

# Trait-Mediated Effects of Parasitic Phorid Flies (Diptera: Phoridae) on Ant (Hymenoptera: Formicidae) Competition and Resource Access in Coffee Agro-ecosystems

STACY M. PHILPOTT<sup>1</sup>

Department of Ecology and Evolutionary Biology, 830 N. University Ave., University of Michigan, Ann Arbor, MI 48109

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**ABSTRACT** Predator effects on prey traits change competitive interactions between prey species affecting resource use. Parasitic phorid flies limit competitive-dominant ant activity, potentially mediating competitive interactions between ant species, changing competitive hierarchies, or affecting ant communities. I considered interactions between phorids (*Pseudacteon* sp.), their ant host (*Azteca instabilis* F. Smith), and co-occurring ant species in coffee agro-ecosystems testing whether phorids (1) limit *A. instabilis* recruitment activity, (2) affect competitive interaction between ant species, and (3) are associated with other species' resource access and therefore have the potential to change competitive hierarchies. I monitored recruitment of *A. instabilis* and other ants to baits over 90 min on canopy trees with or without phorids. *A. instabilis* were one-half as abundant with phorids. Other species gained access to baits 12 times more often and were only able to take over baits when phorids were present. Furthermore, many more species (13 versus 2) gained access to resources when phorids were present. These results indicate that phorids mediate competitive interactions between ant species and may influence ant communities by affecting resource availability. Considering that phorids limit *A. instabilis* attacks on herbivores and that ant species differ in effects on arthropod communities, phorids may have strong community-level effects in coffee agro-ecosystems.

**KEY WORDS** *Azteca instabilis*, *Pseudacteon* sp., multitrophic interaction, trait-mediated effect, competitive hierarchy

TRAIT-MEDIATED EFFECTS OF PREDATORS and parasites strongly regulate trophic interactions. In particular, predators or parasites may mediate competitive interactions between prey species and allow certain species to invade communities they are otherwise not able to (Werner and Peacor 2003). Parasites are often functionally similar to predators in trophic models and may also influence food webs through density or trait-mediated effects. For example, parasitic phorid flies specialize on a limited number of ant species and have strong negative effects on host ants—primarily by limiting foraging activity (Feener and Brown 1992, Orr et al. 1995, Folgarait and Gilbert 1999, Morrison et al. 2000, Philpott et al. 2004b). Theory predicts that phorid-induced changes in ant behavior may mediate ant diversity or change competitive hierarchies because phorid flies often attack competitively superior ants (Feener 2000). Empirical evidence shows that ants under attack by phorids are unable to dominate baits easily dominated in the absence of phorids (Orr et al. 1995) and that other ant species, not attacked by phorids, may take over resources more often (Feener

1981, LeBrun and Feener 2002). However, although some bait losses may result from phorid presence, phorids do not always change the outcome of interspecific contests (Morrison 1999, 2000, Morrison et al. 2000, Orr et al. 2003). Here, I examined whether phorid presence affects (1) host-ant foraging, (2) competitive outcomes between host- and nonhost ants, and (3) the number of nonhost ant species gaining access to resources.

In coffee plantations in southern Mexico, *Azteca instabilis* F. Smith (Hymenoptera: Formicidae), a competitively dominant ant, are attacked by phorid flies. *A. instabilis* are abundant, visible on ≈20% of shade trees in the canopy growing over coffee plants. They are aggressive and competitively superior to other ant species through both interference and exploitative interference competition (unpublished data), and depend on sugary resources (Davidson et al. 2003) that are common in coffee farms in the form of scale insects and *Inga* spp. (Fabaceae: Mimosoideae) extrafloral nectar. In the same farms, >60 ant species, in addition to *A. instabilis*, occur on shade trees and coffee plants, and although not often, sometimes are found on trees dominated by *A. instabilis* (Philpott 2004). Colony size and foraging behavior of *A. instabilis*, and potentially those of other ants, may be modified by a phorid fly (an undescribed species of

<sup>1</sup> Corresponding author. Smithsonian Migratory Bird Center, National Zoological Park, 3001 Connecticut Ave. NW, Washington, DC 20008 (e-mail: philpotts@si.edu).

*Pseudacteon* [Diptera: Phoridae]). This *Pseudacteon* sp. seems to be a specialist on *A. instabilis* in these sites (Philpott et al. 2004b). Phorids limit recruitment activity of *A. instabilis* workers and reduce *A. instabilis* abilities to prey on herbivores resulting in a species-level trophic cascade (Polis et al. 2000, Philpott et al. 2004b). Given that phorids in these sites have strong effects on host ants and lower trophic levels, I asked if phorids also change *A. instabilis*' competitive interactions with other ants. I investigated whether interactions of *A. instabilis* and other ant species change in the presence of phorid flies and if phorid presence is associated with increased resource access for other ant species coexisting with *A. instabilis*.

## Materials and Methods

**Site Description and Natural History.** I worked in two coffee farms of the Soconusco region of Chiapas, Mexico: (1) Finca Irlanda ( $15^{\circ}11'N$ ,  $92^{\circ}20'W$ ) and (2) Finca Belen ( $15^{\circ}15'N$ ,  $92^{\circ}22'W$ ). Both are shaded, organically managed farms, located between 950 and 1,150 m elevation, and receive  $\approx 4,500$  mm of rain annually. Each farm has  $>100$  species of shade trees, providing from 50 to 90% shade cover to a coffee understory (1–3.5 m height). *A. instabilis* ants commonly nest in the shade trees and forage in nearby coffee trees, thereby forming large patches of *A. instabilis* dominance (Philpott 2004). More than 60 other ant species occur in the shade trees, including other numerical dominants (*Camponotus senex textor* Forel, *C. novogranadensis* Mayr, and *Crematogaster* spp.) and other nondominant ants (*Pseudomyrmex* spp., *Cephalotes* spp., *Nesomyrmex* spp., *Procryptocerus* spp.) (Philpott 2004). *Pseudacteon* spp. phorid flies parasitize ants by laying eggs in ant bodies where larvae and pupae develop, thus killing their ant hosts (Feener 2000, Consoli et al. 2001). Phorid flies also affect host behavior by limiting ant foraging and food acquisition behaviors (Feener and Brown 1992, Porter et al. 1995, Folgarait and Gilbert 1999, Feener 2000, Wuellner et al. 2002, Philpott et al. 2004b).

**Effect of Phorids on Ant Recruitment.** In July 2003, I investigated whether phorid presence changed competitive interactions between *A. instabilis* ants and any co-occurring ants by observing the number of different ant species recruiting to tuna baits. Between 0800 and 1430 hours, I located shade trees on which *A. instabilis* were abundant and placed five tuna baits,  $\approx 5$  g each, 1.5 m above ground, on each tree. Every 2 min for 90 min, I recorded the number and species of each ant at baits and recorded if phorids were present or absent. In Finca Irlanda, I observed 27 trees with phorids and 16 trees without; in Finca Belen, I observed 22 trees with phorids and 6 trees without, for a total of 49 trees with and 22 trees without phorids. Each tree was only used once. Shade trees used represented several species and were selected solely on the presence of *A. instabilis* nests. The most commonly used were *Inga* spp. (26 trees), *Alchornea latifolia* Swartz (Euphorbiaceae) (15), *Corodia stellifera* L.M. Johnston (Boraginaceae) (5), *Yucca*

*elephantipes* Regel (Liliaceae) (4), *Nectandra* spp. (Lauraceae) (3), and *Quercus* spp. (Fagaceae) (3). Eleven additional tree species accounted for the other 18 trees sampled.

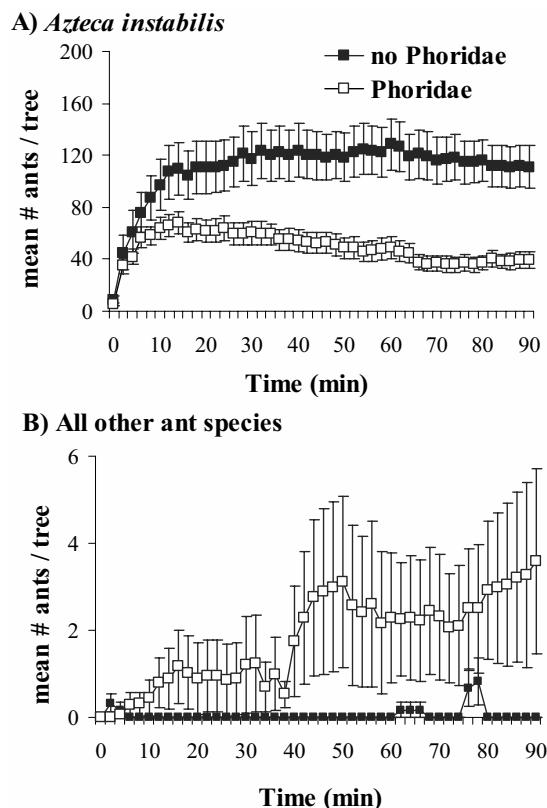
To compare recruitment of *A. instabilis* and other ants on trees with and without phorids, I used repeated-measures analysis of variance (ANOVA; one for *A. instabilis*, one for all other ants) with minute as the repeated factor and phorid presence and absence as a between-subject factor. I used a subset of repeated measures for the analysis using measurements for every 10 min (i.e., 10, 20, 30, 40, 50, 60, 70, 80, and 90 min) rather than every 2 min. I saw few workers of other species at baits, thus these were summed across all other species. Because assumptions of sphericity were not met (*A. instabilis*, Mauchley's  $W = 0$ ; other ants, Mauchley's  $W = 0$ ), I also report Greenhouse-Geisser and Huynh-Feldt corrections to test for significance of phorid presence for ant recruitment (Scheiner and Gurevitch 1993).

**Effect of Phorids on Ant Competitive Interactions.** I used Fisher exact tests to determine if other ant species gained access to resources more or less often on trees with or without phorids. To determine if competitive interactions changed in the presence of phorid flies, I compared numbers of workers of *A. instabilis* and each other ant species on a per tree basis. If another ant species was more abundant than *A. instabilis* after 90 min, this event was counted as a takeover. If *A. instabilis* was more abundant, this was counted as a no takeover situation. I summed all takeover and no takeover events on trees with and without phorids and compared frequencies using Fisher exact tests. To assess whether more species of ants gained access to resources with phorid flies, I compared ant richness at baits on trees with and without phorids. To do this, I created species sample curves using EstimateS (Colwell and Coddington 1994).

## Results

In the study sites, phorids were common; they were found attacking *A. instabilis* on 69% of trees dominated by that ant. The likelihood of encountering phorids on a tree depended on tree identity when examining all 17 tree species used (Mann-Whitney U,  $z = -2.512$ ,  $P = 0.012$ ). However, when only looking at those six tree species that were used for three or more trials (i.e., three individuals), phorids were equally as likely to be found or not on each species (Mann-Whitney U,  $z = -1.048$ ,  $P = 0.295$ ).

On trees where phorids were present, *A. instabilis* abundance at tuna baits was 1.5–3.5 times lower than on trees without phorids from 12 min through the end of the trial period (90 min), a significant reduction in ant numbers (Fig. 1; Table 1). Abundance of other ant species, however, increased by 3–17 times in the presence of phorid flies (Fig. 1; Table 1), yet this was not a significant change overall or for any time period, likely because of high variation in ant numbers. Other ants, however, were significantly more likely to be present on tuna baits (regardless of abundance) on



**Fig. 1.** Ant recruitment with and without phorid flies. Numbers of ants (A, *A. instabilis*; B, all other species) recruiting to tuna baits on shade trees over 90 min in the presence (open symbols) or absence (black symbols) of phorid flies. Error bars show SE.

*A. instabilis*-dominated trees when phorid flies were present. Other ants were found at baits on only 10% of trees where phorids were absent but gained access to baits in one-half of the trees where phorid flies were attacking *A. instabilis* ( $P = 0.001$ ).

The majority of interactions between *A. instabilis* and other ant species did not result in takeovers either on trees with (76%) or without phorids (100%) (Table 2). Nevertheless, all trials in which other species took over baits were in the presence of phorids (Table 2). Four of 13 species found on trees with phorids took over baits from *A. instabilis*. *Pheidole* sp. 1 took over baits in 67% of interactions, *Cephalotes* sp. 1 in 40% of trials, *Solenopsis* sp. 1 in 33% of trials, and *Camponotus novogranadensis* in 29% of trials.

Phorid fly presence was also associated with increased resource access for a number of ant species (Fig. 2). Across all trees, a total of 13 other ant species were observed on baits on trees with *A. instabilis* and phorid flies, but only 2 other species were seen foraging on baits on trees without phorid flies.

## Discussion

Phorid fly presence was associated with significantly decreased recruitment activity of *A. instabilis* as previously shown (Philpott et al. 2004b), and although numbers of other ant species did not significantly increase, other ants were significantly more likely to gain access to baits on trees with phorids. In most cases, *A. instabilis* did not loose competitive interactions with other species, even when phorids were present. However, bait takeovers from *A. instabilis* ants only occurred in the presence of phorids. *A. instabilis* lost competitive contests with one species, *Pheidole* sp. 1, in a majority of interactions when phorids were present, but this finding should be taken with caution because of low sample size. Thus, although presence of phorid flies was not associated with higher likelihood of *A. instabilis* to lose competitive interactions with most species, phorid flies may affect competitive hierarchies between some ants. These results show that phorids may be an important factor mediating competition of *A. instabilis* with other ant species, primarily because the other ants gained access to

**Table 1.** Effects of *Pseudacteon* sp. phorid flies on recruitment of *A. instabilis* and other ants

	df	MS	F	P	Adjusted P	
					Greenhouse-Geisser	Huynh-Feldt
<i>A. instabilis</i>						
Phorid presence	1	2,616,012.447	17.13	<0.001		
Error (phorid presence)	69	32,852.742				
Minute	8	2,017,369	2.301	0.02	0.071	0.066
Minute × phorid	8	3,834,198	4.374	<0.001	<0.001	<0.001
Error (minute)	552	876.636				
Epsilon					0.421	0.452
All other ants						
Phorid presence	1	194.985	0.546	0.464		
Error (phorid presence)	40	357.347				
Minute	8	5.846	0.196	0.991	0.730	0.742
Minute × phorid	8	5.846	0.196	0.991	0.730	0.742
Error (minute)	320	29.853				
Epsilon					0.174	0.183

Numbers show results of repeated-measures ANOVA tests testing whether abundance of *A. instabilis* or summed for all other ant species varied with phorid presence, if ant numbers changed over time, or if there was a significant interaction between the two factors. Numbers of *A. instabilis* decreased, and numbers of other ants increased (not significant) with phorids

Table 2. Phorid-mediated bait takeovers

	With phorid		No phorid	
	No takeover	Takeover	No takeover	Takeover
<i>Camponotus novogranadensis</i> Mayr	10	4	2	0
<i>Camponotus sexdens</i> Forel	4	0	1	0
<i>Camponotus sericeiventris</i> Gužrin	1	0	NA	NA
<i>Cephalotes</i> sp. 1	3	2	3	0
<i>Nesomyrmex echinatoides</i> Forel	1	0	NA	NA
<i>Pachycondyla</i> sp. 1	2	0	NA	NA
<i>Phidole</i> sp. 1	1	2	NA	NA
Top of form <i>Procryptocerus scabriusculus</i> Forel	1	0	NA	NA
<i>Pseudomyrmex</i> sp. 1	1	0	NA	NA
<i>Pseudomyrmex gracilis</i> F.	1	0	NA	NA
<i>Pseudomyrmex simplex</i> F. Smith	1	0	NA	NA
<i>Pseudomyrmex</i> sp. 2	1	0	NA	NA
<i>Solenopsis</i> sp. 1	2	1	NA	NA
Total	29	9	6	0
Fisher's exact test	<i>P</i> = 0.230			

Number of trials in which other ant species took over or did not take over baits from *A. instabilis* ants in the presence or absence of phorid flies.

NA, cases where a given ant species did not interact with *A. instabilis* in the absence of phorid flies.

resources significantly more often where phorids were present.

The abilities of phorids to mediate ant competitive interactions may strongly vary temporally. I observed ants and phorids for 90 min, during which time phorids strongly limited *A. instabilis* recruitment activity. Fire ants (*Solenopsis invicta* Buren) attacked by phorids hide near baits, in areas protected from phorids, and quickly return to baits as soon as phorids disappear (Orr et al. 1997). Similarly, *A. instabilis* ants may return to baits when phorids disappear and exclude most other ant species foraging there. Additionally, phorids are strictly diurnal, whereas ants frequently forage over 24 h, and ants attacked by phorids may show increased foraging activity at night (Orr et al. 2003, Wuellner and Saunders 2003). In fact, *A. instabilis* activity increased at night in at least one of the study sites (S. Uno, personal communication).

Although *A. instabilis* recruitment was strongly limited on trees with phorids, *A. instabilis* did not disappear. *A. instabilis* workers were frequently observed

hiding close to baits and leaving refuges to go to tuna baits. Other ant species attacked by phorids, although also strongly limited, may nonetheless leave behind workers to protect baits from other ants (Orr et al. 1997). Possibly, *A. instabilis* workers remaining near baits during phorid attacks may have been abundant and aggressive enough to limit recruitment of other ant species, thus maintaining *A. instabilis* competitive dominance of baits. In fact, other ant species averaged at most four workers per tree, whereas *A. instabilis* ants, even with phorids, still numbered  $\approx 40$  ants per tree. Thus, *A. instabilis* may leave behind enough workers, risking phorid attack, to win competitive interactions with other ants and effectively maintain control of resources, even in the presence of phorids.

One important additional factor to consider, however, is the size of baits used in trials. Baits were too large ( $\approx 5$  g each) for a single worker (of *A. instabilis* or other ant species) to try to remove. Perhaps as a consequence, some *A. instabilis* workers may have remained to protect this available resource. *A. instabilis*, however, may more readily lose smaller resources to other species when phorids are present—i.e., some other ant species may be able to preempt small (but not large) resources from *A. instabilis* when they are under attack from phorids and thereby win competitive interactions. In fact, in examining behavioral dominance hierarchies with respect to phorid presence and resource size, LeBrun (2005) found that the relative success of phorid-attacked ant species (also behavioral dominants in the system) in encounters with competitors was lowest for smaller resources especially in the presence of phorids. Little is known about the most common food sources for ants in the system presented here, but when removed from shade trees in the same sites, ants had stronger negative effects on small ( $<3$  mm) arthropods and did not affect densities of large ( $>5$  mm) arthropods (Philpott et al. 2004a). Ant diets in the system are thus presumably made up of small food items, creating the

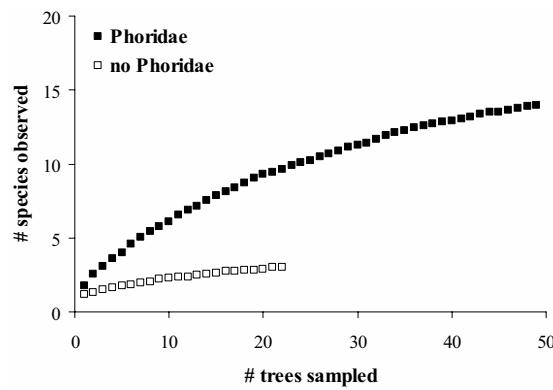


Fig. 2. Number of ants gaining access to resources on shade tree with *A. instabilis* and with (open bars) or without (black bars) phorid flies. Species accumulation curves created with EstimateS show observed species richness.

potential that other ant species gain advantages in exploitative competition in the presence of phorids (Mehdiabadi et al. 2004a).

The results presented here show interesting patterns, indicating that phorids may have large community-level effects in coffee agro-ecosystems. In coffee systems, phorid presence is associated with reduced numbers of *A. instabilis*, increased numbers of other species, and increased resource access for a number of species. Phorid flies did not change *A. instabilis* ability to dominate resources. Nonetheless, workers of other species, and workers of more species were able to access resources when phorid flies were present. These factors taken together may indicate that over a longer time interval, phorid flies may have effects on the ability of the colony to gather resources (Feener and Brown 1992, Porter et al. 1995, Folgarait and Gilbert 1999, Wuellner et al. 2002, Philpott et al. 2004b) and may affect colony expansion and survival. Phorid attacks may thus start a gradual process during which *A. instabilis* ants are replaced by other species that are able to coexist at low numbers for long before *A. instabilis* colonies disappear.

Whether phorids may in fact affect colonies (i.e., population sizes) of host or nonhost ants, however, is a matter of debate and may not be detected over short time scales. Mehdiabadi et al. (2004a) found that host ants, while under attack by phorids, decreased production of workers (foragers) and increased production of soldiers (protectors), hypothesizing that this would impact colony survival through reduced resource acquisition. These findings, however, taken from a laboratory experiment, may have limited applicability in the field because of differences in the pheromones used by phorids to locate ant hosts (Morrison and King 2004). Even if phorid attacks may increase the competitive capabilities of nonhost ants in contests with host ants, this may not translate into decreased survivorship for host ant colonies (Mottern et al. 2004) or increased colony growth of nonhost ants (Mehdiabadi et al. 2004a). Both of these studies examined the effects of phorids on relatively short time scales (28 and 50 d, respectively). Such a short time scale, relevant for studying if phorid flies will be quick-acting biological control agents of exotic host ants, does not address the possibility for long-term dynamics between ant species and phorid flies. In fact, many such interactions across spatial and temporal scales are difficult to assess using experimental techniques are better addressed with models (Steinberg and Kareiva 1997). This study documenting effects of phorids on host ant foraging, competitive interactions between ant species, and increased resource access for ant species in the presence of phorids does not directly address if phorids impact colony survival. For the case of *A. instabilis*, its phorid parasite, and a majority of possible ant competitors, all native to the study region, investigating long-term dynamics and using models with parameters based on the effects documented here may be useful in assessing changes in population densities and colony distributions difficult to determine experimentally.

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