

# Colony-level impacts of parasitoid flies on fire ants

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The red imported fire ant is becoming a global ecological problem, having invaded the United States, Puerto Rico, New Zealand and, most recently, Australia. In its established areas, this pest is devastating natural biodiversity. Early attempts to halt fire ant expansion with pesticides actually enhanced its spread. Phorid fly parasitoids from South America have now been introduced into the United States as potential biological control agents of the red imported fire ant, but the impact of these flies on fire ant populations is currently unknown. In the laboratory, we show that an average phorid density of as little as one attacking fly per 200 foraging ants decreased colony protein consumption nearly twofold and significantly reduced numbers of large-sized workers 50 days later. The high impact of a single phorid occurred mainly because ants decreased foraging rates in the presence of the flies. Our experiments, the first (to our knowledge) to link indirect and direct effects of phorids on fire ants, demonstrate that colonies can be stressed with surprisingly low parasitoid densities. We interpret our findings with regard to the more complex fire ant–phorid interactions in the field.

**Keywords:** biological control; colony-level effects; phorid fly parasitism; interspecific competition; Hymenoptera; fire ants

## 1. INTRODUCTION

Biological invasions threaten global biodiversity and disrupt natural systems (Elton 1958; Pimm 1991; Vitousek *et al.* 1996; Mooney & Cleland 2001). Invasive social insects are particularly harmful (Vinson 1986; Williams 1994). The red imported fire ant, *Solenopsis invicta* Buren, native to South America, has established populations in two continents, North America (Vinson 1997) and, recently, Australia. In North America, the southern United States is significantly affected. Pesticides, which cost the United States millions of dollars annually (Thompson *et al.* 1995), have failed to control fire ants effectively (Summerlin *et al.* 1977). Because of its detrimental effects on native invertebrates and vertebrates (Wojcik *et al.* 2001), this invasive ant is also ecologically costly. One plausible reason why *S. invicta* is so successful in its introduced range may be due to the absence of nearly all of its natural enemies, which include parasitic phorid flies. Research therefore has increasingly focused on biocontrol agents, such as phorids.

Despite some successes (Williamson & Fitter 1996; Belloti *et al.* 1999), biological control has remained controversial. The careless introduction of one species to control another may not lessen, but actually exacerbate the problem (Louda *et al.* 1997). Therefore, understanding the potential impacts of a biocontrol agent is crucial to its success. Biological control of social insects, such as *S. invicta*, is complex because sterile workers of a eusocial insect colony are more like cells of a typical organism (Hölldobler & Wilson 1990). Thus, linking impacts of natural enemies on individual workers to the entire colony (i.e. superorganism) is central in assessing the suitability of these organisms as biocontrol agents. Although two

species of phorid flies that are parasitoids of *S. invicta* have already been introduced into the southern United States, to our knowledge no published study to date has investigated whether phorids reduce colony growth of fire ants. Here, we provide the first quantification of the potential colony-level impacts of phorids on fire ants.

Several genera of the dipteran family Phoridae are specialized parasitoids of ant workers. These include *Pseudacteon*, most species of which specialize on *Solenopsis* spp. (Disney 1994). *Pseudacteon* females oviposit their eggs into ants performing activities outside the nest, such as foraging and defence. About 20 days later, the host dies because the larva has consumed its internal tissues and has pupated in the decapitated ant's head, the site of adult fly emergence.

Previous work demonstrated that the behavioural responses of foragers to attacking phorids may substantially reduce diurnal food harvesting (Feener 1981; Feener & Brown 1992; Orr *et al.* 1995; Porter *et al.* 1995; Morrison 1999). Since the amount of food an ant colony collects is greatly influenced by competition with other species (Hölldobler & Wilson 1990), and since phorids modify such interactions (Feener 1981; Feener & Brown 1992; Orr *et al.* 1995; Porter *et al.* 1995; Morrison 1999), we included a native ant competitor in our experiments. *Forelius mccooki* is one of several native ants in Texas not reduced in overall range in fire ant invasion zones (Camilo & Phillips 1990). *Forelius mccooki* continues to coexist with *S. invicta*, possibly because of its greater heat tolerance and its ability to displace fire ants from food in the heat of the day. In the presence of *S. invicta*-specific phorids, *F. mccooki* might gain an overall competitive advantage.

We tested the effects of phorids on foraging success and colony growth of *S. invicta* by exposing laboratory fire ant colonies to the parasitoid, *Pseudacteon tricuspis* Borgmeier, and to an interspecific competitor, *F. mccooki*. Treatments

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included parasitism and competition independently and together, plus a control.

## 2. MATERIAL AND METHODS

### (a) Collection and splitting of colonies

We collected 12 polygynous (i.e. multiple-queen) colonies of *S. invicta* and 13 polygynous colonies of *F. mccooki* in Austin, Texas between April and August 2000. All field-collected *S. invicta* colonies were divided into four colony fragments for a total of 48 sub-colonies, each consisting of one mated queen, ca. 5000 workers (ca. 4250 minors, 400 small majors and 350 large majors) and 2.5 g of brood. Minors and small and large majors were classified as workers weighing 0.5–1.5, 1.5–2.5, and greater than 2.5 mg, respectively. For *S. invicta*, we used a blocking factor (i.e. each field-collected colony was divided into four sub-colonies, one for each of the four treatments) since workers from different colonies may vary in brood-rearing capabilities (Porter & Tschinkel 1985). *Forelius mccooki* colonies had at least one queen, ca. 5000 workers and brood; we created as many sub-colonies from a field colony as possible. We chose to equalize numbers, not biomass, of *F. mccooki* (which is a relatively small ant compared with *S. invicta*) for a realistic estimate of competition pressure.

### (b) Maintenance of colonies

Individual sub-colonies were housed in plastic nest-boxes (43.2 cm × 27.9 cm × 7.6 cm), which were connected by transparent tubing to foraging arenas (55.9 cm × 43.2 cm × 7.6 cm). In treatments with both *S. invicta* and *F. mccooki*, colonies shared one foraging arena. All boxes were lined with Fluon to prevent ants from escaping. We reared colonies under a 12 L : 12 D cycle at 30 °C. We placed water and sugar-water test-tubes in the nest-boxes *ad libitum*.

### (c) Foraging observations

Foraging observations occurred on alternate days, two days per week, for 50 days. Each foraging period lasted ca. 2 h. During foraging periods, we placed one freeze-killed cricket and a sugar-water test-tube in all the foraging arenas. Sub-colonies received sugar water in both the nest-boxes and foraging arenas, whereas they received protein (crickets being the sole source in our experiments) only in the foraging arenas. All sub-colonies were protein limited since resource limitation frequently mediates synergistic interactions between stress and parasitism in causing population declines in hosts (Sheldon & Verhulst 1996; Leung *et al.* 2001). At each foraging observation, we also introduced four female and two male phorids and removed the barrier between *S. invicta* and *F. mccooki* for the appropriate sub-colonies.

### (d) Data collection and analyses

We quantified total worker population size (numbers of surviving workers), numbers in each worker caste and brood production for each fire ant sub-colony after 50 days. We also recorded phorid attack rates, abundance and rates of foraging ants, and mass of protein harvested during each feeding period. Phorid attack rates were collected three times throughout a 2 h foraging period, after 30 min, after 1 h and after 2 h. We counted the number of attacking flies within a 30 s scan. Abundance of foraging ants was quantified at the end of the foraging observations; however, rate of foraging ants was measured after

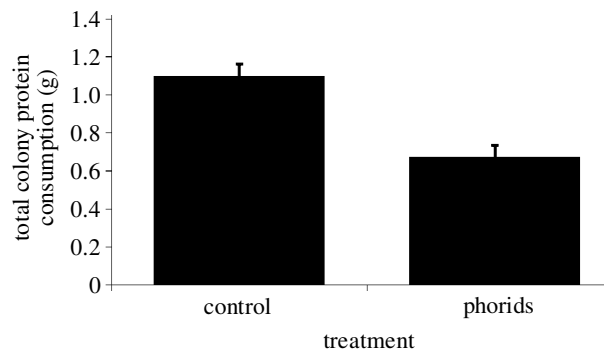


Figure 1. Mean total colony protein consumption (g; + s.e.) for controls and sub-colonies with phorids. Control sub-colonies harvested more protein than sub-colonies with phorids ( $t_{32} = 6.47$ ;  $p < 0.0001$ ).

30 min and after 1 h by counting the number of workers crossing an arbitrary line to and from the crickets. Protein consumption was calculated by weighing crickets before and after foraging observations. Additional crickets were placed in boxes without ants in order to measure loss of cricket biomass due to desiccation. Crickets were dismembered before presentation to the sub-colonies.

Data were analysed with a mixed model ANOVA using SAS (Littell *et al.* 1996; Singer 1998). For analyses of protein consumption and foraging rates, the fixed effects were group (control, phorids, competition and phorids + competition) and observation (14 foraging periods), and the random effect was colony (each of the 12 field-collected colonies). For analyses of phorid pressure, the fixed and random effects were the same as above, except group contained only the control and phorid treatments. For analyses of worker population size, caste and brood production, the fixed effect was group (all four treatments), seasonality (summer and autumn) and queen survival. Experimental treatments showed no significant effect on the last dependent variable. Seasonality was included in the analyses since not all 12 replicates were experimented on at the same time, and queen survival was included since some of the queens from sub-colonies died before the experiment ended. All  $p$ -values are reported using Tukey–Kramer adjustments to control for type I error.

## 3. RESULTS

*Solenopsis invicta* sub-colonies from control groups harvested almost twice as much protein as *S. invicta* sub-colonies encumbered by parasitism, even though average parasite abundance was as little as one attacking fly per foraging observation (figure 1). (Protein consumption data are not reported for groups with competition and groups with phorids + competition since both *S. invicta* and *F. mccooki* foraged on the cricket.) Interestingly, we detected an effect of phorids on fire ant foraging behaviour even at times when phorids were not observed attacking the ants (figure 2). These effects on protein consumption were almost entirely behavioural, in that the rate of foraging ants decreased when phorids were present and even more so when phorids and competition were present (figure 3).

Exposure to phorid parasitoids affected colony growth. Total worker populations decreased in groups exposed to

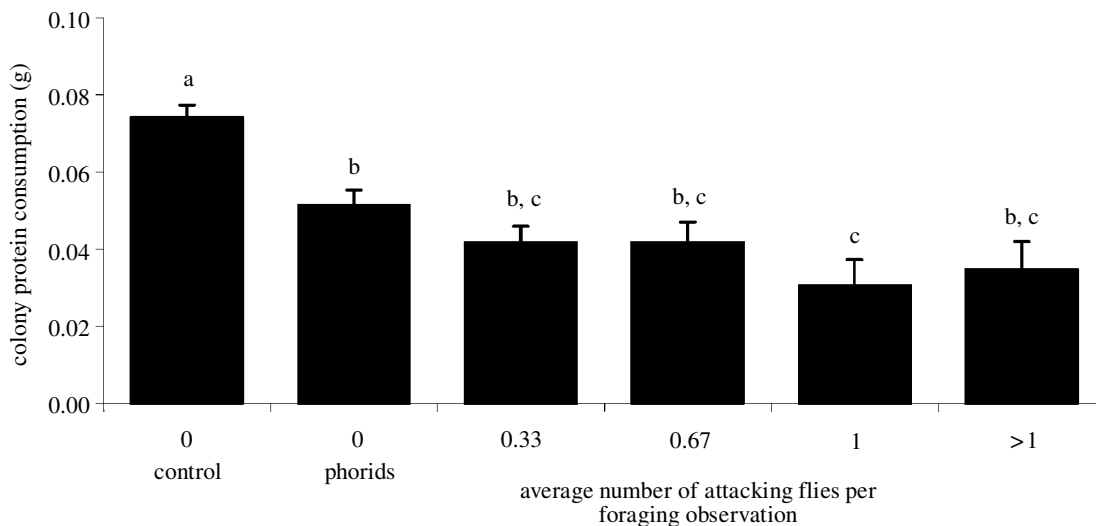


Figure 2. Effects of mean phorid pressure (average number of attacking flies per foraging observation; + s.e.) on colony protein consumption for sub-colonies with phorids in comparison to controls. Phorid pressure was calculated by averaging the three 30 s scans of numbers of attacking flies throughout a 2 h foraging period. Bars with different letters are statistically different using Tukey–Kramer adjusted  $p$ -values. (i) control versus phorids (0),  $t_{31} = 4.46$ ,  $p = 0.0013$ ; (ii) control versus 0.33,  $t_{31} = 5.93$ ,  $p = 0.0001$ ; control versus 0.67,  $t_{31} = 5.19$ ,  $p = 0.0002$ ; control versus 1,  $t_{31} = 5.89$ ,  $p = 0.0001$ ; control versus greater than 1,  $t_{31} = 4.83$ ,  $p = 0.0005$ ; phorids (0) versus 1,  $t_{31} = 3.17$ ,  $p = 0.0370$ .

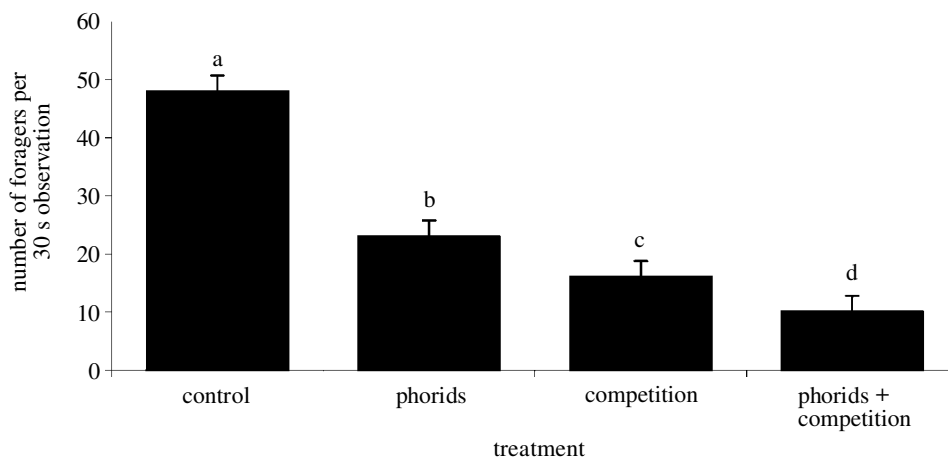


Figure 3. Mean foraging rates (average number of ants going to and from protein in 30 s per foraging observation; + s.e.) for groups in all four treatments. Foraging rates were calculated by averaging the two 30 s scans of numbers of foraging ants crossing an arbitrary line to and from the crickets: (i) control versus phorids,  $t_{653} = 14.41$ ,  $p = 0.0001$ ; control versus competition,  $t_{653} = -18.72$ ,  $p = 0.0001$ ; control versus phorids + competition,  $t_{653} = -22.13$ ,  $p = 0.0001$ ; phorids versus competition,  $t_{653} = -4.31$ ,  $p = 0.0001$ ; phorids versus phorids + competition,  $t_{653} = -7.71$ ,  $p = 0.0001$ ; competition versus phorids + competition,  $t_{653} = -3.41$ ,  $p = 0.0039$ .

competition and in groups exposed to phorids + competition relative to controls (table 1; Tukey–Kramer adjusted  $p$ -values:  $t_{32} = -3.50$ ,  $p = 0.0072$ ;  $t_{32} = 3.08$ ,  $p = 0.0208$ ). However, total worker population size was not significantly reduced in groups with phorids relative to controls, after using Tukey–Kramer adjusted  $p$ -values (table 1;  $t_{32} = 2.46$ ,  $p = 0.0860$ ).

Experimental treatments had the following impacts on the three different worker size classes. The numbers of the smallest-sized workers ('minors') were reduced for groups in competition and for groups in phorids + competition compared to controls (table 1;  $t_{32} = 3.03$ ,  $p = 0.0234$ ;  $t_{32} = 2.71$ ,  $p = 0.0495$ ). Once again, numbers of minors were not significantly different between groups with phorids and controls (table 1;  $t_{32} = 2.24$ ,  $p = 0.1336$ ). Since

minors make up the largest proportion of the colony, it is not surprising that we obtained similar results to those for total worker population size. Intermediate-sized workers ('small majors'), which *P. tricuspidis* preferentially attack (Morrison *et al.* 1997), suffered higher mortality in groups with phorids, competition, and phorids + competition in comparison to controls (table 1;  $t_{32} = 2.90$ ,  $p = 0.0325$ ;  $t_{32} = -4.94$ ,  $p = 0.0001$ ;  $t_{32} = 4.64$ ,  $p = 0.0003$ ). However, numbers of large majors were not significantly different among any of the four treatments.

#### 4. DISCUSSION

Our short-term experiment revealed two significant parasitoid impacts that could dramatically affect colony

Table 1. Mean numbers ( $\pm$  s.e.) of minors, small majors, large majors and all workers for the four treatments.

treatment	number of sub-colonies	mean ( $\pm$ s.e.) minors	mean ( $\pm$ s.e.) small majors	mean ( $\pm$ s.e.) large majors	mean ( $\pm$ s.e.) all workers
control	12	2442 ( $\pm$ 228)	248 ( $\pm$ 24)	214 ( $\pm$ 22)	2904 ( $\pm$ 253)
phorids	12	2075 ( $\pm$ 233)	201 ( $\pm$ 25)	199 ( $\pm$ 23)	2475 ( $\pm$ 253)
competition	12	1946 ( $\pm$ 233)	168 ( $\pm$ 25)	181 ( $\pm$ 23)	2295 ( $\pm$ 259)
phorids + competition	12	1998 ( $\pm$ 233)	172 ( $\pm$ 25)	196 ( $\pm$ 23)	2368 ( $\pm$ 259)

fitness in the long term. First, the continued reduction in protein flow at the levels observed could decrease brood production because larvae require protein for growth (Sorenson *et al.* 1983). Moreover, if phorid-harassed *S. invicta* abandon food resources, other predatory organisms, including competing ants, may forage, increase their colony growth and thus intensify competitive effects on *S. invicta*. Indeed, in our experiments, phorids of *S. invicta* seemed to provide a competitive advantage to *F. mccoocki* (N. J. Mehdiabadi, unpublished data). Second, by killing small majors, both directly as well as indirectly (i.e. by lowering colony protein intake), phorids reduce worker populations. Protein-limited colonies may replace these costly, yet invaluable, majors as observed for other ant species (Hölldobler & Wilson 1990; Passera *et al.* 1996) when encountering severe environmental stresses (e.g. such as intense competition), but at the probable expense of investment in other castes, including reproductives. Conversely, if colonies do not replace these workers, they may be less likely to overcome such stresses (Hölldobler & Wilson 1990) and may lose task efficiency because this caste specializes in foraging and defence (Wilson 1978). Our finding that numbers of large majors were not significantly impacted by any of the experimental treatments may be due to two reasons. First, large majors represent the smallest proportion of all worker size classes. Second, *P. tricuspis* does not prefer to attack this largest size class (Morrison *et al.* 1997). Thus, changes in colony composition were probably due to a combination of reduced colony food intake (through changes in foraging behaviour or competition) and mortality from phorids.

Worker populations were more negatively impacted by competition than by parasitism (table 1). One possible explanation is that the intense interference competition observed between the two ant species resulted in quicker mortality of *S. invicta* workers in comparison to their mortality due to phorid flies (i.e. almost 20 days for larvae to kill hosts and potentially longer for phorids to decrease worker population size due to reduced protein intake).

Nevertheless, our findings that phorids alone were effective at reducing protein consumption and colony growth is important since *S. invicta* has successfully displaced many native ant species in parts of its introduced range (Wojcik *et al.* 2001), thereby decreasing potential competitors. *Pseudacteon tricuspis* is efficient in imposing a negative impact on *S. invicta* because one attacking fly per 193 foragers, on average, was capable of significantly reducing colony protein intake; for every ant attacked, other workers responded by posturing defensively or retreating to the nest, which diminished colony foraging rates. Abundance of flies in our experiments were similar to those experienced by colonies in their native range (Orr *et al.* 1995;

Folgarait & Gilbert 1999); however, in South America, *S. invicta* is exposed to several phorid species that preferentially attack different worker castes (Morrison *et al.* 1997). These results suggest that achieving such densities of phorid attack in North America will vary by ecoregion and by phorid species. For example, *Pseudacteon* species in their native ranges vary in their seasonal phenologies (P. J. Folgarait, unpublished data) and in the degree to which they focus attack on ants at disturbed mounds versus foraging trails (Orr *et al.* 1997). The constant level of phorid pressure in our experimental system may be achieved in nature only with a mix of complementary phorid species that orient to foraging trails.

Field estimates of native fire ant (*Solenopsis geminata*) worker infection rates in Texas indicate that no more than 2% of foragers (including minors and majors) will die of their host-specific *Pseudacteon* parasitoids (Morrison *et al.* 1997). Rather than direct mortality, it is the indirect behavioural responses of foraging *S. invicta* workers to phorid attack, which is proposed to be most significant in altering colony fitness in the field. Our experiments provide predictions of possible pathways that connect indirect (behavioural modification of fire ant foraging) and direct (mortality of workers) effects of phorids on imported fire ants. For example, a reduction in colony protein intake due to behavioural modifications in fire ant foraging may cause a reduction in the production of large-sized workers, which in turn could cause a reduction in the ability of affected colonies to forage effectively. Likewise, direct caste-specific mortality due to phorid infection may also affect foraging and the outcome of competition but on a different time-scale.

Despite generations of relaxed selection in the absence of phorids, fly avoidance behaviours are intact in introduced fire ants. The aggressive behaviours of *S. invicta* are also intact in invasive populations, allowing this species to dominate native ant communities (Wojcik *et al.* 2001). Whereas non-pest native fire ants are also aggressive, they are encumbered by their own specific *Pseudacteon* parasitoids. Thus, freedom from the risk of phorids has been a favoured hypothesis for the ecological success of exotic fire ants, and is the basis for current efforts to introduce *Pseudacteon* flies into North America before any direct field demonstration of their effectiveness (Feener 1981; Feener & Brown 1992; Orr *et al.* 1995; Porter *et al.* 1995; Morrison 1999; Porter 1998).

Because few alternatives for the sustainable ecological control of imported fire ants are viable, the introduction of host-specific *Pseudacteon* flies will continue. Thus, we need a quantitative basis for predicting the potential impacts of the flies on invasive fire ant populations. Quantifying and linking the indirect and direct effects of phorids

using colonies from introduced fire ant populations allow for the evaluation of these parasitoids as biocontrol agents.

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