and South America. Pseudacteon affinis Borgmeier, P. borgeieri Schmitz, P. comatus Borgmeier, P. conicorns Borgmeier, P. convexicauda Borgmeier, P. culellatus Borgmeier, P. curvatus Borgmeier, P. dentiger Borgmeier, P. lenkoi Borgmeier and Prado, P. litoralis Borgmeier, P. nocens Borgmeier, P. nudicornis Borgmeier, P. obtusus Borgmeier, P. pradei Borgmeier, P. solenopsis (Schmitz), P. tricuspis Borgmeier, and P. wasmanni (Schmitz), along with two undescribed species, are known from S. saevissima complex hosts in South America (5, 6, 22, 70, B. Brown, personal communication). Pseudacteon antiquensis (Malloch), P. arcuatus Borgmeier, P. bifidus Brown and Morrison, P. bispinosus Borgmeier and Prado, P. browni Disney, P. crawfordi Coquillett, P. grandis Greene, P. longicauda Borgmeier and Prado, and P. spatulatus (Malloch) are known from S. geminata complex hosts in North and Central America, including the Caribbean (10, 21, 22).

Because Pseudacteon phorids are so small and many species appear to be temporally or spatially rare (33, 59, 70), additional Pseudacteon species that parasitize Solenopsis workers probably await discovery. For example, a new species, P. bifidus, was described in 1999 (10) and known initially only from Travis County, Texas, although it has since been collected in Costa Rica (B. Brown, personal communication). Additionally, some described Pseudacteon species with unknown hosts may ultimately be determined to parasitize Solenopsis species. For example, P. conicorns was described in 1962 (5) but only recently was found to be associated with Solenopsis-ants (B. Brown, personal communication).

Many Pseudacteon species have broad geographical ranges (6, 21, 70), and insufficient information exists to delimit the distributions of individual Pseudacteon species. Enough regional variation exists in some South American species to suggest that these species may need to be split (70).

Although regional species diversity patterns of Pseudacteon are not yet well-documented, several studies have elucidated species diversity patterns at the level of alpha diversity (i.e., within homogenous habitats). In South America, several Pseudacteon species (three to eight) often coexist at the same site (33, 65). One species is often much more abundant than the rest, comprising > 70% of the females collected (the males of most species have not been described) (33, 65).

Similar patterns of species diversity have been described from North America. Several species may be found at a single site, but the number is usually lower (two to four), probably because the North American Pseudacteon fauna is not as speciose. One species is usually much more abundant than the others (59).

Multiple Pseudacteon species may coexist on a single Solenopsis host species by partitioning the host resources along several axes: First, Pseudacteon species of different sizes parasitize different size worker ants (14, 32, 56, 57). (Solenopsis workers are polymorphic and the largest workers are about 3 times larger than the smallest [79]). Second, some Pseudacteon species have complementary diurnal activity patterns (67). Third, some Pseudacteon species appear predominantly at disturbed mounds, while others appear more frequently at foraging trails (65). The first mechanism of coexistence has been documented for Pseudacteon species attacking S. saevissima complex species in South America as well as for Pseudacteon species attacking S. geminata complex species in North America. The second and third mechanism have so far only been documented for the more speciose South American fauna.

**PSEUDACTEON-SOLENOPISIS INTERACTIONS**

**Host Specificity**

All Pseudacteon species are apparently...
parasitoids of ants, and individual *Pseudacteon* species appear to be almost always specific to a single genus of ants (22, 75). Many *Pseudacteon* species that parasitize *Solenopsis* are specific to, or reveal preferences for, an individual species or species complex. Field tests of host specificity among *Pseudacteon* phorids in South America with 26 ant species in 13 different genera revealed that *Pseudacteon* phorids were attracted only to *Solenopsis* species (75). The *Pseudacteon* species primarily attacked fire ant workers of the *S. saevissima* complex, and only rarely attacked *S. geminata* complex workers (71, 75). Conversely, none of the *Pseudacteon* species present in North America that attack native North American fire ants in the *S. geminata* complex have ever been observed to attack the imported *S. invicta* or *S. richteri*, both in the *S. saevissima* complex (35).

In laboratory tests conducted in the United States, *Pseudacteon* species imported from host *S. saevissima* complex populations in South America revealed a range of relative host specificity when presented with a choice between *S. invicta* and *S. geminata*. Four species, *P. tricuspis*, *P. litoralis*, *P. wasmannii*, and *P. obtusus*, exhibited a high degree of specificity for *S. invicta*, rarely or never attacking *S. geminata* (35, 58, 73). Two other species, *P. curvatus* and *P. borgei*, attacked *S. geminata* relatively frequently in laboratory tests (58, 72). *Pseudacteon curvatus* attacked *S. xyloni*, another native Texas fire ant, to a greater degree than *S. geminata* (72). Neither *P. curvatus* nor *P. borgei* attacked any native fire ant as frequently as they attacked *S. invicta*, however (35, 58, 72).

At least some *Pseudacteon* species from South America (*P. tricuspis* and *P. curvatus*) can complete development in *S. geminata* hosts (72, 73). Because the main effect of *Pseudacteon* phorids is not a direct effect of mortality, but rather a behavioral change at the colony level that leads to changes in competitive outcomes (see below), the crucial question in evaluating the safety of exotic *Pseudacteon* species is whether the species in question will attempt oviposition on native ants. If so, even if oviposition or development is unsuccessful, harassment by exotic *Pseudacteon* species may have negative impacts on native ant populations (58).

**Oviposition behavior**

Adult *Pseudacteon* females are attracted to aggregations of host *Solenopsis* worker ants at foraging trails, food resources, disturbed mounds, or mating flights (25, 65, 66, 92). When males are attracted to host ants, aggressive male-male interactions, as well as matings, are observed (25, 27, 59, 81). Males initiate matings by clasping a female while in flight. Copulation is usually completed in a fraction of a second, and the pair often falls to the ground before breaking up and flying away (82). Both sexes may mate multiple times (70). It is unknown where mating occurs in species in which males are not attracted to host ants.

Females inject a single egg into the side of a worker ant's thorax by use of a hypodermic-style ovipositor in a rapid aerial attack. In most species, oviposition occurs in a fraction of a second (77). In *P. crawfordi*, however, the female often "rides" the worker ant for several seconds while ovipositing (25, 56).

In a laboratory setting with unlimited hosts, most *Pseudacteon* species attacked several ants per minute, and significant variation existed among species in attack rates (35, 56, 58). Attack rates in the field are probably lower, however, and dependent upon the availability of hosts. *Pseudacteon* females attack numerous workers in oviposition bouts which may last from several minutes to over an hour. *Pseudacteon* females may exhibit multiple periods of such oviposition activity, perching for several minutes between bouts (56, 92). In the laboratory with unlimited hosts, females have been observed to attack more or less continuously for an hour or more, making >100 parasitization attempts (56).

Not all parasitization attempts are successful, or at least do not result in
development to a second or third instar. Success rates (number of parasitized workers/number of parasitization attempts) are often low, and have been documented in the range of 11 to 35% (56, 77, 82). Success rates are likely to depend upon a number of factors, including the difficulties associated with alignment of the ovipositor and injection of an egg into a live ant in a very rapid attack, and aborting oviposition at the last moment because the worker is determined to be of an inappropriate size (77).

It has been reported that *Pseudacteon* phorids prefer to oviposit on large workers (25, 77, 90). The size of worker preferred, however, varies among *Pseudacteon* species, and a positive correlation exists between size of phorid species and size of ant worker attacked (14, 32, 56, 57). The smallest *Pseudacteon* species prefer workers that are smaller than the colony average, particularly in the case of monogyne (single queen) colonies (56, 57).

Phorid parasitoids of ants, including *Pseudacteon*, appear to initially locate host workers at a distance by olfactory cues (9, 23, 28, 35, 65). One study indicates *Pseudacteon* are attracted to host workers from distances of <50 m in the short term (~15 min) (59), but this probably depends on a number of factors including wind speed and direction (60). Visual cues become more important at close range for oviposition, although olfactory cues may still be important (70, 73).

**Effects on Host Workers**

**Behavioral Reactions**

*Pseudacteon* phorids do not inflict high levels of mortality on host ant colonies through parasitization. Observations in both South and North America have indicated that relatively few ants are parasitized (45, 56). The only quantitative study to date documented that ≤3% of the workers in a *S. geminata* colony in central Texas were parasitized at a given time (56).

*Pseudacteon* phorids may exert a relatively large effect on competitive interactions among the host and competing ant species by altering the behavior of the host *Solenopsis* workers. The specific responses of workers to phorid attack, however, vary depending upon the *Pseudacteon* species in question (10, 31, 59, 65), and even among *Solenopsis* colonies (81).

When *Pseudacteon* phorids are present, *Solenopsis* workers often curl their abdomen under the thorax and elevate their head, remaining motionless or moving only very slowly (25). This posture apparently makes it more difficult for phorids to successfully oviposit, and has only been observed in ants under phorid attack. This C-shaped defensive posture has been frequently observed in *S. geminata* workers (25, 27, 54), but appears to be less common in *S. saevissima* complex species (56, 81).

Other individual level behaviors that are reactions to the presence of phorids have also been observed, although they may not be specific to *Pseudacteon* harassment. For example, workers may exhibit a standing, "stilted" posture, or elevate their gasters to disperse venom (81, 90, 92), a behavior known as gaster flagging (62). In the laboratory, I have observed workers crouching down and laterally extending their legs in the direction of an attacking phorid, apparently in an attempt to prevent the phorid from approaching (unpublished observations).

Both male and female phorids have been observed to elicit behavioral responses in workers (27, 81). Although the presence of a single male may effect the behavior of numerous workers (27), the most dramatic effects on colony-level foraging occur when females are actively attacking workers (65). Attacked ants apparently release an alarm pheromone that induces phorid-specific behaviors in nearby workers (18).

Some *Pseudacteon* species attack workers quickly and with such force that the worker is knocked over and appears visibly stunned for several seconds (56, 81, 92). In contrast, *P. crawfordi* rides its host for 1-2 seconds while ovipositing and causes a much less violent reaction (25, 56, 59). After a
worker has been attacked, it usually appears stunned and often will remain motionless for several minutes, or engage in gaster flagging behavior (65, 92). The attacked worker is often surrounded by nestmates, which appear to be engaged in grooming behavior that may last for several minutes (81).

The defensive postures, in addition to the stunned reaction and grooming behavior, may result in a large proportion of workers being "frozen" in place, and not actively foraging or defending food resources. In addition, the presence of phorids often results in workers hiding under leaves, or an overall decrease in worker recruitment (31, 64, 81). Some worker ants may react offensively to the presence of phorids, however, snapping their mandibles at them and catching and killing the flies if they are able (81). Such aggressive behavior by harassed worker ants may even result in an overall increase in worker activity (10), although such instances appear to be rare.

**Effects on Competition**

Most studies of the effects of *Pseudacteon* phorids on ant interspecific competition involving host *Solenopsis* species have focused on exploitative competition (i.e., competition for food). In Costa Rica, the presence of *Pseudacteon* phorids decreased the number of *S. geminata* workers retrieving visible food particles by 84% (27). In South America, *Pseudacteon* phorids were shown to decrease worker recruitment of *S. saevissima* complex species to food baits in a number of studies (31, 64, 65, 81). In Texas, a study in which food baits were weighed before and after exposure to foraging *Solenopsis* workers found that the presence of *Pseudacteon* phorids decreased the amount of solid and liquid food retrieved by as much as 50% (54). *Pseudacteon* phorids may reduce resource retrieval rates by decreasing the number of workers recruiting to a food resource, decreasing forager activity, or decreasing the average size of forager (31, 54, 55).

The effect of *Pseudacteon* phorids on individual-level foraging (i.e., food particles small enough for a single worker to retrieve) has not been studied. Because phorids are apparently initially attracted to odors of the host ants, and foragers retrieving single food items would not be expected to recruit other workers by pheromones, the effect of phorids on individual-level foraging may be very small.

Fewer studies have focused on the effect of phorids on the pure interference component of interspecific competition (i.e., direct aggressive interactions). Most evidence for this effect is derived from studies using baits to attract ants, and both exploitative and interference competition is observed. In Brazil, the presence of *Pseudacteon* phorids during initial recruitment of *S. invicta* workers to food resources often led to the loss of those resources to competing ant species (64). If recruitment to a food item had become established, however, *S. saevissima* complex species were usually able to defend the food item from other species (65, 81). In a study of the behavioral reactions of *S. richteri* to *Pseudacteon* phorids at food baits of varying sizes in Argentina, workers did not abandon food items in the presence of phorids. More foragers were recruited to larger food items, and phorids reduced ant foraging activity by the same factor independently of food quantity (31), a foraging strategy characterized as 'risk-adjusting' (34).

In Texas, the presence of *Pseudacteon* flies had no effect on the outcome of interference competition at baits. *Solenopsis geminata*, which was host to attacking phorids, won as many contests against *S. invicta* (which was not a host of the phorids present) in the presence as in the absence of phorids. The defensive behaviors usually observed in *S. geminata* under phorid attack were very rare in the presence of *S. invicta*, and most *S. geminata* workers ignored the flies and fought aggressively with *S. invicta* (54). The converse of this experiment was conducted in the laboratory. *Solenopsis invicta* and *S. geminata* were observed in the presence and absence of *P. tricuspis*, a phorid that is highly specific to *S. invicta*. Unlike other studies, this
experiment examined pure interference competition (no food resource was present), and the outcome was quantified by territorial gain or loss. The presence of *P. tricuspid* had no effect on the short-term outcome of interference competition (55).

Another study in Texas on the effect of *Pseudacteon* species on *S. geminata* revealed that the presence of phorids did not change the structure of community-wide dominance hierarchies, and *S. geminata* won the majority of its interspecific interactions in the presence of phorids (60). This study did suggest that the identity of competing ants may play an important role in determining the outcome of aggressive interactions in the presence of phorids, however, and this interaction warrants further investigation.

Thus, it appears that in general *Pseudacteon* flies have a relatively small direct effect of mortality on their host ants, but may have a relatively large indirect effect on the outcome of interspecific competition. This indirect effect appears to operate primarily through the exploitative component of interspecific competition. Although no strong evidence of an effect on interference competition has yet been obtained, this effect has only been evaluated under limited conditions. Relatively small direct and large indirect effects may characterize other phorid-ant parasitoid-host interactions as well. For example, Feener (24, 26) has shown that parasitism rates of *Apocephalus* phorids on *Pheidole* ants are low (5%), but relatively large indirect effects on both exploitative and interference competition have been documented.

**Host Ant Defenses**

All evaluations of the effect of *Pseudacteon* phorids on *Solenopsis* fire ant foraging to date have been over the very short term (on the order of a few hours) (27, 31, 54, 60, 64, 65, 81). The cumulative, longer term effects are not known, and it is difficult to extrapolate from the short-term data. It appears that the effect of *Pseudacteon* phorids on fire ant foraging is usually greatest in the first hour or two after a food item has been discovered. Although foraging is depressed due to phorid presence, workers are often busy tunneling under the food item and piling bits of dirt and debris on top of it (54). Other workers remain around the food item, often in a defensive posture, apparently guarding the food resource from enemy ants (81). In time workers may be able to access the food from below with little exposure to phorids. Along foraging trails, a resurgence of above-ground foraging after an initial decrease has been documented in *S. invicta* in the continued presence of *P. solenopsidis* (65).

*Solenopsis* ants display a number of behaviors that may reflect, to some degree, adaptations to the presence of diurnally active phorid flies, and which may decrease the impact of these parasitoids. These include the defensive posturing behavior (25, 27, 54, 81), an extensive underground tunnel system (50), and covering food items with dirt and debris, as described above. Additionally, *Solenopsis* workers obtain some unknown proportion of their food from underground sources (85) safe from phorid attack, and at night (15, 16, 54) when phorids are not active.

One study has revealed that *Solenopsis* workers are able to compensate for the presence of phorids at one food resource by increasing food consumption at a phorid-free food resource (55). This suggests that *Solenopsis* workers may be able to increase the relative amount of diurnal underground foraging, or nocturnal aboveground foraging, to avoid *Pseudacteon* parasitism pressure, although this hypothesis has not been investigated in the field.

**IMPLICATIONS FOR BIOLOGICAL CONTROL**

Imported fire ants, *S. invicta* and *S. richteri*, were accidentally introduced into the United States from South America beginning in 1918. These exotic pests currently occupy over 114 million hectares in 11 southeastern states and Puerto Rico and are continuing to
spread (13). *Solenopsis invicta* has also invaded the Bahamas (53). *Solenopsis invicta* and *S. richteri* have hybridized in Alabama, Mississippi and Georgia (19). Both *Solenopsis* species and the hybrid are major agricultural pests in their introduced ranges; they also adversely affect biodiversity and human health (1, 2, 46, 88). Imported fire ant populations in the United States are about 4-7 times higher than in South America, and escape from natural enemies is a leading hypothesis in explaining such unusually high densities (76, 83).

The potentially strong indirect effect of *Pseudactepon* phorids on *Solenopsis* fire ants, along with high levels of host specificity, have generated interest in introducing *Pseudactepon* species from South America to serve as biocontrol agents for imported fire ants in North America (27, 35, 64, 73, 75, 81). In the first laboratory test of the effect of *P. tricuspid* (a South American species) on North American *S. invicta* populations, a single *P. tricuspid* female significantly affected *S. invicta* foraging (54). Subsequent laboratory experiments revealed that the presence of *P. tricuspid* females can reduce food retrieval in North American *S. invicta* populations by as much as 50%. The main mechanisms were a reduction in recruitment and a decrease in average forager size (55).

Studies elucidating how *Pseudactepon* phorids partition host resources indicate that the introduction of multiple species will put more parasitism pressure on host *Solenopsis* ants than would a single *Pseudactepon* species (56, 57, 65, 67). The combination of *Pseudactepon* species that produces the greatest impact on the host *Solenopsis* species may vary between monogyne and polygyne social forms (57).

Ultimately, the only way to determine the efficacy of *Pseudactepon* phorids as biocontrol agents of *Solenopsis* fire ants will be to evaluate the long-term success of field releases in various areas. Field releases of *P. tricuspid* are currently underway in several southeastern states, and at least one population of *P. tricuspid* has been established for over 2 years in Florida (S. Porter, personal communication).

Because the factors limiting a population often vary over the population's geographic range (11), *Pseudactepon* phorids may have a differential effect throughout the introduced range of imported fire ants in the U.S. The overall effect of *Pseudactepon* species in limiting *Solenopsis* fire ants is likely to depend crucially upon the presence and relative competitive ability of other ants (and potentially other types of organisms) that will compete with the host ant species for the same food resources (54, 60). Food resources not immediately usurped by competing species will likely be eventually obtained by *Solenopsis* ants, either through the construction of underground tunnels or nocturnal foraging.

In many areas of the southeastern U.S., imported *Solenopsis* fire ants have greatly reduced the species richness and abundance of other ant and arthropod species (78). Because the primary effect of *Pseudactepon* phorids is an indirect one, mediated through competing species, the impact of phorids may not be very strong in depauperate areas with dense *Solenopsis* populations. If parasitism pressure by *Pseudactepon* phorids on imported fire ants is strong enough to allow for an increase in the population size of competing ants, however, host *Solenopsis* populations may slowly decrease over time until a new equilibrium is reached. This process may take years, if not decades.

In addition to the applied interest in decreasing imported fire ant populations, the introduction of exotic *Pseudactepon* species represents an important basic experiment in community ecology. Ant communities are known to be structured to a large degree by interspecific competition (43). Predators, pathogens, and parasites may also be important regulators of ant communities, however, at least under some conditions (8, 24, 37, 48). The widespread introduction of exotic *Pseudactepon* species to the southeastern U.S. and long-term monitoring of recipient ant and arthropod communities represents a rare opportunity to elucidate factors regulating ant
communities over broad spatial and temporal scales.

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