

Lloyd W. Morrison

Indirect effects of phorid fly parasitoids on the mechanisms of interspecific competition among ants

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Abstract Indirect effects, which occur when the impact of one species upon another requires the existence of an intermediary species, are apparently very common and may be of greater magnitude than direct effects. Behaviorally mediated indirect effects occur when one species affects the behavior of a second, which in turn affects how that species interacts with a third. I studied behaviorally mediated indirect effects on the mechanisms of competition in two congeneric fire ant species in the presence and absence of parasitoid phorid flies, which parasitized only one ant species. In observational and experimental field studies, the presence of native Texas phorid flies in the genus *Pseudacteon* decreased food retrieval by their host, *Solenopsis geminata* (F.), by as much as 50%. In the presence of phorid flies, many *S. geminata* workers assumed a stationary, curled defensive posture and did not forage. Although the phorid parasitoids had a relatively large effect on exploitative competition, there was no measurable effect on interference competition. Fierce interspecific aggression was observed between *S. geminata* and *S. invicta* Buren, and the presence of phorids had no effect on the outcome of these contests. The indirect effects of *Pseudacteon* parasitoids on *Solenopsis* fire ant resource retrieval appear to be larger than the direct effect of mortality. Some aspects of the foraging behavior of these *Solenopsis* species may be, in part, evolutionary adaptations to phorid parasitoid pressure. Because of the relatively large indirect effects, South American *Pseudacteon* phorids may be promising biocontrol agents of imported fire ants, *S. invicta*, in the USA. In a laboratory study, a single South American *Pseudacteon* female was able to significantly decrease food retrieval rates of a North American population of the imported fire ant, *S. invicta*.

Key words Direct effects · Exploitative competition · Indirect effects · Interference competition · Parasitism

Introduction

Much ecological work, both past and present, has focused on pairs of species and the direct effects, such as predation and interference competition, of one species on another (Kareiva 1994). Recently, however, the importance and abundance of indirect effects have attracted the attention of many ecologists (see Strauss 1991; Schoener 1993; Wootton 1994a; Menge 1995 for reviews). Indirect effects arise when the impact that one species has upon another requires the existence of an intermediary species. Although the terminology used in recent reviews varies, two major categories of indirect effects have been recognized.

- (1) Indirect effects may be transmitted through changes in population densities (i.e., the change in abundance of one species alters the abundance of a second species through the change in abundance of a third species with which the first two species interact). These types of indirect effects have been termed abundance indirect effects (Strauss 1991), interaction chains (Wootton 1994a), trophic linkage indirect effects (Menge 1995), and density-mediated indirect effects (Abrams et al. 1996).
- (2) Indirect effects may be transmitted through changes in behavior (i.e., the presence of one species changes the behavior of a second species which in turn modifies its interactions with a third species). These types of indirect effects have been referred to as behavioral indirect effects (Strauss 1991; Menge 1995) and interaction modifications (Wootton 1994a). Abrams (1995) broadened this category to include traits other than behavior (i.e., morphology and life history) using the terminology trait-mediated indirect effects.

Indirect effects are also considered to arise when the presence of a species alters the interaction between two

L.W. Morrison (✉)
Department of Zoology and Brackenridge Field Laboratory,
University of Texas,
Austin, TX 78712, USA
e-mail: lmorrison@mail.utexas.edu, Fax: +1-512-4756286

other species through either chemical or abiotic pathways (Wootton 1994a; Menge 1995).

Although there is some semantic confusion associated with the various definitions of different types of indirect effects (Billick and Case 1994; Abrams 1995), theoreticians and empiricists seem to concur on the apparent ubiquity of indirect effects in general. Abrams (1987, 1992), for example, has shown that the variety of possible types of indirect effects is theoretically almost unlimited. In a review of marine rocky intertidal studies, Menge (1995) found that indirect effects accounted for ~40% of the change in community structure resulting from experimental manipulations.

Indirect effects may be either stronger or weaker than direct effects, and operate in the same or opposite direction. Thus indirect effects may increase or diminish direct effects. Schoener (1993) found that indirect effects were stronger than direct effects in about 25% of the experimental studies he reviewed.

Most empirical work has focused primarily on the first category of indirect effects, those mediated through changes in abundance, while a smaller body of work has targeted indirect effects mediated through behavior (Wootton 1994a; Menge 1995). A mechanistic, rather than mathematical, approach has been emphasized in the study of behaviorally mediated indirect effects, and it has been suggested that, at present, natural history observations are likely to provide the most rapid progress (Wootton 1994b). A number of studies have demonstrated that the behavior of prey species is altered by the presence of predators (reviewed by Lima and Dill 1990), indicating that behaviorally mediated indirect effects are quite common. Thus the question of interest is not merely one of their existence, but rather of their relative strength in structuring ecological communities (Wootton 1994b).

I undertook a study of the indirect effects of parasitic phorid flies (Diptera: Phoridae) on the mechanisms of interspecific competition among ant species. Although the importance of interspecific competition in structuring animal communities in general has been debated among ecologists (Connell 1975, 1983; Wiens 1977; Schoener 1982, 1983), interspecific competition among ant species has been widely documented and is thought to be an important factor structuring ant communities (Hölldobler and Wilson 1990). Interspecific competition has traditionally been divided into two mechanisms: exploitative (when the consumption of a resource by one species deprives another species of this resource) and interference (when one species is harmed by direct interaction with another species) (Schoener 1983). Exploitative competition is itself a type of indirect effect: One species indirectly decreases the abundance of another species by reducing the abundance of a shared resource. Although the competitive interactions among some types of organisms may fall wholly within one type of competition or another, both exploitative and interference competition are common among ants (Hölldobler and Wilson 1990), including the species of this study

(Bhatkar 1988; Porter et al. 1988; Tennant and Porter 1991).

The *Pseudacteon* flies studied are parasitoids of *Solenopsis* workers. The adult female fly injects an egg into the thorax of a worker ant using a hypodermic-like ovipositor in a rapid aerial attack. The larva migrates to the head capsule and pupariates, killing the host in the process (Porter et al. 1995a). In the presence of phorid flies, *Solenopsis* workers assume a curled defensive posture and are relatively immobile, which apparently decreases the likelihood that they will be successfully parasitized (Feener 1987; Feener and Brown 1992; Orr et al. 1995; Porter et al. 1995b).

The change in behavior of the host ant species in the presence of phorid flies affects how the host ant species interacts with other ant species, and is thus a type of behaviorally mediated indirect effect. The direct and indirect effect sequences in this system are illustrated in Fig. 1. Parasitism of host ants by phorid flies represents a direct effect, providing food for the developing larvae. The host ant species competes directly with other ant species (interference competition) and indirectly through competition for the same resources (exploitative competition). Parasitism pressure on the host ant species modifies interspecific competition among ants, resulting in a positive indirect effect of the phorid flies on the non-host ant species.

This study addresses the following questions. (1) How are the mechanisms of interspecific competition among ant species affected by the presence of phorid flies? (2) What is the relative magnitude of the indirect effect? (3) How does the strength of the indirect effect compare with the measured direct effect? (4) What are the

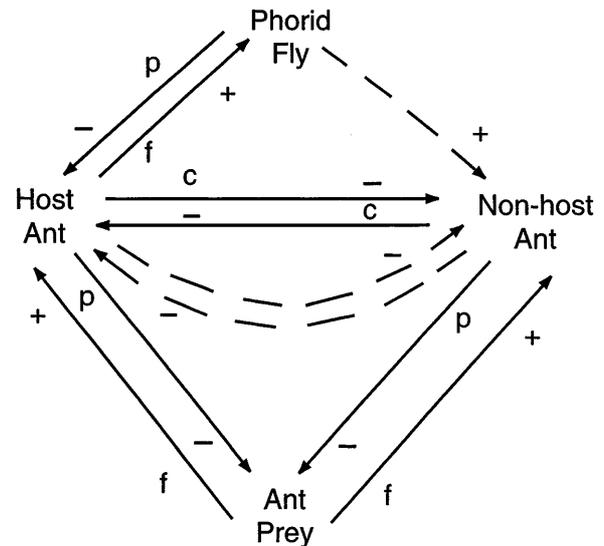


Fig. 1 Direct and indirect effects in the phorid parasitoid-fire ant system. *Solid lines* indicate direct effects, *dashed lines* indicate indirect effects (+ positive effect, - negative effect, *p* predation/parasitism, *f* provision of food, *c* interference competition). The *dashed lines* between host and non-host ants indicate exploitative competition (see text)

evolutionary implications of direct and indirect effects in this system? (5) What are the implications for successful biocontrol of fire ants using parasitoid phorid flies?

Materials and methods

Field experiments

All field work was done in September–October 1995 and September–October 1996 at the City of Austin's Indian Grass Prairie Preserve on the north shore of Lake Walter Long, Travis County, Texas. A small population of the native fire ant, *Solenopsis geminata* (F.), inhabited a wooded area on the lake shore, surrounded by the red imported fire ant, *S. invicta* Buren. In the late 1970s/early 1980s, *S. invicta* invaded the Austin area and excluded *S. geminata* from much of its former range (Porter et al. 1988). *S. geminata* now exists in the Austin area only in small, isolated populations (Morrison et al. 1999).

Two species of parasitoid phorid flies, *Pseudacteon browni* Disney and *P. bifidus* Brown and Morrison (Brown and Morrison 1999), were present at the study site. *P. browni* was far more common, by a 14:1 ratio. Both *Pseudacteon* species parasitized the native fire ant, *S. geminata*, but ignored the imported fire ant, *S. invicta*. Both fire ant species foraged diurnally and nocturnally, whereas the phorids were only active by day.

Exploitative competition

To compare resource retrieval rates and document interactions between fire ant and phorid fly species, a series of observational and experimental baiting trials were conducted. Resource retrieval rates were measured as the decrease in biomass of baits due to foraging ants. The baits used were Oscar Mayer Wieners (pork and turkey), which were sliced into ~3.0 g sections and placed out on 5 × 5 cm cards. Baits were left out for 90 min, and weighed with an electronic balance before and after exposure to foraging ants. Baits were weighed in the laboratory 2–3 h prior to and after the trials. Each bait was placed inside a Ziploc bag and all baits were transported to and from the field inside a cooler at ~10°C.

During each trial, a control set of ten baits was left out for the 90-min period to measure weight loss by desiccation in the absence of ant foraging. The average weight loss of this control group was then subtracted from the weight loss of the experimental baits.

All baiting trials done during the “day” were conducted in the evening, in the shade, within 3 h before sunset. All baiting trials done at “night” were conducted within 3 h after sunset. This timing reduced variation in variables such as temperature and humidity that are known to affect ant foraging activity (Hölldobler and Wilson 1990).

Diurnal resource retrieval was measured at three different natural levels of phorid parasitism pressure: high, medium, and low. If many phorids were present at >90% of the baits, phorid pressure was classified as “high.” If a single phorid was present at >90% of the baits, but many phorids were present at <20% of the baits, phorid pressure was classified as “medium.” If phorids were present at <20% of the baits (almost always a single phorid per bait), phorid pressure was classified as “low.”

During the first series of observational baiting trials, conducted in September 1995, many *Pseudacteon* phorids were almost always present at all baits, and abundances fit the criteria of the “high”-pressure category. In contrast, *Pseudacteon* phorids at this site were much less abundant in 1996. A drought occurred in central Texas between the fall of 1995 and fall of 1996, and rainfall recorded at Austin for the 12-month period between August 1995 and July 1996 was 27% below the 30-year average. By contrast, rainfall for the 12-month period between August 1994 and July 1995 was 57% above the 30-year average (National Climatic Data Center, Asheville, N.C.). The pupal stages of these *Pseudacteon* species are susceptible to desiccation at low humidities in the laboratory

(unpublished data), and it is likely that *Pseudacteon* population densities in nature are adversely affected by dry conditions. Dry conditions are probably also associated with less diurnal ant activity on the surface and thus fewer available hosts.

In early September 1996, very few *Pseudacteon* phorids were present at the study site, and phorid abundances fit the criteria of the “low”-pressure category. Although phorids were seen in the direct vicinity of very few baits, a low level of posturing was observed at many baits, indicating that ants were aware of the general presence of phorids in the area. (The posturing behavior may be a response to chemical cues released by other workers; see Discussion). In late October 1996 when a third set of baiting trials was conducted, phorids were more numerous, although many were males, to which the ants did not respond as strongly. Phorid abundances fit the criteria of the “medium”-pressure category for this period.

To further elucidate the effect of phorid pressure on food retrieval by *S. geminata*, the presence of phorids was manipulated in two sets of experiments. (1) Phorids were excluded from baits during the day by covering the baits with a transparent plastic enclosure, which still allowed ants to access the baits through tiny cracks where the bottom of the enclosure did not lie flush with the ground, and by underground foraging tunnels. A control series of baits were covered by plastic enclosures which had large holes cut in the top that allowed phorids to enter. (2) Baits were illuminated with fluorescent lights at night that allowed phorids to remain at the baits after dark. A control series of baits was not illuminated.

In both observational and experimental trials, numbers of individual workers on each bait card and percentage of *S. geminata* workers assuming a defensive posture were recorded every 15 min. Numbers of workers were estimated within the following ten abundance intervals: 1–4, 5–9, 10–19, 20–29, 30–49, 50–74, 75–99, 100–149, 150–199, and 200+.

A one-way ANOVA was applied to the data on resource retrieval for the observational trials in both years, and the Holm simultaneous testing procedure was used to detect significant differences among a set of ten pairwise comparisons and contrasts of interest (Neter et al. 1996). In the experimental manipulations, two-tailed *t*-tests were used to compare the two treatments in each experiment to determine if there was a significant difference in resource retrieval.

The number of individuals at baits after 90 min was compared by Kruskal-Wallis one-way analyses of variance by ranks tests within three groups of observations: (1) 1995 observational trials, (2) 1995 experimental trials, and (3) 1996 observational trials. A multiple-comparison procedure was conducted for all possible pairs of treatments within each group at an experimentwise error rate of $\alpha = 0.15$ (Daniel 1990).

Data on percentage of *S. geminata* workers posturing after 90 min were arcsine square root transformed and analyzed with ANOVAs within two groups of observations: (1) the three different levels of phorid parasitism pressure, and (2) the experimental manipulations. The Tukey method of multiple comparisons was applied to all possible pairs of treatments within each group (Neter et al. 1996).

Interference competition

The effect of phorids on the interference component of interspecific competition was examined by observing interactions of the two *Solenopsis* species when they co-occurred at baits, in the presence and absence of phorids. *S. invicta* and *S. geminata* occupied mutually exclusive territories, and in a preliminary trial, baits were placed out in a 2 × 2 m grid along the intersection of the foraging territories of the two species to locate the boundary. After 3 days, baits were placed along this boundary at locations where they were judged to have an equal chance of being initially discovered or ultimately controlled by either *S. invicta* or *S. geminata*. When both species were present at the same bait, the ensuing interactions were monitored. The *Solenopsis* species that displaced the other from the card was considered the winner of the interaction. Trials were conducted in late September 1995 and late September 1996.

Laboratory experiments

To quantify the effect of South American *Pseudacteon* phorids on resource acquisition by North American *S. invicta* populations, laboratory experiments were conducted at the University of Texas' Brackenridge Field Laboratory (BFL) in July 1996. Polygynous (multiple-queen) *S. invicta* colonies were obtained from the grounds of BFL, and experimental sub-colonies consisting of 4 g of workers (~8000 individuals), 2 g of brood, and one egg-laying queen were separated. Experimental colonies were maintained in plastic trays (24 × 17 × 7 cm, length × width × depth; Panel Controls Corporation, Detroit, Mich.) with Fluon (polytetrafluoroethylene; ICI Fluoropolymers, Exton, Pa.) on the sides to prevent escapes. A petri dish (90 mm in diameter, 15 mm high), two-thirds filled with damp plaster to maintain humidity, was provided as a nesting chamber. All experimental colonies were provided with water and sugar water ad libitum and given one freeze-killed cricket every other day. After 1 week, the experimental colonies were starved (given water only) for 2 days before the experimental trials, to produce a uniform state of hunger.

Resource retrieval rates were measured by allowing an experimental colony access to a bait (~3.0-g section of Oscar Mayer Wiener, as used in the field experiments) for 90 min. Each colony tray was connected by a 12-cm length of Tygon tubing (1 cm inside diameter) to a foraging tray containing a bait. As in the field trials, all baits were weighed with an electronic balance before and after exposure to ants, and a control set of baits was used to correct for desiccation. A single *P. tricuspis* female was placed in the foraging tray, and the top was covered with glass to prevent escape. In a set of control trials, the same procedure was repeated without the phorid. An experimental trial and a control trial were conducted on each colony; half of the colonies were subjected to the experimental trial first, the other half to the control trial first. Paired one-tailed *t*-tests were used to analyze the data.

Results

Field experiments

Exploitative competition

The amount of food retrieved in a 90-min period was used as a measure of exploitative competition between the two fire ant species. Food retrieval was measured for both *S. invicta* and *S. geminata* during the day and at night in both years. Additionally, since phorid pressure

varied over the study period, diurnal food retrieval for *S. geminata* was quantified for three categories of phorid parasitoid pressure: high (in 1995), medium, and low (both in 1996) (Table 1).

The following general patterns are evident in the comparisons presented in Table 2.

- (1) At night, when phorids were not active, *S. invicta* retrieved more food than *S. geminata* in both years, although the difference was significant only in 1995 (comparisons 1 and 2).
- (2) *S. geminata* retrieved more food at night than by day in both years, although the difference was significant only in 1995, when phorid pressure was high (comparisons 3 and 4).
- (3) *S. geminata* retrieved less food under high compared to medium phorid pressure, and under medium compared to low phorid pressure, although only the latter comparison was significant (comparisons 5 and 6).
- (4) Within each year, there were no significant differences in diurnal versus nocturnal food retrieval for *S. invicta* (comparisons 7 and 8).
- (5) *S. invicta* retrieved significantly more food in 1995 than in 1996 (comparison 9); food retrieval rates for

Table 1 Food retrieved (mean ± SD) by fire ant (*Solenopsis*) species at different times of the day and under different amounts of phorid parasitism pressure

Ant species	Time	Phorid pressure	Food retrieved (g)	<i>n</i>
1995				
<i>S. geminata</i>	Day	High	0.151 ± 0.040	29
<i>S. geminata</i>	Night	None	0.295 ± 0.056	25
<i>S. invicta</i>	Day	None	0.522 ± 0.165	28
<i>S. invicta</i>	Night	None	0.595 ± 0.210	30
1996				
<i>S. geminata</i>	Day	Low	0.310 ± 0.104	27
<i>S. geminata</i>	Day	Medium	0.215 ± 0.112	26
<i>S. geminata</i>	Night	None	0.298 ± 0.063	29
<i>S. invicta</i>	Day	None	0.358 ± 0.198	28
<i>S. invicta</i>	Night	None	0.321 ± 0.142	26

Table 2 Pairwise comparisons and contrasts of means from Table 1. The first mean or combination of means listed in each comparison or contrast was the larger of the two (*GEM S. geminata*, *INV S. invicta*)

Comparison	Mean difference or contrast ^a	Statistically significant? ^b
(1) INV (night) vs GEM (night) 1995	0.300	Yes
(2) INV (night) vs GEM (night) 1996	0.023	No
(3) GEM (night) vs GEM (day, high phorid pressure) 1995	0.144	Yes
(4) GEM (night) vs GEM (day, low and medium phorid pressure) 1996	0.036	No
(5) GEM (medium phorid pressure 1996) vs GEM (high phorid pressure 1995)	0.064	No
(6) GEM (low phorid pressure 1996) vs GEM (medium phorid pressure 1996)	0.095	Yes
(7) INV (night) vs INV (day) 1995	0.073	No
(8) INV (day) vs INV (night) 1996	0.037	No
(9) INV (day and night) 1995 vs INV (day and night) 1996	0.219	Yes
(10) GEM (night) 1996 vs GEM (night) 1995	0.003	No

^a Comparisons 1–3, 5–8, and 10 are pairwise comparisons; 4 and 9 are contrasts involving more than two factor level means

^b The Holm simultaneous testing procedure with a family confidence coefficient of 95% was employed after a one-way ANOVA (Neter et al. 1996)

S. geminata were similar between the two years (comparison 10).

Examination of the graphs of numbers of workers at baits over time reveals complementary patterns. In 1995, *S. invicta* recruited more workers to baits than *S. geminata*, and *S. geminata* recruitment was much higher at night than by day (Fig. 2A). In 1996, recruitment was again higher for *S. invicta*. *S. geminata* recruited more workers nocturnally than diurnally, and more workers under low than medium phorid pressure (Fig. 2B). When phorids were present, up to 90% of the *S. geminata* workers at baits assumed a curled defensive posture, remaining motionless for many minutes at a time (Fig. 3A).

In the manipulative experiments, *S. geminata* was able to gather significantly more food diurnally when phorids were excluded from the baits (Table 3). At night, food retrieval rates were significantly lower at baits that were illuminated and allowed phorids to remain active after sunset (Table 3). Excluding phorids from baits during the day had no apparent effect on numbers of individual ants at the baits (Fig. 2C). The greater proportion of workers posturing at the open baits (Fig. 3B) probably accounts for the difference in resource retrieval between the two treatments. Some posturing did occur inside the enclosures even though no phorids were seen inside (Fig. 3B). At night, fewer *S. geminata* workers were present at the illuminated baits where phorids remained active (Fig. 2C), and more of the workers at the illuminated baits were posturing rather than actively retrieving food (Fig. 3B).

Interference competition

Baits placed along the boundary of the two *Solenopsis* species territories were usually found by foragers of one or other species, which quickly recruited additional workers in high numbers, effectively monopolizing the bait. Some baits were discovered by both *Solenopsis* species at about the same time, however, and aggressive interactions were observed.

In late September 1995, phorids were always present at baits where the two species co-occurred. In trials conducted in late September 1996, phorids were present about 50% of the time. A total of 36 interspecific interactions were observed when phorids were present at the bait and attacking *S. geminata*. Of these 36, 18 were won by *S. invicta*, and 18 were won by *S. geminata*. Twenty-one interspecific interactions were observed in

the absence of phorids (all in 1996). Eleven were won by *S. geminata*, and *S. invicta* was the winner of 10. The presence of phorids had no effect on the outcome of

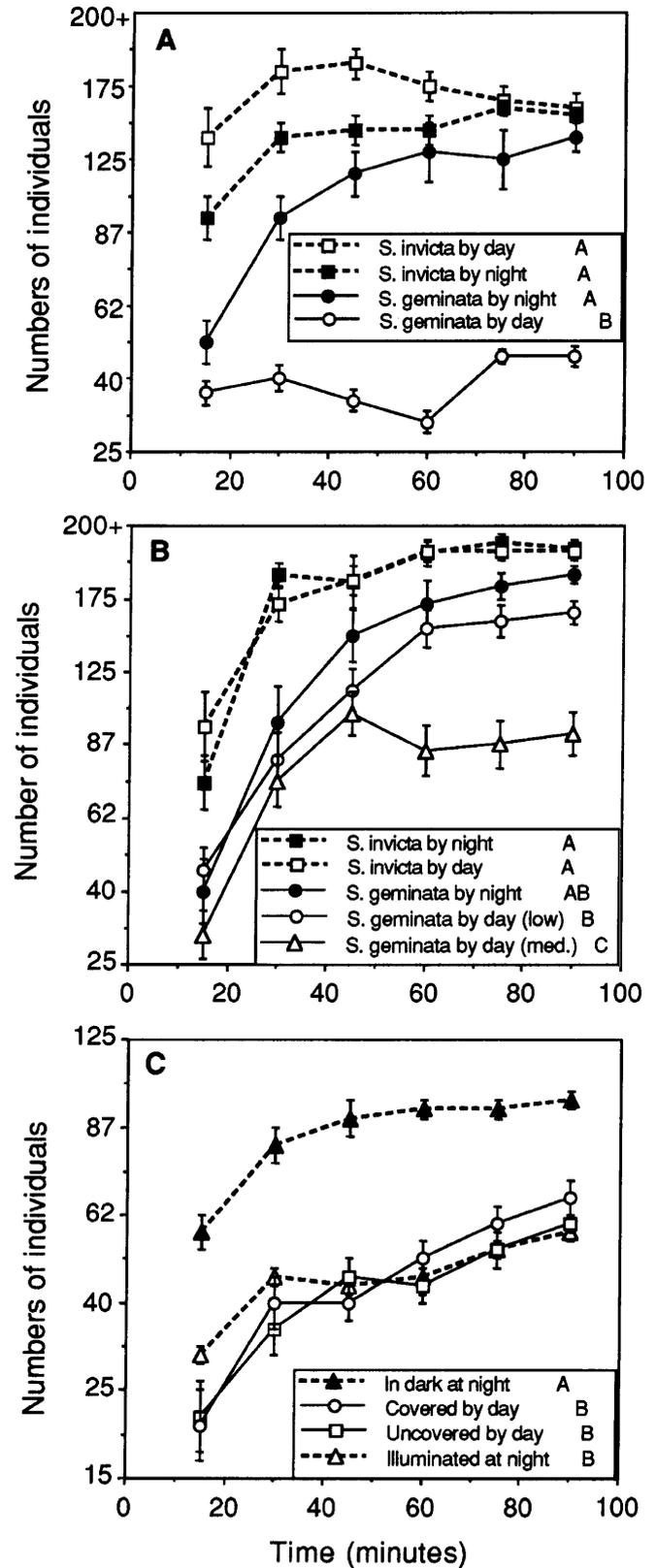


Fig. 2 Number of individual worker ants (*Solenopsis* spp.) on bait cards at 15-min time intervals. Midpoints of abundance intervals are indicated on the y-axes. Error bars represent SEs. Different letters represent significant differences in numbers of individuals at baits after 90 min, within each graph. **A** Observations in 1995. **B** Observations in 1996 (low low phorid pressure, medium medium phorid pressure). **C** *S. geminata* in manipulative experiments (see text)

these interspecific interactions ($\chi^2 = 0.03$, $P = 0.8623$, $df = 1$).

Although many *S. geminata* individuals assumed a defensive posture in the presence of phorids when

S. invicta was not present, the change in the behavior of *S. geminata* when *S. invicta* was detected was dramatic. *S. geminata* workers rarely assumed a defensive posture, but instead actively fought with *S. invicta* workers, even though phorids were in the area vigorously attacking *S. geminata*.

Effects of exotic phorids on *S. invicta* in laboratory experiments

Pseudacteon species native to South America attack a number of *Solenopsis* species in the South American *saevissima* complex, including *S. invicta*. In laboratory experiments, colonies of North American *S. invicta* obtained significantly less food when a single *P. tricuspidis* female was present in the foraging tray than when no phorid was present (mean \pm SD: 0.078 ± 0.017 vs 0.091 ± 0.002 g, respectively; $P = 0.043$, $n = 13$, paired *t*-test, one-tailed). *P. tricuspidis* prefers to parasitize larger than average-size workers (Morrison et al. 1997; Morrison and Gilbert 1998), and the average worker in this experiment (0.62 ± 0.12 mm mean \pm SD, $n = 110$) was smaller than the average size of worker preferred by *P. tricuspidis* (~ 0.93 mm; Morrison and Gilbert 1998). In the experimental trials, minor workers entered the foraging tray and foraged largely unmolested, whereas most majors remained in the connecting tube or in the colony tray. The phorid often hovered at the entrance of the connecting tube to the colony tray, and in several trials actually flew into the tube or through the tube to the colony tray and attacked larger workers.

Most majors that entered the foraging tray were attacked, after which they typically remained immobile for several seconds to several minutes. Nearby workers of all sizes were often attracted to the attacked ant, or assumed an immobile posture themselves. Similar observations of the response of *Solenopsis* workers to *Pseudacteon* attack have been reported from the field in South America (Porter et al. 1995b). In the context of this experiment, it is likely that *Pseudacteon* species which parasitize smaller workers would have had an even greater effect, or that *P. tricuspidis* would have had a greater effect if the average worker size was larger, as would be the case for monogyne (single-queen) colonies (Morrison et al. 1997; Morrison and Gilbert 1998).

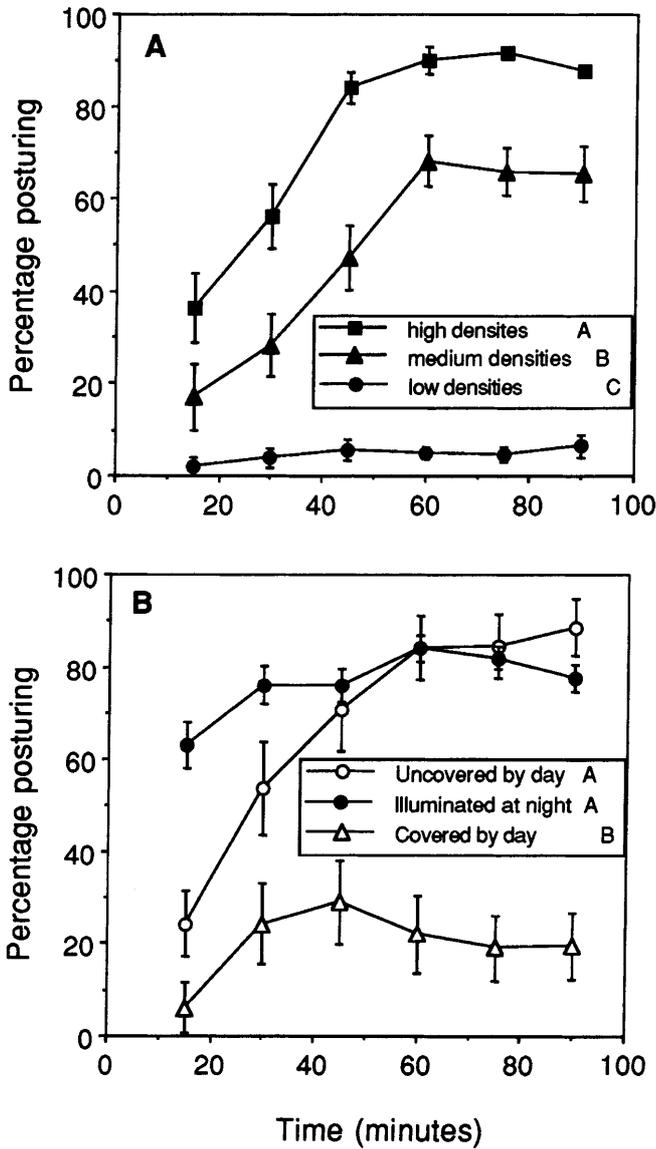


Fig. 3 Percentage of *S. geminata* individuals posturing at 15-min intervals. Error bars represent SEs. Different letters represent significant differences in numbers of workers posturing after 90 min, within each graph. **A** Under three different natural levels of phorid pressure. **B** Experimental manipulations (see text)

Table 3 Food retrieved (mean \pm SD) by *S. geminata* in manipulative experiments

Treatment	Food retrieved (g)	Statistical significance (two-tailed <i>t</i> -test)	<i>n</i>
Experiment 1 (day)			
Baits covered (no phorids)	0.175 \pm 0.062	$P = 0.0172$	20
Baits uncovered (+ phorids)	0.133 \pm 0.043		20
Experiment 2 (night)			
Artificial illumination (+ phorids)	0.196 \pm 0.050	$P = 0.0065$	20
Dark (no phorids)	0.264 \pm 0.091		20

Discussion

Indirect effects of phorid flies on interspecific ant competition

Feener (1981) presented the first evidence that phorid flies can influence the outcome of direct interference competition among ants. A number of succeeding studies have documented that the presence of phorids can affect resource retrieval rates of ants, counting either food particles retrieved (Feener and Brown 1992) or number of foragers at baits (Orr et al. 1995; Porter et al. 1995b). Foraging fire ant workers collect both solid and liquid foods, however, and one detailed study found that the liquid component made up the majority of the food collected by foraging *S. geminata* and *S. invicta* workers (Tennant and Porter 1991). Liquid food is stored in the crop during transport back to the colony, and is not visible to a human observer. Thus, the technique of weighing baits before and after exposure to foraging ants, as used in this study, represents the first attempt to precisely quantify the amount of food acquired, measuring both solid and liquid components. This is also the first study to elucidate how both mechanisms of interspecific competition among ants are differentially affected by the presence of phorid flies.

Comparison of food retrieval rates for *S. geminata* in the presence and absence of *Pseudacteon* phorids revealed that resource acquisition was decreased by as much as 50% when phorids were present (compare *S. geminata* in 1995 in the presence of phorids by day versus the absence of phorids by night, and diurnally under high phorid pressure in 1995 versus low phorid pressure in 1996). This decrease was due both to lower recruitment rates and to the defensive posturing behavior exhibited by workers in the presence of the flies. Although the largest effects were documented when many phorids were present at food resources, the presence of a single female phorid can have a large effect on ant foraging. The difference between low and medium pressure, for example, was proportionately greater than the difference between medium and high pressure (Table 2, comparisons 5 and 6; Fig. 3A).

S. geminata and *S. invicta* are highly territorial and tend to have mutually exclusive distributions (Porter et al. 1988; Tschinkel 1988). A comparative study of the diets of *S. geminata* and *S. invicta* in central Texas revealed a 59% overlap in solid food (Tennant and Porter 1991), indicating that there is substantial resource competition between these two fire ant species. Observations of intense fighting between *S. invicta* and *S. geminata* (Bhatkar 1988; L.W. Morrison, unpublished data) indicate that interference competition also characterizes interactions between these two congeners. The distribution of *S. geminata* has decreased dramatically since the introduction of *S. invicta* from South America and its subsequent spread across the southeastern USA, and much evidence suggests that the mechanism of re-

placement is competitive exclusion (Wilson and Brown 1958; Porter et al. 1988).

Although elucidation of the ultimate factors limiting ant populations is beyond the scope of this study, many researchers have found evidence that competition, particularly competition for food resources, is a strong, ubiquitous force structuring ant communities (reviewed by Hölldobler and Wilson 1990). In the observational baiting trials of this study, >98% of all baits attracted ants. This fact, along with the interspecific conflicts between *S. invicta* and *S. geminata* observed along the territorial boundary, indicates that resources not gathered by one ant species will be obtained by another. Thus, a decrease in resource retrieval by *S. geminata* will likely translate into more resources available to *S. invicta* and other competing species. The presence of *Pseudacteon* flies may therefore place *S. geminata* at a competitive disadvantage in the exploitative component of interspecific competition, and a positive indirect effect will be conferred to competitors of *S. geminata*. In contrast, no indirect effect of the parasitoids was observed on the interference component of interference competition under the conditions of this study.

Direct effects of phorid flies on ants

At this same field site, we found that $\leq 3\%$ of the *S. geminata* workers in a colony were infected with *Pseudacteon* larvae (Morrison et al. 1997). These infection rates were obtained during the fall of 1995, when phorid density was highest. Low rates of parasitism have also been reported for *Pseudacteon* spp. on *S. saevissima* complex ants in South America (Jouvenaz et al. 1981). Low rates of infection may result from the mechanical difficulties associated with injecting eggs into workers. Studies have documented that $\leq 35\%$ of apparent attacks result in development to the larval stage, where verification of infection is possible (Porter et al. 1995a, 1997a; Morrison et al. 1997). Additionally, the defensive behaviors of workers – retreating underground and a curled posture which decreases the likelihood that a worker will be attacked – decrease opportunities for parasitism. Yet these defensive behaviors interfere with foraging and decrease resource acquisition rates.

Overall effects of phorid flies on ants

The 50% decrease in resource acquisition by *S. geminata* in the presence of phorids observed in some comparisons of this study may represent the maximum indirect effect of phorids on fire ant foraging, and the overall magnitude of this type of indirect effect is likely to be less, for a number of reasons.

- (1) *Pseudacteon* phorids only interfere with diurnal, aboveground foraging. However, both *Solenopsis* species forage nocturnally, perhaps more than diur-

nally, at least in the summer months (Claborn and Phillips 1986; Claborn et al. 1988).

- (2) A study of the diets of these two *Solenopsis* species indicates that an unknown proportion of foraging occurs underground (Tennant and Porter 1991). Diets of both species include a high proportion of liquid foods, which would indicate a relatively immobile food source (e.g., plants or honeydew-producing homopterans), an unknown proportion of which is probably underground (e.g., plant roots or root homopterans).
- (3) Foraging on small food items, which could easily be carried back to the nearest foraging tunnel entrance by one or a few workers, is not likely to be affected by phorids to such a large degree. Thus the size distribution of food items will likely determine the magnitude of this effect. In one ant species with a generalized diet, *Lasius neoniger*, in which the frequency of recruitment in food retrieval was studied, 85% of the total prey biomass was cooperatively retrieved by groups of workers (Traniello 1983). Recruitment to rich food resources is probably also very common in the two *Solenopsis* species studied, as indicated by the high proportion of liquid food of plant origin (plant sap, plant nectar, and homopteran honeydew) in their diets (Tennant and Porter 1991).
- (4) Finally, *Pseudacteon* populations vary in abundance both spatially and temporally (Morrison et al. 1999), which would change the magnitude of both direct and indirect effects.

Pseudacteon species had no significant effect on interference competition between the two fire ant species of this study, as *S. geminata* ignored attacking phorids when *S. invicta* was present. It is likely that such behavior on the part of *S. geminata* led to relatively more successful ovipositions, and thus the immediate presence of *S. invicta* (and possibly other competing ant species) may lead to a relatively greater direct effect.

The presence of phorid parasitoids has been demonstrated to affect the interference component of interspecific competition among other ant species (Feener 1981, 1988). It is possible that *Pseudacteon* parasitoids may have some significant effect on interference competition between the two *Solenopsis* species of this study under different circumstances than simulated experimentally. It is also possible that *S. geminata* exhibits various degrees of enemy specification (Hölldobler and Wilson 1990), reacting more aggressively (and ignoring phorids to a greater degree) to some species of ants than others.

Overall the indirect effect on exploitative competition appears to be the most important effect in this system. The magnitude of this effect, however, will depend to a large extent upon the existence and abundance of other species in the community that can effectively consume resources not gathered by fire ants in the presence of phorids.

Other ant species are hosts to parasitoid phorid flies (Disney 1994), although the host-parasitoid relationships for most other genera have not been studied in

detail. Feener (1981, 1988) has shown that parasitism rates of *Apocephalus* phorids on *Pheidole* ants are low (5%), but the presence of phorids may have substantial indirect effects on resource retrieval and interspecific interactions. Relatively small direct and large indirect effects may characterize phorid-ant interactions over a wide range of genera.

Evolutionary implications

If indirect effects are ecologically important in a community, then they should also have strong evolutionary effects through natural selection (Miller and Travis 1996). In the system studied, both direct and indirect effects operate in the same direction, although the indirect effect on exploitative competition appears to be of greater magnitude. Over evolutionary time, such indirect (along with direct) effects of phorid parasitism could be expected to produce adaptive responses in fire ants. Four behaviors of the *Solenopsis* ants studied may reflect, to some degree, adaptations to the presence of diurnally active phorid flies.

First, the defensive posturing behavior appears to be a specific response to these parasitoids (Feener 1987; Porter et al. 1995b). The low levels of posturing observed within the experimental enclosures even though no phorids were inside suggest that the posturing behavior may be a response to alarm pheromones released by other workers, rather than a direct response to the presence of the flies. Ants that were attacked or harassed by phorids were often observed to "gaster flag," a behavior characterized by raising their abdomen in the air and extruding venom (Obin and Vander Meer 1985). Workers that had been attacked or harassed by phorids outside the enclosures before moving inside may have communicated via pheromones the presence of phorids to those inside the enclosures. This mechanism may also explain the low levels of posturing observed at baits during low phorid pressure when no phorids were seen in the direct vicinity of the baits.

A second potential adaptation is a shift to relatively more nocturnal foraging. Evidence for changes in diel foraging activity resulting from the presence of diurnally active phorid flies has been found in the ant genera *Pheidole* (Feener 1988) and *Atta* (Orr 1992). In the present study, *S. invicta* revealed no significant differences in the amount of resources removed, or numbers of individuals at baits, diurnally versus nocturnally, within each year. In contrast, *S. geminata* almost always retrieved more resources and was more abundant at baits nocturnally. Diel cycles of ant foraging activity are affected by a number of factors, including environmental variables such as temperature and relative humidity (Hölldobler and Wilson 1990). In the present study, because all the observations and experiments were conducted in the shade, and within a few hours of sunset, variation in temperature and relative humidity was minimal. Thus, the presence of phorid flies may be a

factor in the significant differences observed in *S. geminata* foraging activity. It is also possible that over the five decades that *S. invicta* has been in the United States in the absence of phorid parasitoid pressure, a shift back to relatively more diurnal foraging has occurred.

A third potential adaptation is that mounds are surrounded by extensive systems of underground foraging tunnels with numerous exits that provide access to all areas of the foraging territory with minimal above-ground exposure (Markin et al. 1975). The use of such covered trails by ants may have evolved, at least partly, in response to phorid parasitism pressure (Disney 1994).

Finally, workers often cover food sources that cannot be easily transported back to the colony with soil or debris. Liquid food may be absorbed by the debris, and then carried back to the colony; this behavior has been interpreted as tool use (Barber et al. 1989). Workers also cover large solid food sources with debris, however, and feed upon them from underneath through tunnels (personal observations). Phorid parasitism pressure may have played a role in the evolution of this behavior.

Implications for biological control

Since its introduction from South America in the 1930s, *S. invicta* has spread across large areas of the southeastern USA and dramatically decreased biodiversity in infested areas (Porter and Savignano 1990). Throughout much of its present range it has displaced *S. geminata* (Porter et al. 1988) even though the two species are similar in morphology and life history.

One hypothesis for the success of *S. invicta* in North America is escape from natural enemies (Feener 1981; Jouvenaz et al. 1981; Porter et al. 1992, 1997b). Harassment of *S. geminata* by phorid flies may be one factor that has allowed *S. invicta* to competitively displace its congener over much of the southeastern USA. Introduction of phorid flies from South America that attack *S. invicta* may reduce the apparent advantage *S. invicta* has in exploitative competition (Feener and Brown 1992).

Several studies have documented the effect of *Pseudacteon* parasitoids on the foraging behavior of *S. invicta* or other closely related species in the South American *saevissima* complex (Orr et al. 1995, 1997; Porter et al. 1995b; Folgarait and Gilbert 1998). This is the first study, however, to document an effect of a South American *Pseudacteon* species on North American *S. invicta* populations. The fact that a single phorid had a measurable impact on resource retrieval in the laboratory indicates that the indirect effects documented for native Texas phorid flies and fire ants are also likely to exist among South American *Pseudacteon* species and North American *S. invicta* populations.

Biocontrol of any ant species has yet to be successfully implemented (Tschinkel 1993). The results of this study indicate that, because of their strong indirect effects on exploitative competition, *Pseudacteon* phorid

flies possess the potential to reduce abundances of *S. invicta* in the USA. Effects of South American *Pseudacteon* species on North American *S. invicta* populations may be even more dramatic than native Texas *Pseudacteon* species on *S. geminata*, because studies in South America on *saevissima* complex species (including *S. invicta*) have found that workers were more likely to abandon baits than remain and assume a defensive posture (Orr et al. 1995; Porter et al. 1995b). The present study indicates that the impact of phorid flies and the ultimate effectiveness of such a biocontrol program will depend critically upon: (1) the relative foraging activity of *S. invicta* nocturnally versus diurnally, and above-versus belowground; (2) the size distribution of food items in the environment, and (3) the presence of other, diurnally active species that will acquire the resources not gathered by *S. invicta* in the presence of phorids. A more precise prediction is difficult to make at present, since foraging patterns in *S. invicta* are not very well-studied, and the presence of other species which may usurp food resources is likely to vary spatially.

Finally, this study suggests that workers in the field of biological control should consider both direct and indirect effects when screening for potential biocontrol candidates. For example, *Pseudacteon* parasitoids of *S. invicta* fire ants have been known since the early 1970s, but were prematurely dismissed as potential biocontrol agents because only the relatively small direct effects were considered (Jouvenaz et al. 1981).

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