Mechanisms of *Pseudacteon* Parasitoid (Diptera: Phoridae) Effects on Exploitative and Interference Competition in Host *Solenopsis* Ants (Hymenoptera: Formicidae)

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**ABSTRACT**

I conducted a series of laboratory experiments to quantify the effects and elucidate the mechanisms by which *Pseudacteon tricuspis* Borgmeier phorid flies affect the exploitative and interference components of interspecific competition in host *Solenopsis invicta* Buren ants. In manipulative experiments, workers retrieved 50% less food in a foraging tray with phorids present, compared with an equidistant foraging tray with the same food resource but without phorids. The average number of workers actively foraging in the tray with phorids was significantly less than in the tray without phorids. There were no significant differences in either average worker size or average number of workers present at the food resource at the end of the trials in trays with phorids versus trays without phorids. In a control set of trials in which no phorids were added to either foraging tray, the size of foraging workers averaged over both foraging trays was significantly larger than in either the phorid or no-phorid tray of the manipulative experiments. This suggests that colonies can communicate the generalized presence of phorids in an area, which leads to a decrease in foraging by major workers. *S. invicta* workers retrieved an intermediate amount of food in the foraging trays of the control experiment compared with the phorid and no-phorid trays of the manipulative experiment. Moreover, the overall amount of food obtained in both foraging trays was similar for the manipulative and control experiments, suggesting that the *S. invicta* colonies were able to compensate for harassment by phorids by altering their foraging strategy, which resulted in no net loss of food retrieved. When *S. invicta* was paired with *S. geminata* (F.) in interference competition experiments, phorid flies had no effect on the outcome of interspecific interactions. Phorids did not appear to be attracted to host workers once they were engaged in combat with enemy workers, and the spatial distribution of fighting was significantly different than the spatial distribution of parasitization attempts.

**KEY WORDS** *Pseudacteon tricuspis, Solenopsis geminata, Solenopsis invicta*, exploitative competition, interference competition, parasitism

Interspecific competition has been demonstrated to be an important factor limiting many ant populations (reviewed in Hölldobler and Wilson 1990). Predators, pathogens, and parasites may also affect the population dynamics of their prey or hosts (Hölldobler 1970, Edwards et al. 1974, Waller and Moser 1990, Briano et al. 1995, Gotelli 1996), particularly when such organisms also affect the competitive ability of ants (Feener 1981, MacKay 1982). The Phoridae is a diverse group of minute flies, many species of which are parasitoids of ants (Disney 1990). Phorid parasitoids affect their host ants directly, by developing inside infected workers, killing them in the process (Disney 1994, Porter et al. 1995a). Phorid parasitoids may also indirectly affect their hosts, by altering the behavior of workers and changing the outcome of interspecific competition (first described by Feener [1981]). The magnitude of such indirect effects may be greater than the direct effect of mortality for many phorid/ant species pairs (Feener 1988, Morrison 1999).

Both the exploitative and interference components of interspecific competition among ants may be affected by phorid flies, and the exact mechanisms by which phorids indirectly affect competitive interactions are potentially diverse. Phorids may influence worker behavior, caste size ratios, and number of worker ants recruiting to a food resource or enemy ant species (Feener 1981, 1988; Feener and Moss 1990; Feener and Brown 1992; Orr 1992; Orr et al. 1995; Porter et al. 1995b; Orr and Seike 1998; Folgarait and Gilbert 1999, Morrison 1999). The end result of such behavioral modifications is that the host ant species is placed at a competitive disadvantage relative to other ants in the community.

Because of their potential to modify competitive interactions, phorid flies of the genus *Pseudacteon* are being evaluated as biocontrol agents of imported fire ants (*Solenopsis invicta* Buren and *S. richteri* Forel) in the United States. Field observations in South America have revealed that the presence of *Pseudacteon* species...
decreased foraging of *Solenopsis saecissina* complex workers and at times contributed to species turnover at baits (Orr et al. 1995, 1997; Porter et al. 1995b; Folgarait and Gilbert 1999).

Although these field studies measured an overall effect of *Pseudacteon* phorids on *S. saecissina* complex species, a drawback of such studies is that it is not always possible to separate the two components of interspecific competition, and the mechanisms underlying the measured effects are not always apparent.

I conducted a series of laboratory experiments in which I could control variables such as state of hunger, colony size, colony caste ratio, and colony location of ants, as well as number, sex, age, and reproductive status of phorids. I quantified the effects of one *Pseudacteon* species, *P. tricuspis* Borgmeier, on the pure exploitative (i.e., competition for food in the absence of any other species) and pure interference (i.e., direct, aggressive interactions in the absence of food resources) components of interspecific competition in North American populations of *S. invicta*.

The following questions were addressed: (1) What is the magnitude of the effect of *P. tricuspis* on resource retrieval (i.e., exploitative competition component) in *S. invicta*? (2) What is the magnitude of the effect of *P. tricuspis* on aggressive interactions (i.e., interference competition component) between *S. invicta* and its congener *S. geminata* (F.)? (3) What are the important mechanism(s) underlying these effects? (4) How much of an overall limiting factor are *Pseudacteon* phorids to *Solenopsis* ant populations?

**Materials and Methods**

*Solenopsis invicta* colonies were collected from Travis County and *S. geminata* colonies were collected from Hays County, TX. All colonies were of the polygynous, or multiple queen, form. *P. tricuspis* were reared at the University of Texas at Austin’s Brackenridge Field Laboratory (BFL) from stock originally collected in Sao Paulo State, Brazil. This is the northern form of *P. tricuspis* as described by Borgmeier and Prado (1975). Reference specimens of *S. invicta, S. geminata,* and *P. tricuspis* have been placed in the Natural History Museum of Los Angeles County, CA; the Museu de Historia Natural, UNICAMP, Sao Paulo, Brazil; and at BFL.

All experiments were conducted between January and May 1999 at BFL. I set up experimental ant colonies consisting of a measured quantity of workers, brood, and a single queen. An electronic balance was used to weigh all workers and brood. The experimental colonies were placed in open trays (25 by 18 by 7 cm), the sides of which were coated with Fluon (polytetrafluoroethylene; ICI Fluoropolymers, Exton, PA) to prevent escapes. A petri dish (90 mm diameter, 15 mm high) containing damp plaster to maintain humidity was provided as a nesting chamber.

The mother colonies from which the experimental colonies were derived were kept in the laboratory at ~28°C for at least 2 wk before experimental colony formation, fed a standardized diet of water and sugar water ad libitum (in test-tubes plugged with cotton), and provided fresh frozen crickets every day. After initiation, the experimental colonies were maintained at ~28°C, provided with water and sugar water ad libitum, and fed two fresh frozen crickets every other day for 1 wk before the beginning of the experiments. All trays described below except the colony trays contained a layer of plaster on the bottom, which was moistened before the experiments to maintain a relative humidity of ~75%. All experiments were conducted at ~28°C.

**Resource Competition.** I set up experimental *S. invicta* colonies containing 4 g of workers and 2 g of brood. *S. invicta* workers were sieved through a screen with 0.85-mm openings, and each experimental colony received 2 g of "major" workers >0.85 mm and 2 g of "minor" workers <0.85 mm. This procedure resulted in a worker caste size ratio typical of monogyne colonies (see Discussion). Each gram of majors consisted of ~370 workers, and each gram of minors consisted of ~1,600 workers.

Experimental colonies were starved for 48 h before the beginning of the trials to produce a uniform state of hunger. Each tray containing an experimental colony was connected via a 12-cm length of opaque Tygon tubing (1 cm i.d.) to two adjacent foraging trays of the same dimensions on opposite sides of the colony tray, providing a choice of foraging in two equidistant trays containing the same food resource (Fig. 1). The trays were connected for 1 h before introduction of the food resource during which time ants were al-

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**EXPLOITATIVE COMPETITION SET-UP:**

**INTERFERENCE COMPETITION SET-UP:**

Fig. 1. Design of the exploitative (top) and interference (bottom) competition experiments.
lowed to explore both foraging trays. Two freeze-
killed crickets were then placed in the center of each
foraging tray, on white plastic cards (5 by 5 cm). The
crickets were stripped of the legs and antennae, which
could have been dismembered and carried away, and
were pinned down to prevent ants from moving them.
Glass tops were placed over both foraging trays.

Resource retrieval rates were measured by quanti-
fying precisely the amount of food retrieved in 60 min.
Crickets were weighed with an electronic balance
immediately before and after exposure to ants. In each
trial, a control set of crickets was left out for 60 min to
measure weight loss by desiccation. The average
weight loss of the control group was then subtracted
from the weight loss of the experimental group. I also
measured three potential mechanisms underlying this
effect: (1) worker activity, (2) number of workers
recruited to the bait, and (3) worker size. To quantify
worker activity, the number of workers crossing the edge
(nearest to the colony tray) of the 5 by 5-cm card were
counted for 2 min at 10-min intervals. To quantify
number of workers recruited to the bait, all workers on
the 5 by 5-cm cards at the end of the trials were
collected and counted. To quantify worker size, I
measured head widths in a random subsample of 25
workers taken from all workers collected from each
card at the end of the trials.

The average number of actively foraging workers throughout the course of the trials was likely to be
positively correlated with number of workers present
at the baits at the end of the trials. This potentially
strong correlation does not preclude testing for each
effect individually, however, because Pseudacteon
phorids may cause Solenopsis workers to remain im-
mobile for many minutes at a time (Porter et al. 1995b,
Orr et al. 1997, Morrison 1999). This effect on activity
may be manifested independently of number of workers
present.

In the first, or manipulative, set of experimental
trials, five mated, 1-d-old P. tricuspis females were
added to one of the foraging trays 10 min after the
introduction of the food resource. Not all phorids
actively attacking ants, and additional flies were added
time if necessary. I attempted to have at least two
phorids actively attacking workers at all times. No
phorids were added to the opposite foraging tray. The
trials lasted for 60 min after introduction of flies. The
same data were collected from the foraging tray with
phorids and the foraging tray without phorids in each
trial, and were compared with paired t-tests. Because
multiple comparisons were made within the same ex-
periment, the sequential Bonferroni method was used to
control the group-wide type I error rate (Rice 1989).

In a second, or control, set of trials, the same pro-
cedure was followed, except that no phorids were
added to either foraging tray. Paired t-tests revealed
no significant differences ($P > 0.05$) between the two
foraging trays for any of the four measured variables.
Thus, the values for each variable were averaged be-
tween the two foraging trays of the control experi-
ment, and compared with the values for the phorid
and no-phorid treatments in the manipulative experi-
ment, by a one-way analysis of variance (ANOVA).
The Bonferroni method of multiple comparisons with
a family confidence level of 90% was used to compare
the average values of the control experiment to both
the phorid and no-phorid treatments of the manipu-
lation experiment.

Although I attempted to have a constant number of
actively attacking phorids, there was an unavoidable
amount of variation among the trials in the number of
active flies. In foraging trays with phorids present (the
manipulative experiment), the number of actively at-
tacking phorids was counted for 1 min immediately
before and 1 min immediately after counting recruit-
ing ants, as described above. I averaged the number of
actively attacking flies in each trial and, in simple
linear regressions, regressed each of the four variables
described above on average number of attacking flies,
in four separate regressions, to see if more active flies
resulted in a significantly greater effect.

Interference Competition. I tested the effect of
phorids on short-term interference competition by
measuring the spatial dimensions of interspecific com-
bat between S. invicta and S. geminata. Experimental
colonies of S. invicta were set up as described previ-
ously. Workers of S. geminata are on average larger
than workers of S. invicta (Trager 1991), and previous
work has revealed that S. invicta wins interspecific con-
tests in the moderate to long-term when S. invicta
and S. geminata colonies are equivalent by biomass,
but this outcome is reversed when the colonies are
equivalent by worker number (Morrison 2000). This
difference was not significant in the short term, how-
ever, and the outcome of short-term interspecific in-
teractions was more equal when colonies were equiva-
 lent by worker number (Morrison 2000). Thus, I set
up S. geminata colonies that were equivalent in worker
number to the S. invicta colonies. I sieved S. geminata
workers through the 0.85-mm screen, and found that
each gram of “majors” consisted of ~190 workers, and
each gram of “minors” consisted of ~1,380 workers. I
then set up colonies consisting of 3.9 g of S. geminata
majors, and 2.3 g of S. geminata minors. This procedure
resulted in ~740 majors and ~3,180 minors per colony
tray, for both S. invicta and S. geminata.

A S. geminata colony and a S. invicta colony were
each connected to opposite ends of a larger (37 by 24
by 7 cm) tray via 12-cm lengths of opaque Tygon
tubing (1 cm i.d.). This tray contained eight opaque
walls that turned the central tray into a maze (Fig. 1).
The walls and sides of the tray were white, and coated
with Fluon to prevent the ants from escaping or scal-
ing the walls. The bottom of the tray was covered with
white plaster. A grid containing 72 squares, in nine
rows and eight columns, was marked off in the maze
tray. A gate coated with Fluon was placed in the center
of the tray. The S. geminata and S. invicta colonies were
equidistant from the gate, with 36 squares between the
gate and each colony tray.

Workers from each colony were allowed to explore
the maze tray for 15 min. In this time, workers of both
species traveled throughout the maze to the central
For the first three variables, the average values of the phorid treatments in the manipulative experiment were averaged between foraging trays, and no differences between the two trays in any of the measured variables were significant at α = 0.05 (paired t-tests). The interaction was also not significant (F = 0.96, df = 1, P = 0.33). The interaction was also not significant (F = 0.05, df = 1, P = 0.83).

Table 1. Effects of phorids on resource retrieval, and the underlying mechanisms, in S. invicta

<table>
<thead>
<tr>
<th>Mechanism</th>
<th>Mannitol retrieval (g)</th>
<th>No. of active workers</th>
<th>No. of workers at bait</th>
<th>Avg worker size (HW in mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Phors present</td>
<td>0.028 ± 0.016</td>
<td>142.0 ± 73.2</td>
<td>0.699 ± 0.084</td>
<td></td>
</tr>
<tr>
<td>Phorids absent</td>
<td>0.055 ± 0.029</td>
<td>189.8 ± 41.2</td>
<td>0.728 ± 0.090</td>
<td></td>
</tr>
<tr>
<td>P</td>
<td>0.0064*</td>
<td>0.0152*</td>
<td>0.3898</td>
<td></td>
</tr>
<tr>
<td>Avg of 2 trays</td>
<td>0.043 ± 0.018</td>
<td>180.2 ± 60.7</td>
<td>176.5 ± 56.0</td>
<td></td>
</tr>
</tbody>
</table>

* Significant at α = 0.05 by the sequential Bonferroni method. Four comparisons were made within the same experiment.

Resource retrieval was significantly greater in the phorid treatment compared with the no-phorid treatment (Table 1). Average worker size at the end of the trials, however, was larger for the control than either treatment of the manipulative trials.

In the control experiment, in which phorids were present in either tray, numbers represent means ± SD. P-values are from two-tailed, paired t-tests.
specific aggression. Workers of the two ant species began grappling with each other quickly after the gate was opened, clamping on to each other with their mandibles. Most phorids did not seem interested in attacking host workers attached to enemy workers. In fact, most of the phorids spent most of their time attempting to parasitize host workers recruiting to the battle from the colony tray. Thus, although the majority of fighting occurred in the center of the maze, the distribution of parasitization attempts was skewed toward the *S. invicta* colony tray (Fig. 3). This variation in the distribution of attacks versus the distribution of fighting was highly significant ($\chi^2 = 26.16, df = 8, P = 0.001$, chi-square test of homogeneity).

Phorids often hovered around the entrance tube to the colony, attempting to parasitize workers entering the maze. In some experimental trials, *S. invicta* recruitment to the fighting was very low, and could have been a result of phorid presence, although this was not quantified.

**Discussion**

**Overview of Phorid/Ant Interactions.** A number of field studies have documented the effects of parasitic phorids on their host worker ants. *Apecephalus* phorids have been documented to affect both foraging and defense behavior of host *Pheidole* ants (Feener 1981, 1988), as well as the frequency of hitchhiking minim workers in the leaf-cutting *Atta colombica* (Feener and Moss 1990). *Neodohrniphora* phorids have been shown to influence caste ratios and numbers of foraging *Atta cephalotes* (Orr 1992, Feener and Brown 1993). *Pseudacteon* phorids (*P. pusillum* and an undescribed species) have been documented to decrease foraging in the Argentine ant, *L. humile* (Orr and Seike 1998).

Many recent studies of ant/phorid interactions have focused on *Solenopsis* fire ants and their associated *Pseudacteon* parasitoids. In South America, the presence of *Pseudacteon* flies that parasitize *S. saevissima* complex ants has been shown to decrease worker foraging, and contribute to food resources being lost to competing ant species (Orr et al. 1995, 1997; Porter et al. 1995b; Folgarait and Gilbert 1999). In Central and North America, *Pseudacteon* flies that parasitize *S. geminata* complex ants have also been documented to decrease food retrieval (Feener and Brown 1992, Morrison 1999). An effect of *Pseudacteon* phorids on interference competition involving *S. geminata* has not been found, however (Morrison 1999).

All of the above studies have been conducted in the field, with phorid and ant species native to the respective areas. Separating the exploitative and interference components of interspecific competition in the field is often difficult, however, as is precisely evaluating the magnitude of the effects. It may not be possible, for example, to manipulate the presence or abundance of phorids, or control for differences in the size and location of host ant colonies, or presence of enemy ants. Thus, the experiments described in this article represent the first detailed laboratory study of the effects of phorids on the pure exploitative and interference components of interspecific competition, and the underlying mechanisms.

**Exploitative Competition.** When *S. invicta* workers were given a choice to forage in trays with or without *P. tricuspis* flies, resource retrieval was 50% less in the tray with phorids. Significantly fewer workers actively
foraged in the tray with phorids. Fewer, and smaller, workers were present at the end of the trials in the tray with phorids, but these differences were not significant. In control trials, when no phorids were present in either tray, the amount of resource retrieved was intermediate to that of the phorid versus no-phorid treatments, indicating that the colonies were obtaining more food from the no-phorid tray to compensate for decreased food retrieval in the phorid tray. This is the first evidence that host ants may be able to compensate for diminished food retrieval caused by phorid harassment.

In nature, this mechanism may be manifested by a spatial shift to increased underground foraging during the day when phorids are active, or a temporal shift to increased aboveground foraging at night, when phorids are not active. A study of the diet of S. invicta and S. geminata revealed that a large proportion of their diet may be obtained from subterranean sources (Tennant and Porter 1991), and both species commonly forage diurnally as well as nocturnally (Glaborn and Phillips 1986, Morrison 1999).

Significantly larger workers foraged in the control trials than in either treatment of the experimental trials. Solenopsis workers appear to be able to communicate the presence of phorids to nestmates by alarm pheromones (C. G. Dall’Aglio-Holvorcem, unpublished data). Thus, the colonies may have been aware of the general presence of phorids in the area, and larger workers did not forage in the no-phorid trays because of the ultimate, rather than proximate, risk of parasitization.

In the foraging trays of the experimental set-up, there was no significant relationship between variation in the number of actively attacking phorids and variation in any of the measured variables. Although the presence of a single female is often sufficient to disrupt worker foraging at a localized food resource (Feener and Brown 1992, Orr et al. 1995), higher phorid densities have been associated with lower resource retrieval rates in the field (Morrison 1999). Variation in attack frequency among individual phorids may obscure this relationship, however. Orr et al. (1997) reported that the degree of response in workers was more closely related to number of attacks than amount of time that a phorid was present. Likewise, in the context of the laboratory experiments of this study, the degree of response of S. invicta may be more closely associated to the number of attacks than the number of phorids attacking. It is also possible that an effect of phorid number may emerge over a wider range of fly densities.

Although only females were used in the experimental trials, P. tricuspis males may have similar effects on worker behavior. P. tricuspis males are attracted to worker ants, apparently to find mates, and appear to feign attacks on workers (unpublished data), possibly to increase worker excitement and release of pheromones which may attract P. tricuspis females. The presence of both male and female Pseudacteon phorids has been documented to disrupt foraging of Solenopsis workers in the field (Feener and Brown 1992, Porter et al. 1995b).

**Interference Competition.** The presence of P. tricuspis had no effect on the outcome of short-term interspecific competition, based on the spatial location of fighting. Interspecific interactions between S. invicta and S. geminata usually involved workers of each species clasping each other with their mandibles and grappling for extended periods (several minutes to the end of the trials). At times, three or more workers were attached to each other. (Detailed descriptions of the interspecific interactions of S. geminata and S. invicta are given in Bhatkar [1988] and Morrison [2000].) The phorids did not appear interested in these clusters of workers. Pseudacteon phorids exhibit size-specific preferences for host ants (Morrison et al. 1997, Morrison and Gilbert 1998), and two or more workers grappling together probably do not fit their search image for hosts.

There was a significant difference between the spatial distribution of fighting and the spatial distribution of parasitization attempts. Most parasitism attempts occurred between the active fighting and the tube leading to the S. invicta colony tray, where individual S. invicta workers could be found. Thus, the effect of Pseudacteon phorids on the interference component of interspecific competition in the field is likely to depend upon the spatial location of interspecific interactions relative to the host Solenopsis colony. S. geminata and S. invicta use extensive underground tunnel systems (Markin et al. 1975), however, and are able to reach areas distant from the colony with little above-ground exposure. Thus, the effect of phorids on interference competition is likely to be relatively small in most cases. In a field study of interference competition between S. geminata and S. invicta at rich food resources, S. geminata workers were observed to travel only short distances above ground from underground tunnel entrances to the contested resources (Morrison 1999).

The identity of competing ant species may also be important in determining the effect of phorids on interference competition. If interspecific interactions with other ant species involve less grappling of workers attached to each other, the effect of phorids may be greater. For example, Monomorium is a genus found in sympatry with S. invicta that relies heavily on chemical defense, rather than physical grappling (Baroni-Urbani and Kannowski 1974). Such an interaction may result in more parasitization pressure on S. invicta, although the dispersal of airborne venom could negatively affect Pseudacteon parasitization.

The effects of phorids on interference interactions were evaluated over a relatively short period in this laboratory study. A previous study indicated that the ultimate winner (based on reduction of colony size) of interference interactions could usually, but not always, be predicted based on the short-term distribution of fighting (Morrison 1999). In the previous study, S. geminata and S. invicta workers were observed to fight for several days before such territorial disputes were resolved, and it was not practical to run the
experiments of the current study for such a long period. It is possible that phorids may have a greater effect over a longer period in nature, but any potential effects will be limited by the spatio-temporal dimensions of the interference interactions. In nature many interactions may not be accessible to phorids at all, such as fighting occurring underground or at night.

Implications for Biocontrol. In the first test of the effects of South American *Pseudacteon* phorids on resource retrieval by North American *S. invicta* populations, a single *P. tricuspis* female decreased food retrieval by 15% in laboratory trials, although the mechanisms underlying the decrease in food retrieval were not identified (Morrison 1999). It was qualitatively observed that few majors entered the foraging trays, however, and minors foraged largely unmonitored. Random samples of polygyne *S. invicta* were used, in which the average worker size was only 0.62 mm. *P. tricuspis*, however, prefers workers with a head width of ~0.93 mm (Morrison et al. 1997, Morrison and Gilbert 1998). The experiment in Morrison (1999) was designed differently than the current study, and did not allow a simultaneous choice of phorid or no-phorid food sources. Each colony was instead tested sequentially with phorid and no-phorid treatments.

In pilot trials of the experimental set-up of the current study, *P. tricuspis* females rarely attacked *S. invicta* workers in foraging trays when offered a random subsample of polygyne *S. invicta* workers. The most likely reason was that the foraging workers were too small. Only ~12% of the workers in the typical polygyne *S. invicta* colony in Travis County, TX, have head widths >0.93 mm (unpublished data). By sieving workers and adding a relatively larger proportion of majors, I obtained worker size distributions more typical of the monogyne form. In a previous study, the average head width of monogyne *S. invicta* workers was 0.86 mm (Morrison and Gilbert 1998). The screen used to separate *S. invicta* majors from minors had 0.85-mm openings. Natural monogyne colonies were not used because they are rare in central Texas. *P. tricuspis* is likely to have a larger effect on monogyne, rather than polygyne, *S. invicta* colonies. A smaller species of *Pseudacteon*, such as *P. obtusus* (Morrison and Gilbert 1999) or *P. curvatus* (S. D. Porter, 2000), apparently would be more effective in controlling polygyne *S. invicta* populations, all else being equal.

The results of the laboratory experiments elucidate the mechanisms by which *P. tricuspis* decreases short-term resource retrieval in *S. invicta*. Whether this will translate into long-term food limitation for the colony is difficult to predict. *S. invicta* workers never abandoned any baits in the laboratory trials, and revealed an ability to compensate for phorid harassment by foraging on alternate resources. The first report of the effect of *Pseudacteon* phorids on *Solenopsis* fire ant foraging in South America found evidence that phorid presence resulted in *S. invicta* abandoning baits to competing ant species (Orr et al. 1995). Such a strong suppressive effect may occur primarily during initial recruitment to food resources, however, and subsequent studies have found that after recruitment is established, enough workers usually remain at the resource in the presence of phorids to successfully defend the resource from competing ants (Porter et al. 1995a, Orr et al. 1997).

In field experiments conducted in central Texas with *S. geminata* and associated *Pseudacteon* phorids, *S. geminata* workers were observed never (Morrison 1999) or only very rarely (Morrison et al. 2000) abandoning a food resource to competing ants, even under harassment by multiple *Pseudacteon* females. Some workers (primarily minors) remained at the food resource, guarding it and covering it with soil and bits of debris, while other workers tunneled under the food resource, decreasing exposure to phorids. It is difficult to make a generalized prediction regarding the overall effect of *Pseudacteon* phorids on *Solenopsis* ants. All studies to date have focused on short-term, behavioral effects lasting at most several hours (Feener and Brown 1992; Orr et al. 1995, 1997; Porter et al. 1995b; Folgarait and Gilbert 1999; Morrison 1999). *Solenopsis* workers exhibit a number of characteristics or frequently observed behaviors that appear to decrease the impact of *Pseudacteon* phorids, however, and may be to some degree adaptations to *Pseudacteon* parasitism pressure. These include underground foraging tunnels or covered walkways, covering food with dirt or debris, and defensive posturing (reviewed in Morrison 1999). Altering foraging strategies to avoid phorid flies, as revealed in this study, may also be frequently employed. Yet the presence of *Pseudacteon*-specific defensive behaviors is evidence that these parasitoids are capable of having population-level impacts on their *Solenopsis* hosts, or such behaviors would not have evolved. Long-term field studies are needed to assess the magnitude of the population-level effects of *Pseudacteon* phorids on *Solenopsis* fire ants.

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