

## Host Location Behavior in a Parasitoid of Imported Fire Ants

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*Female parasitoids use a hierarchy of cues to locate suitable hosts. We conducted a series of field observations and experiments to examine host location behavior in *Pseudacteon tricuspis* Borgmeier, a phorid parasitoid of *Solenopsis invicta* Buren worker ants. The parasitoids were frequently attracted to host workers at disturbed colonies, but were almost never attracted to host workers foraging at baits. When conspecific nonnestmate workers were introduced to baits, resulting in aggressive interactions, parasitoids appeared at the majority of baits. Moreover, larger numbers of parasitoids appeared at baits to which greater numbers of nonnestmate workers had been added. Addition of nonnestmate workers to disturbed colonies resulted in increased numbers of parasitoids attracted. *Pseudacteon tricuspis* did not display a pattern of uniform distribution at disturbed colonies but often was very abundant at some colony locations while absent or rare at nearby colony locations. *Solenopsis invicta* workers release alarm pheromones in aggressive interactions with nonnestmates, and this substance is likely an important chemical cue that attracts *P. tricuspis* flies to host workers from a distance.*

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## INTRODUCTION

Female parasitoids rely on a hierarchy of physical or chemical stimuli to locate suitable hosts (Vinson, 1976; Weseloh, 1981). Such host searching behavior is strongly influenced by natural selection, and has been used in tests of optimal foraging theory (Godfray, 1994). The small size of many parasitoid species, however, makes field observations difficult, often restricting such work to the laboratory (van Alphen and Vet, 1986; but see Casas *et al.*, 2000). Nearly 78% of the estimated number of parasitoid species are hymenopterans (Feener and Brown, 1997), and almost all recent research on insect parasitoids has focused on this taxon (Waage and Greathead, 1986; Godfray, 1994; Hawkins and Sheehan, 1994).

Dipterans comprise approximately 20% of the known parasitoid species and appear to be exceedingly diverse in their biology and interactions with their hosts, although they have been studied far less intensively than their hymenopteran counterparts (Feener and Brown, 1997). Many species in the dipteran family Phoridae are parasitoids of ants (Disney, 1990, 1994) and represent an interesting group for the study of host location. Although adult phorids are small, many species attack live workers and may congregate in the vicinity of their hosts in relatively large numbers, making field observation possible. Parasitic phorid flies are known to use olfactory cues in ant host location (Donisthorpe, 1927; Brown and Feener, 1991; Morehead and Feener, 2000). Studies of several *Pseudacteon* species that are parasitoids of *Solenopsis* fire ants suggest that these parasitoids initially locate their hosts from a distance by olfaction and then switch to visual cues at close distances to inject an egg into a live worker ant (Gilbert and Morrison, 1997; Orr *et al.*, 1997; Porter, 1998b; Porter and Alonso, 1999).

Here we present, from a series of field observations and experiments, the first systematic account of host location behavior in a *Pseudacteon* species (*P. tricuspis* Borgmeier) that is a parasitoid of a *Solenopsis* fire ant (*S. invicta* Buren). These two species represent a unique dipteran parasitoid-host ant interaction. *S. invicta*, an invasive pest, was unintentionally introduced into the United States in the 1930s (Callcott and Collins, 1996), escaping from numerous *Pseudacteon* parasitoid species in South America. *P. tricuspis* has been recently introduced into the United States as a potential biocontrol agent (Porter *et al.*, 2004). Thus, an understanding of the host location behavior of *P. tricuspis* represents not only a valuable contribution to our knowledge of dipteran parasitoid-host interactions, but also insight into the potential efficacy of this species as a biocontrol agent.

To better understand the basic patterns of host location in *P. tricuspis* in the field, we addressed the following five questions: (1) Is *P. tricuspis* differentially attracted to worker ants at colony disturbances compared to

foragers at rich food resources? (2) Is *P. tricuspsis* differentially attracted to foragers at rich food resources in the presence vs. absence of intraspecific interactions? (3) Does increasing the intensity of interspecific interactions at rich food resources affect the number of *P. tricuspsis* individuals attracted? (4) Is *P. tricuspsis* differentially attracted to workers at colony disturbances in the presence vs. absence of intraspecific interactions? and (5) Are some *S. invicta* colony locations more attractive than others to *P. tricuspsis*?

## MATERIALS AND METHODS

This study was conducted at four sites in Alachua County, Florida. Site A was located in a mown field near a small creek (29°38'N, 82°23'W). Sites B and D were located in grazed pastures near ponds (29°49'N, 82°25'W, and 29°42'N, 82°28'W, respectively). Site C was located in a grazed pasture near a wooded area (29°49'N, 82°25'W). All four sites had monogyne (i.e., single queen) colonies of imported fire ants, *S. invicta*, and introduced phorid flies, *P. tricuspsis*. Introductions of *P. tricuspsis* were first made at site A in September 1997, at sites B and C in April 1998, and at site D in November 1999 (Porter *et al.*, 2004). No other phorids that parasitized *S. invicta* were present at any sites.

Field observations and experiments addressing the questions above were conducted during the following periods at the following sites: questions 1, 2, and 4: October–December 2000, sites A, B, and C; question 3: July–August 2001, sites A and B; and question 5: July–October 2001, sites A, B, and D. Because adult *Pseudacteon* flies are not active on cool days (<20°C [Morrison *et al.*, 1999, 2000]), all field experiments were conducted when air temperatures were  $\geq 25^\circ\text{C}$ .

*Question 1—Attraction to Workers: Colony Disturbances vs. Rich Food Resources.* We set out transects of 30 baits, spaced 5 m apart, at each of the three sites. Baits consisted of  $\approx 4$ -g sections of Oscar Mayer Wieners (pork and turkey) placed on laminated 5  $\times$  5-cm cards. Baits were monitored for the presence of *P. tricuspsis* at 20-min intervals for 1 h. Baits that were not discovered or did not elicit moderate recruitment were excluded from the analyses. Only baits at which >75 *S. invicta* workers (estimated) were present at the end of the hour or at which phorids were observed at some point were included. Baits with <75 workers were included if phorids were present because the presence of phorids usually decreases worker abundance at baits (Orr *et al.*, 1995; Porter *et al.*, 1995). Baits to which *S. invicta* recruited usually had >200 workers (estimated) at the end of the hour.

We disturbed 25–30 *S. invicta* colonies at each site by digging a crater  $\approx 20$  cm in diameter and  $\approx 15$  cm deep with a small shovel. We monitored

the disturbed colonies for *P. tricuspis* at 10-min intervals for 30 min. The colony disturbances were conducted at different times than the baiting trials, to prevent exposure of the flies to two different types of host stimuli simultaneously. We used chi-square tests of homogeneity (Daniel, 1990) to determine whether significant variation existed in attraction of flies to colony disturbances versus attraction of flies to foragers at baits. Separate tests were conducted for each of the three sites.

*Question 2—Attraction to Workers at Rich Food Resources: Presence vs. Absence of Intraspecific Interactions.* We set out transects of 30 baits at each of the three sites as described above. After 1 h, we identified baits to which *S. invicta* was recruiting ( $>75$  workers; although  $>200$  were usually present). To half of these baits we added  $\approx 200$  nonnestmate *S. invicta* workers transported to the field from a (monogyne) laboratory colony. The remaining baits were not altered. The abundance of added workers was determined by weighing workers and estimating numbers based on a previously determined weight–abundance relationship. Treatments were alternated along the transect, with every other bait receiving non-nestmate workers. We monitored the baits for the presence of *P. tricuspis* at 15-min intervals for 45 min. Chi-square tests of homogeneity were employed as in question 1.

The manipulation of the nonnestmate ants associated with introductions to baits (questions 2 and 3) could have triggered the release of alarm pheromones independent of aggressive interactions. Thus, we conducted two experiments to determine whether such manipulations in the absence of competing ants attracted phorids. In the first, we set out 20 cards (as above) with baits on every other card. After  $>75$  *S. invicta* workers (but usually  $\approx 200$ ) were present at each baited card,  $\approx 250$  nonnestmate *S. invicta* workers from a laboratory colony (estimated by weighing, as above) were introduced to all cards. Cards were monitored for the presence of phorids at 5-min intervals for 20 min. Because introduced ants often abandoned the cards before the end of 20 min, a second experiment was conducted in which the cards were contained within petri dishes, the sides of which were coated with Fluon (polytetrafluoroethylene; AG Fluoropolymers, Chadds Ford, PA) to prevent nonnestmate ants from easily leaving the cards. A small hole was placed in the side of the petri dish to allow ants from the field site to find and recruit to the baits. These experiments were conducted at site D.

*Question 3—Attraction to Workers at Rich Food Resources: Abundance Effects.* We laid out baits as described above (question 1) and, after 35–45 min, identified baits with high densities ( $>200$  workers) of *S. invicta*. We then added nonnestmate *S. invicta* workers from a (monogyne) laboratory colony. Five different treatments were employed, consisting of 5, 25, 50, 100, and 250 workers. Groups of 5 and 25 workers were counted individually;

larger treatment sizes were estimated by weighing (as above). Baits were monitored for *P. tricuspis* at 5-min intervals for 20 min. Eight replications of each treatment were obtained per site.

Because *P. tricuspis* was absent at many baits (i.e., the data set contained many zeros), we used Kruskal–Wallis tests to compare fly densities. For the dependent variable, we examined both average number of flies present (over four observation periods) and maximum number of flies present at any single observation interval for each treatment level. Maximum number of flies is probably a more realistic measure of parasitism pressure because once phorids were attracted to hosts they usually remained in the area as long as the hosts were active. During some observations, however, some flies may have been in the vicinity of baits but simply not seen due to dense vegetation or perching. Separate analyses were conducted for each dependent variable (maximum and average number of flies) and for each site. Following the Kruskal–Wallis procedures, we used multiple pairwise comparisons of all treatment levels at an experimentwise error rate of  $\alpha = 0.15$  (Daniel, 1990) to determine which treatment levels were different.

*Question 4—Attraction to Workers at Colony Disturbances: Presence vs. Absence of Intraspecific Interactions.* We disturbed 10 *S. invicta* colonies at each site by digging into them with a small shovel, as above. All colonies were at least 5 m apart. We added  $\approx 300$  *S. invicta* workers (determined by weighing, as above) from a (monogyne) laboratory colony to each of five field colonies selected at random; the remaining five were not treated. We monitored all 10 colony disturbances for *P. tricuspis* at 10-min intervals for 30 min.

Because *P. tricuspis* was present at almost all colonies in this experiment (100% of the treatment and 80% of the control colonies), our analyses focused on the number of flies at colony disturbances. We used a two-way ANOVA to compare abundances of *P. tricuspis* following a log transformation of the data.

*Question 5—Relative Attractiveness of Different Colonies.* We disturbed 10 *S. invicta* colonies of a similar size and shape, spaced at least 5 m apart, by digging into them with a small shovel (as in question 1, above). We used aspirators to collect all *P. tricuspis* individuals attracted to each disturbed colony for 30 min. At the end of 30 min, if there were still *P. tricuspis* flies hovering over the colony (i.e., too many to collect within the specified time), we counted the number of remaining flies. We then counted and sexed all flies that had been aspirated for each colony.

We measured the areas and volumes of the earthen mounds constructed by the colonies to test whether the number of flies attracted was related to the number of workers present. The total number of workers in a *S. invicta* colony is strongly correlated with the mound size (Tschinkel, 1993; Macom

and Porter, 1996). We calculated the two-dimensional area of the mounds by using the formula for an ellipse [ $A = \pi * (a/2) * (b/2)$ , where  $a$  = length (long axis) and  $b$  = width (short axis)]. The volume of the mounds was calculated using the formula for half a spheroid [ $V = 2/3 * \pi * (a/2) * (b/2) * c$ , where  $c$  = mound height]. Number of flies was regressed against both mound area and volume in separate simple linear regressions.

Each site was sampled four times at 1-month intervals. We used chi-square goodness-of-fit tests (Daniel, 1990) to determine whether the distribution of flies at colonies differed from a uniform pattern. Separate tests were conducted for each date at each site. Only dates on which  $\geq 50$  flies were present at a site were included in the analyses.

## RESULTS

*Question 1: Is P. tricuspid Differentially Attracted to Worker Ants at Colony Disturbances Compared to Foragers at Rich Food Resources? Pseudacteon tricuspis* was not attracted to any of the 62 total baits (summing over all sites) that contained  $>75$  *S. invicta* workers. *P. tricuspid* was found at the vicinity of two baits, however, with smaller numbers of workers. At one, fighting between *S. invicta* and another ant species was observed. At the other, no aggressive interactions were apparent at the bait during our observation intervals, although such interactions may have occurred in the surrounding vicinity. Very low abundances of *S. invicta* at this bait (always  $<20$  workers, even after one hour) may have resulted from the presence of other ant species, phorid flies, or both.

In all other cases, we never observed *P. tricuspid* to be attracted to foragers of *S. invicta*, even when large numbers ( $>200$  workers) were present. Nor were phorids ever observed along foraging trails between baits and foraging tunnel entrances, although it was not always possible to observe the entire length of these trails through the vegetation. In contrast, the majority of colony disturbances attracted *P. tricuspid*. The differences were highly significant at all three sites (Table I).

*Question 2: Is P. tricuspid Differentially Attracted to Foragers at Rich Food Resources in the Presence vs. Absence of Intraspecific Interactions?* When nonnestmate *S. invicta* workers were added to baits already occupied by *S. invicta* foragers, resulting in aggressive intraspecific interactions, *P. tricuspid* appeared at the majority of baits. In contrast, *P. tricuspid* never appeared at baits without intraspecific interactions. The differences were highly significant at all sites (Table II).

In the experiments to determine whether introductions of ants per se could result in attraction of phorids, introductions of nonnestmate *S. invicta*

**Table I.** Number of Occasions on Which *Pseudacteon tricuspidis* Flies Were Attracted or Not Attracted to Host *Solenopsis invicta* Ants at Colony Disturbances or Baits, in the Absence of Competition from Other Ant Colonies

Site	Colony disturbances		Baits		$\chi^2$	P
	Flies present	Flies absent	Flies present	Flies absent		
A (mown field)	18	12	1	27	20.94	0.0001
B (pasture near pond)	14	11	0	22	17.55	0.0001
C (pasture near woods)	20	10	1	13	13.56	0.0002

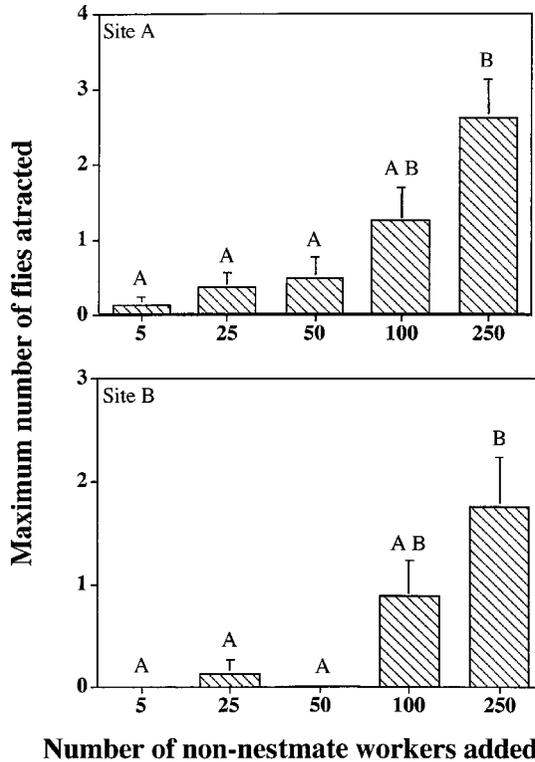
workers to cards without competing *S. invicta* workers never attracted phorids. In contrast, when interspecific interactions were staged at baits, phorids appeared at 10 of 10 baits in experiment one (cards only) and 8 of 10 baits in experiment two (cards within petri dishes). This demonstrates that phorids were attracted to cues resulting from aggressive interspecific interactions and not simply from agitation of ants resulting from the introduction procedure.

*Question 3: Does Increasing the Intensity of Intraspecific Interactions at Rich Food Resources Affect the Number of P. tricuspidis Individuals Attracted?* In general, the more nonnestmate workers added to *S. invicta* foragers at rich food resources, the more *P. tricuspidis* individuals were attracted (Fig. 1). Significant differences among the treatment levels existed at both sites for both maximum number of flies present ( $P = 0.0064$  for site A,  $P = 0.0105$  for site B; Kruskal–Wallis tests) and average number of flies present ( $P = 0.0063$  for site A,  $P = 0.0123$  for site B). Multiple pairwise comparisons of all treatment levels revealed the same results at both sites. Each of the three smallest groups of nonnestmate workers ( $n = 5, 25,$  and  $50$ ) was significantly different from the largest group of workers ( $n = 250$ ; Fig. 1). The results for

**Table II.** Number of Occasions on Which *Pseudacteon tricuspidis* Flies Were Attracted or Not Attracted to Host *Solenopsis invicta* Ants at Baits

Site	Fighting <sup>a</sup>		No fighting		$\chi^2$	P
	Flies present	Flies absent	Flies present	Flies absent		
A (mown field)	9	5	0	12	11.80	0.0006
B (pasture near pond)	7	4	0	12	10.98	0.0009
C (pasture near woods)	7	0	0	6	13.0	0.0003

<sup>a</sup>“Fighting” indicates that nonnestmate *S. invicta* workers were added to baits to induce intraspecific interactions.



**Fig. 1.** Numbers of *P. tricuspis* flies attracted to baits for varying intensities of intraspecific interactions. Bars represent 1 SE. Treatments with different letters were significantly different by a multiple pairwise comparison of all treatment levels at an experimentwise error rate of  $\alpha = 0.15$  following a Kruskal–Wallis test (Daniel, 1990).

maximum number of flies are shown; the comparisons of average number of flies were similar.

*Question 4: Is P. tricuspis Differentially Attracted to Workers at Colony Disturbances in the Presence vs. Absence of Intraspecific Interactions?* *Pseudacteon tricuspis* appeared in higher densities at colony disturbances where nonnestmate *S. invicta* workers were added, resulting in intraspecific interactions (Fig. 2). There was a significant effect of treatment (addition of nonnestmate ants) ( $P = 0.0001$ ) but no effect of site ( $P = 0.33$ ). The interaction term was not significant ( $P = 0.61$ ).

*Question 5: Are Some S. invicta Colony Locations More Attractive Than Others to P. tricuspis?* The total number of flies attracted to 10 disturbed

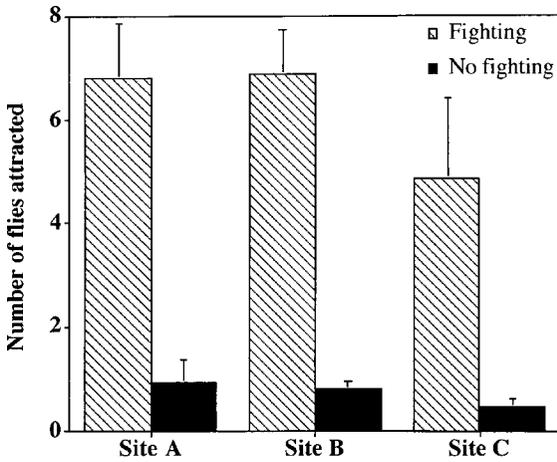


Fig. 2. Numbers of *P. tricuspid* flies attracted to 10 disturbed *S. invicta* colonies with and without intraspecific interactions ( $n = 5$  for each), at three different sites. Bars represent 1 SE.

colonies often varied greatly from site to site and date to date (Table III). At all sites and dates, however, the distribution of flies attracted to colony disturbances was significantly different from a uniform distribution.

No significant correlation was found between mound area or mound volume and *P. tricuspid* abundance for any site or date (all  $P$ 's  $\gg 0.05$ ). Thus

Table III. Numbers of Flies Present at 10 Disturbed *S. invicta* Mounds

Site date	No. Total flies at 10 mounds	Max. No. flies per mound	Min. No. flies per mound	$\chi^2$	$P$	Sex ratio
Site A						
July	54	13	0	33.7	<0.0001	3.0
September	62	22	0	68.3	<0.0001	2.9
October	181	75	0	260.8	<0.0001	2.2
Site B						
July	122	44	0	144.0	<0.0001	4.2
October	113	26	4	39.1	<0.0001	1.6
Site D						
July	122	51	0	200.0	<0.0001	3.1
September	196	39	5	55.2	<0.0001	2.9
October	453	81	9	173.6	<0.0001	4.2

Note. Chi-square goodness-of-fit tests were used to test whether the spatial pattern of parasitoid abundance differed significantly from a uniform distribution ( $df = 9$  for all). All comparisons were significant ( $P < 0.05$ ) after correcting for multiple comparisons by the sequential Bonferroni method (Rice 1989). Sex ratio is numbers of males per female.

there is no evidence that the number of host workers in the colony affected the number of flies attracted, at least within the range of colony sizes tested. Both males and females were found at disturbed colonies, and males always outnumbered females by a ratio of two to four males for every female.

## DISCUSSION

*Mechanisms of Host Location.* *Pseudacteon* phorids appear to use olfactory cues to locate host *Solenopsis* workers from a distance (Gilbert and Morrison, 1997; Orr *et al.*, 1997; Porter and Alonso, 1999). The chemical signals released by worker ants in our field observations and experiments varied both qualitatively and quantitatively. Workers foraging at baits would have released recruitment pheromones traveling from the bait back toward the colony, whereas workers at disturbed colonies or those involved in intraspecific interactions would have released alarm pheromones or venom alkaloids. Workers at baits, although usually numbering in the hundreds of individuals, represented only a small fraction of the workers present at colonies, so that a greater amount of chemical signal would have been released from disturbed colonies. Additionally, in the baiting trials in which increasing numbers of nonnestmate workers were added, greater quantities of defensive chemicals would have been released as the number of aggressive interactions increased.

These field results suggest that *P. tricuspis* is strongly attracted to host worker alarm pheromones or other defensive compounds but not to recruitment pheromones or chemical signals associated with foraging activities. In the rare instances in which *P. tricuspis* was found at baits where nonnestmate workers had not been added, other species of ants were present in the vicinity of the baits and interspecific interactions could not be ruled out. The results also indicate that a positive correlation exists between the amount of chemical signal released and the number of flies attracted.

*Pseudacteon tricuspis* is also attracted to mating flights of host *Solenopsis* ants (Pesquero *et al.*, 1993). The male and female alates initiate heightened activity among workers by releasing excitant pheromones, and workers in turn release alarm pheromones (Obin and Vander Meer, 1994; Alonso and Vander Meer, 1997). Thus the observed attraction to mating flights is consistent with the chemical mechanism of alarm pheromone underlying the attraction of *P. tricuspis* to hosts.

Laboratory experiments conducted with *P. tricuspis* and *S. invicta* have yielded complementary results to those found in the field, documenting increased fly activity in response to alarm pheromones released by their hosts, but not to extracts of venom alkaloids or recruitment pheromones

(R. Vander Meer and S. Porter, unpublished data). In an analogous ant-phorid parasitoid system, an investigation of attraction of *Apocephalus paraponerae* to its host *Paraponera clavata* revealed that the parasitoids were attracted to chemicals produced in the mandibular gland, which serve as alarm pheromones in many ant species (Feener *et al.*, 1996).

Perhaps the most puzzling result presented here is that large numbers of *P. tricuspis* were present at some disturbed colony locations, while few or none were present at nearby colony locations. The flies may simply be distributed unevenly in response to some microhabitat factor. Alternatively, the flies may be more abundant in the vicinity of colonies that have experienced a recent disturbance or a mating flight, having been attracted to these colony locations previously and remaining in the vicinity. Another, yet uninvestigated, possibility is that *P. tricuspis* may somehow signal conspecifics to congregate, analogous to some hymenopteran parasitoids (van den Assem, 1986).

Whatever the mechanism, such congregation could be adaptive in finding mates. Mating in *P. tricuspis* occurs in flight (Porter *et al.*, 1997). Both sexes appear to be attracted to host ants and mating has been observed over disturbed colonies and at host ant mating flights (L.W.M., personal observations). Males of a number of phorid parasitoids of ants are attracted to hosts apparently for finding mates (Feener and Brown, 1997). Thus, it may be advantageous for flies to congregate at certain colonies rather than to disperse randomly or uniformly among colonies. This would be especially important in scenarios where host colonies are abundant but flies are rare.

*Host Location in Other Pseudacteon Species.* The pattern of host location behavior presented here for *P. tricuspis* does not appear to characterize host location behavior in all *Pseudacteon* fire ant parasitoids. Eighteen *Pseudacteon* species in South America and nine *Pseudacteon* species in North and Central America are known parasitoids of *Solenopsis* ants (Porter, 1998a; Porter and Pesquero, 2001). Two *Pseudacteon* species native to Texas, *P. browni* Disney and *P. bifidus* Brown & Morrison, were frequently attracted to host workers of the tropical fire ant, *S. geminata* (F.), at baits in the absence of any competitive interactions (Morrison, 1999). These two species were also frequently attracted to colony disturbances (Morrison *et al.*, 1999).

In South America, numerous *Pseudacteon* species have been reported attacking foraging host *Solenopsis* workers at baits or along foraging trails (Williams and Banks, 1987; Orr *et al.*, 1995, 1997; Porter *et al.*, 1995; Folgarait and Gilbert, 1999). Thus far, however, the only attempt to describe the variation in host location behavior in *Pseudacteon* parasitoids of fire ants is the work of Orr *et al.* (1997), conducted at the community level. Orr *et al.* (1997) found that some *Pseudacteon* species were more commonly found at disturbed mounds, while others were more frequent at foraging trails.

*Pseudacteon tricuspis* was more frequently encountered at disturbed mounds than foraging trails, although Orr *et al.* (1997) were not always able to distinguish *P. tricuspis* from its congener *P. litoralis*.

In other studies conducted in South America, *P. tricuspis*, among other *Pseudacteon* species, has been reported to attack *Solenopsis* workers along foraging trails (Porter *et al.*, 1995; Folgarait and Gilbert, 1999). Other species of ants, and potential interspecific interactions, were apparently present in the vicinity of the trails, however. Numerous species of *Pseudacteon* that parasitize *Solenopsis* ants exist sympatrically in South America, and because of difficulties involved in field identification, studies conducted there have often grouped *Pseudacteon* species together and focused on collective effects on ant foraging (Porter *et al.*, 1995; Folgarait and Gilbert, 1999). A limitation of such an approach is that it obfuscates differences in behavior among *Pseudacteon* species. An advantage of our study was that the focal parasitoid species was the only parasitoid species present.

It is perhaps not surprising that such variation in host location behavior exists in this parasitoid, particularly in South America, where multiple *Pseudacteon* species are often present in the same community parasitizing the same host *Solenopsis* species. Patterns of host-specificity in parasitic phorids may be related to the degree of species specificity in the pheromones of their hosts, and selection by phorids for increased specificity of host pheromones could result in increased diversity of parasitoid lineages (Brown and Feener, 1991). Multiple *Pseudacteon* species parasitizing the same host may coexist by partitioning host resources along different axes. For example, *Pseudacteon* species are known to parasitize workers of different size classes (Morrison *et al.*, 1997; Morrison and Gilbert, 1998) and be active at different times of the day (Pesquero *et al.*, 1996).

Phorids that parasitize other genera of ants also appear to be attracted to chemicals released by their hosts during interspecific interactions. *Pseudacteon pusillus* flies were attracted to host *Linepithema* workers in greater numbers at baits in the presence of competing ants than at baits that were not contested (Orr *et al.*, 2003). Similar results have been reported for *Apoccephalus* phorids and host *Pheidole* workers (LeBrun and Feener, 2002). In both cases, phorids were attracted in relatively low numbers to hosts foraging in the absence of interspecific competition, suggesting that a combination of recruitment and alarm pheromones are used by these species of parasitoids in host location. In contrast, we found that *P. tricuspis* was almost never attracted to host *S. invicta* foraging activity *per se*. Thus, phorid parasitoids of ants in general may utilize more than one type of pheromone to locate hosts, with the relative importance of multiple cues varying among species.

*Implications.* It has been suggested that phorid flies may mediate interspecific interactions among ants strongly enough to affect diversity patterns

at the community level (Feener, 1981, 2000) and that phorid parasitoids could be used as biocontrol agents of pest ants (Feener and Brown, 1992). A number of South American *Pseudacteon* species are currently being evaluated for control of imported fire ants in the United States (see reviews by Porter, 1998a; Morrison, 2000a), and *P. tricuspis* is now well established in Florida (Porter *et al.*, 2004). Studies of host location behavior, among other aspects of phorid biology, are important as they indicate which species may be most effective or which suite of species would complement each other in a biocontrol program. For example, some *Pseudacteon* species (e.g., *P. tricuspis*) may be more likely to influence aggressive interactions involving their hosts, whereas others may primarily affect foraging efficiency.

Most studies of phorid impacts on host ants have focused on the effects of phorids on host foraging behavior (Feener and Brown, 1992; Orr, 1992; Orr *et al.*, 1995, 1997; Porter *et al.*, 1995; Folgarait and Gilbert, 1999; Tonhasca *et al.*, 2001). Relatively few studies, however, have investigated the effects of phorids on direct interspecific interactions between their hosts and other ants. In laboratory and field studies comparing both potential effects of *Pseudacteon* phorids on *Solenopsis* ants, the flies strongly impacted host foraging success, although no evidence was found to indicate that the outcome of interspecific interactions was affected, at least within the dimensions of the experiments (Morrison, 1999, 2000b). Other species of phorids have been found to affect the defensive behavior of their hosts, however, in interactions with competing ant species (Feener, 1981, 1988).

In the laboratory, *P. tricuspis* introduced into small foraging chambers parasitized *S. invicta* and disrupted foraging even in the absence of enemy workers (Morrison, 2000b). Thus it appears that while *P. tricuspis* is not attracted over great distances by the foraging activities of its host, once it is in the near vicinity it uses visual cues or possibly some type of close-range olfactory signals to recognize its host, and it will then parasitize foraging workers. Because *P. tricuspis* is not attracted to *S. invicta* foraging *per se* in the field, any indirect effects this species may have on target fire ant populations will be mediated through interference with activities other than foraging, unless interspecific interactions occur at the food resources.

The use of alarm pheromones as cues in host location may be adaptive to *P. tricuspis* if host *S. invicta* workers are more abundant or more available for parasitization in situations where alarm pheromones are released. Foraging *Solenopsis* workers react dramatically to the presence of *Pseudacteon* phorids at rich food resources, leading to decreases in the abundance, size, and activity of workers in the vicinity of the resource and ultimately to lower host availability (Feener and Brown, 1992; Orr *et al.*, 1995; Porter *et al.*, 1995; Folgarait and Gilbert, 1999; Morrison, 1999, 2000b). Conversely, the parasitization avoidance behavior observed in workers at food resources is largely

absent in the context of aggressive interactions (Morrison, 1999, 2000b). Thus worker ants involved in fighting may represent a richer host resource than workers involved in foraging. Given that host location cues vary among *Pseudacteon* species in South America (Orr *et al.*, 1997), it is of interest that *P. tricuspis* is frequently the most common species in the *Pseudacteon* assemblage (Fowler *et al.*, 1995; Pesquero *et al.*, 1996; Orr *et al.*, 1997; Porter, 1998a). This differential abundance may be due, at least in part, to relatively greater success in locating suitable hosts.

Although all the mechanisms by which *Pseudacteon* phorids affect *Solenopsis* fire ants are as yet unknown, the results of these field observations and experiments elucidate conditions under which *P. tricuspis* would be most effective in a biological control program. For example, *P. tricuspis* would likely be more effective in areas where host *Solenopsis* colonies are frequently disturbed or where host *Solenopsis* workers commonly compete with other ants. The predominant social form of *Solenopsis* may also play an important role. In areas where the monogyne form is prevalent, intraspecific interactions among colonies would provide opportunities for *P. tricuspis* attack. In areas with primarily polygyne populations, the lack of intracolony aggression would lead to relatively fewer oviposition opportunities. Finally, the release of additional *Pseudacteon* species utilizing differing host location cues would increase the overall amount of parasitism pressure on pest *Solenopsis* species.

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