

Phorid Flies, *Pseudacteon* spp. (Diptera: Phoridae), Affect Forager Size Ratios of Red Imported Fire Ants *Solenopsis invicta* (Hymenoptera: Formicidae) in Texas

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ABSTRACT Multiple species of *Pseudacteon* phorid flies (Diptera: Phoridae) are currently being released throughout the southern United States to aid biological control of red imported fire ants, *Solenopsis invicta* Buren (Hymenoptera: Formicidae). It is anticipated that these flies will interfere with *S. invicta* foraging, allowing native ant assemblages to outcompete *S. invicta* for available resources. Numerous studies have shown a decrease in *S. invicta* foraging intensity when exposed to phorids. This study documents a behavioral change in phorid-exposed *S. invicta* colonies at a phorid release site in central Texas. Significant differences in forager size ratios were detected between phorid-exposed and phorid-absent colonies. A similar phenomenon was recently documented in the native range of these insects in South America as well. Experimental manipulation of ratios of *S. invicta* worker sizes has been shown to have important effects on colony success. This newly documented phorid-mediated *S. invicta* colony-level effect represents a significant shift in *S. invicta* foraging dynamics and may provide an additional mechanism by which phorids can influence *S. invicta* populations in their United States range.

KEY WORDS *Pseudacteon*, phorid, *Solenopsis*, fire ant

The red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae), is a widespread invasive pest in the southern United States and elsewhere, posing a significant ecological and economic threat to invaded systems (Lofgren 1986, Porter et al. 1992). Native to South America, these ants were discovered in Mobile, AL, in the 1930s (Vinson 1997). With the exception of the microsporidian parasite *Thelohania solenopsae* (Jouvenaz et al. 1977), *S. invicta* arrived in the United States with no natural enemies. *S. invicta* are very efficient foragers that routinely outcompete native ants in invaded territories (Wojcik et al. 2001, Helms and Vinson 2005), and they are more successful in invading disturbed habitats than are most native ant species (Tschinkel 2006).

Pseudacteon spp. phorid flies (Diptera: Phoridae) are part of an important assemblage of natural enemies of *S. invicta* in their native South American range. These flies parasitize adult *S. invicta* workers and are currently being imported and released in the southern United States to aid biological control of *S. invicta*. Numerous studies have documented the reduction of foraging *S. invicta* adults in the presence of these parasitoids (Feener 1981, Orr et al. 1995, Porter et al. 1995, Morrison 1999). These studies demonstrate that

S. invicta foraging intensity is diminished during, and for a period after *Pseudacteon* spp. phorids are present. Successful competitive interactions with other ant species are of paramount importance with regard to the ability of an ant colony to obtain the resources necessary to support colony activity (Holldobler and Wilson 1990). Thus, it is presumed that *S. invicta*-specific phorid-mediated competitive interference may allow native ant assemblages to become more competitive with *S. invicta* for available resources, and that this may begin tipping the ecological balance in favor of native ants.

This work provides evidence that *S. invicta* forager size ratios in field-released phorid fly ranges may be affected by phorid fly presence and activity. Chirino et al. (2009) demonstrated that in their native South American range, *Pseudacteon curvatus* Borgmeier affects the size ratios of foraging *S. invicta*. That is, in the presence of phorid flies, a greater proportion of small workers was observed. The investigations reported in this study were designed to determine whether *S. invicta* colonies are affected similarly by the introduced phorid species *Pseudacteon tricuspis* Borgmeier and *P. curvatus* Borgmeier in Texas.

Materials and Methods

Experimental Field Sites. *S. invicta* foraging intensity and foraging size ratios were assessed at two lo-

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cations; the treatment site was 5-Eagle Ranch (30° 34' 54.57" N; 96° 40' 59.77" W) in Caldwell, TX (Burleson Co.), and was phorid infested, and the control site was the Skrivaneck Ranch (30° 28' 49.40" N; 96° 15' 23.00" W) in Wellborn, TX (Brazos Co.), and was phorid free. These ranches occur within the same ecoregion and are physically separated by a distance of ≈ 43 km. Sampling occurred weekly, beginning on 8 August 2007 and ending on 7 November 2007.

Phorid Monitoring. Five PTS-Traps (Puckett et al. 2007) were deployed for the duration of each sampling period to monitor phorid activity at 10-m increments along a transect that ran parallel to, and 50 m from hot-dog bait transects (described below). These traps exploit both the host searching and perching behaviors of phorids to attract them to fire ant midden (dead workers) and then ensnare responding flies on Tanglefoot-coated prongs. Traps were deployed at the initiation of each sampling period, retrieved at the conclusion of each sampling period, and phorid numbers were assessed in the laboratory.

***S. invicta* Monitoring.** Hot-dog baits (Bestelmeyer et al. 2000) were used to assess fire ant foraging intensity and forager size ratios simultaneously at both field sites. Transects of 15 hot-dog bait stations were deployed for 20 min before PM civil twilight and for 20 min after AM civil twilight at both the phorid-infested and phorid-free site. PM civil twilight is defined as the period of time during which the geometric center of the sun travels from an angle parallel with the horizon to 6° below the horizon, whereas AM civil twilight is the period of time during which the geometric center of the sun travels from 6° below the horizon to an angle parallel with the horizon. There was sufficient distance between the two sampling sites used in these studies such that abiotic conditions (light intensity, temperature, relative humidity, etc.) would have been different if sampling was synchronized based on the 24-h clock. Civil twilight was used to synchronize sampling at these two sites to standardize for temporally related variables. For example, on the first sampling date (8 August 2007), PM civil twilight occurred at 2041 hours and 2039 hours at the treatment and control sites (respectively), and the following AM civil twilight occurred at 0623 hours and 0622 hours at the treatment and control sites (respectively); on the final sampling date (7 November 2007), PM civil twilight occurred at 1759 hours and 1758 hours at treatment and control sites (respectively), and the following AM civil twilight occurred at 0621 hours and 0620 hours at treatment and control sites (respectively).

Each hot-dog bait station consisted of one slice (5 mm thick) of Bar-S beef frank placed on a 3" \times 5" index card. Transect locations were 50 m from the PTS-Traps, and these relative positions were maintained throughout the duration of the study. Bait stations were positioned 3 m apart along the transect. After 20 min, the ants, index cards, and hot-dog baits were collected by quickly placing them into large Ziploc bags. These samples were returned to the laboratory, where they were frozen until analysis.

Before analysis, the ants were separated from hot dogs and index cards. Ants were then processed (sieved) through a KECK Instruments SS SandShaker Mechanical Graduated Sieve Field Analysis Kit (Williamston, MI). Samples were separated into four size classes by filtering them through United States Standard Sieve numbers 20, 14, 12, and 10 (respective mesh openings = 0.76, 1.29, 1.54, and 1.82 mm). Size classes are notated as size classes 1, 2, 3, and 4, which relate to United States Standard Sieve numbers 20, 14, 12, and 10, respectively. All surfaces of the sieve equipment were coated with talcum powder to reduce friction, and each sample was sieved for 3 min. As in Porter and Tschinkel 1985, and Wood and Tschinkel 1981, mesh sizes were chosen to distinguish between foraging ant sizes along a continuum that encompassed the majority of workers' sizes such that the smallest foragers were collected in a dish below all sieves (<number 20), medium-small foragers were retained by sieve number 20, large foragers from sieve number 14, and largest foragers from sieve number 12 (all foragers were small enough to pass through sieve number 10). This design allowed for a direct comparison of overall as well as size-specific foraging rates between sites. Each hot-dog bait sample represented one replicate in this study. Temperature and humidity data corresponding to sampling periods were obtained from historical records from weather stations in the vicinity of each study site: ≈ 12 km southwest of the treatment site (30° 37' 57.98" N; 96° 41' 15.03" W) and 9 km northwest (30° 33' 5.00" N; 96° 18' 5.00" W) of the control site.

Statistical Analysis. Student's *t* test was used to compare foraging intensity, and *S. invicta* size class separation was assessed using χ^2 analysis (SPSS 2007). Voucher specimens of *S. invicta* and phorid flies collected in this study were deposited in the Texas A&M University Insect Collections.

Results

Foraging Intensity. There was no significant difference in *S. invicta* foraging intensities on hot-dog baits at the treatment site and control site ($t = 0.02$; $df = 1,418$; $P = 0.98$) (Fig. 1). In addition, there was no significant difference in foraging intensities (all size classes) at treatment site and control site when PM and AM civil twilight sampling periods were analyzed independently: PM civil twilight ($t = 1.63$; $df = 1,208$; $P = 0.10$) (Fig. 2) and AM civil twilight ($t = 1.52$; $df = 1,208$; $P = 0.13$) (Fig. 3). These data demonstrate that a statistically equivalent number of ants were foraging at the treatment and control sites regardless of the presence or absence of phorid flies.

***S. invicta* Size Classes.** There were, however, statistically significant differences among size classes between sites ($\chi^2 = 6811.85$, $df = 3$, $P < 0.05$; PM and AM data combined) (Fig. 4). A significantly greater proportion of ants in size class 1, and a significantly smaller proportion of ants in size classes 3 and 4 were foraging at the treatment site, relative to ants at the control site.

PM twilight samples showed statistically significant differences between sites among size classes ($\chi^2 =$

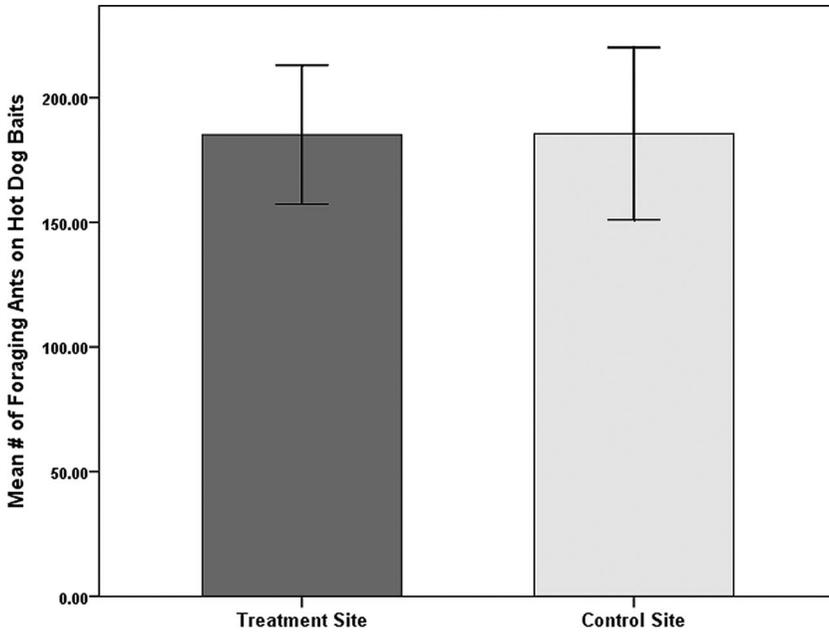


Fig. 1. Mean *S. invicta* (all size classes) foraging intensity on hot-dog baits at treatment and control sites. No significant difference in foraging intensity between sites.

5352.79, $df = 3$, $P < 0.05$) (Fig. 5). As with the combined PM and AM sampling data, a significantly greater proportion of ants in size class 1, as well as a smaller proportion (not significant) of ants in size classes 3 and 4 were foraging at the treatment site, relative to ants at the control site.

AM twilight samples showed statistically significant differences between sites among size classes ($\chi^2 =$

1562.24, $df = 3$, $P < 0.05$; Fig. 6). A greater proportion (not significant) of ants in size class 1, and significantly fewer ants in size class 4 were foraging at the treatment site during AM sampling. The separation between AM forager means is less pronounced than those of the PM data in all size classes except class 1.

Phorid Activity. Phorids were always present during sampling periods at the treatment site, and they were

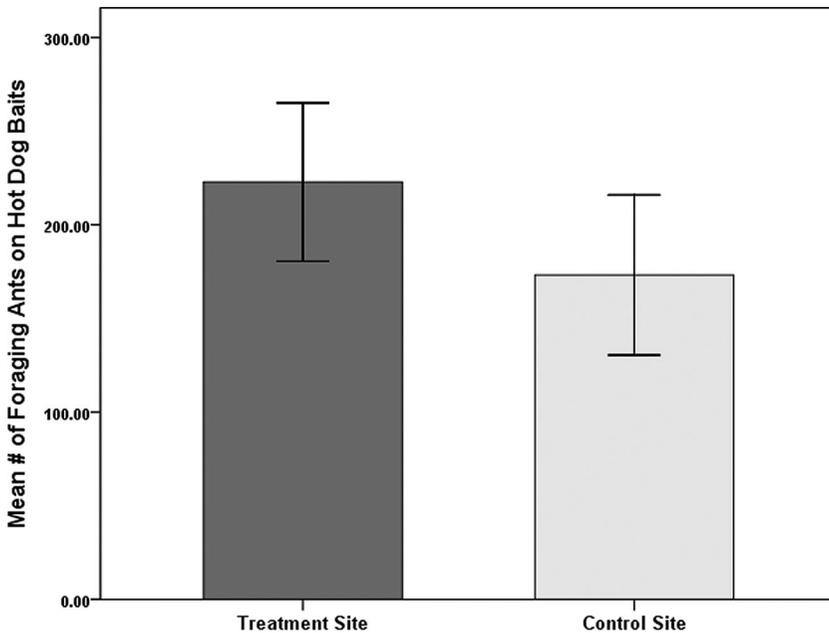


Fig. 2. Mean PM twilight *S. invicta* (all classes) foraging intensity on hot-dog baits at treatment and control sites. No significant difference in foraging intensity between sites.

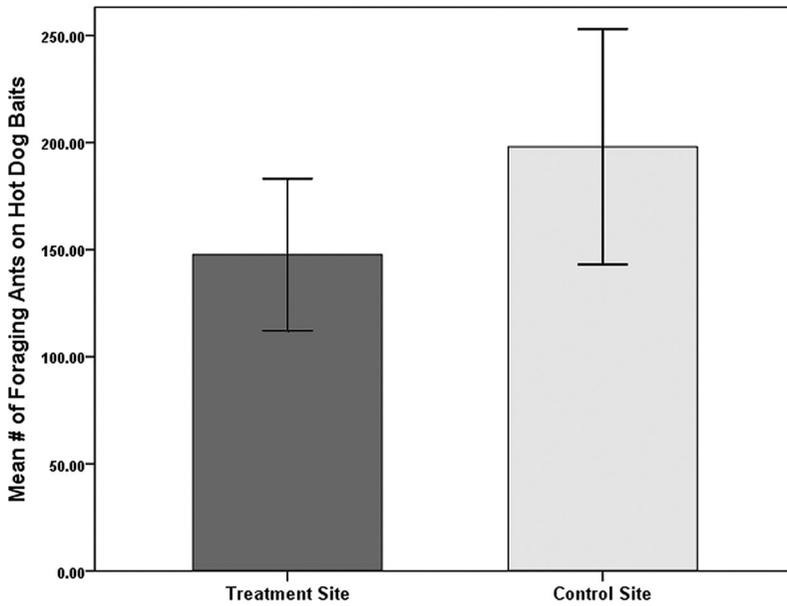


Fig. 3. Mean AM twilight *S. invicta* (all classes) foraging intensity on hot-dog baits at treatment and control sites. No significant difference in foraging intensity between sites.

never collected at the control site (Fig. 7). However, the mean number of phorids collected on PTS-Traps at the treatment site fluctuated dramatically throughout the study. The lowest number of phorids was

collected in August and November, and peaked during early October (Fig. 7).

Temperature and Relative Humidity. There was no significant difference in temperature between the

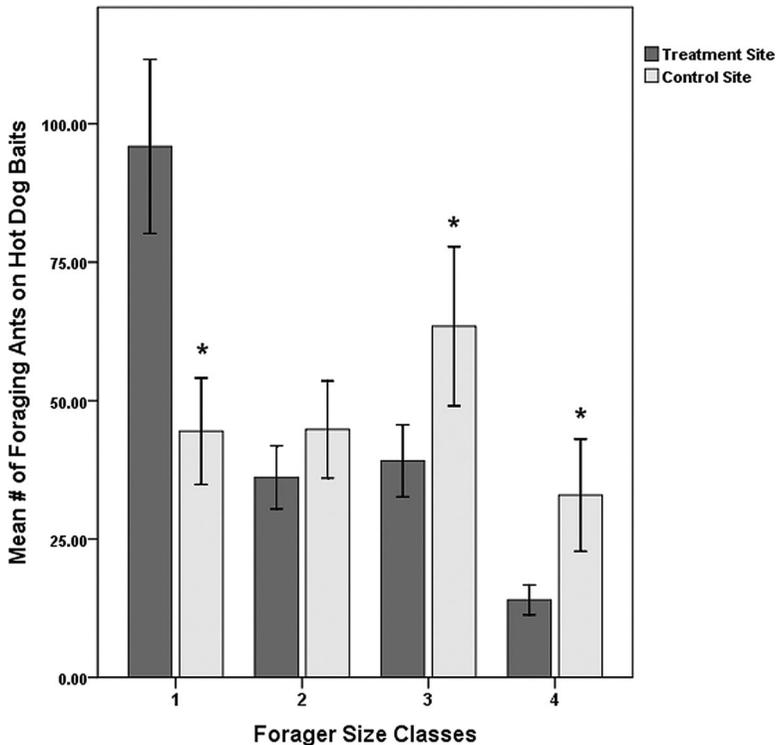


Fig. 4. *S. invicta* forager size class differentials during combined AM and PM sampling periods (*, indicates significant difference between sites; $P < 0.05$).

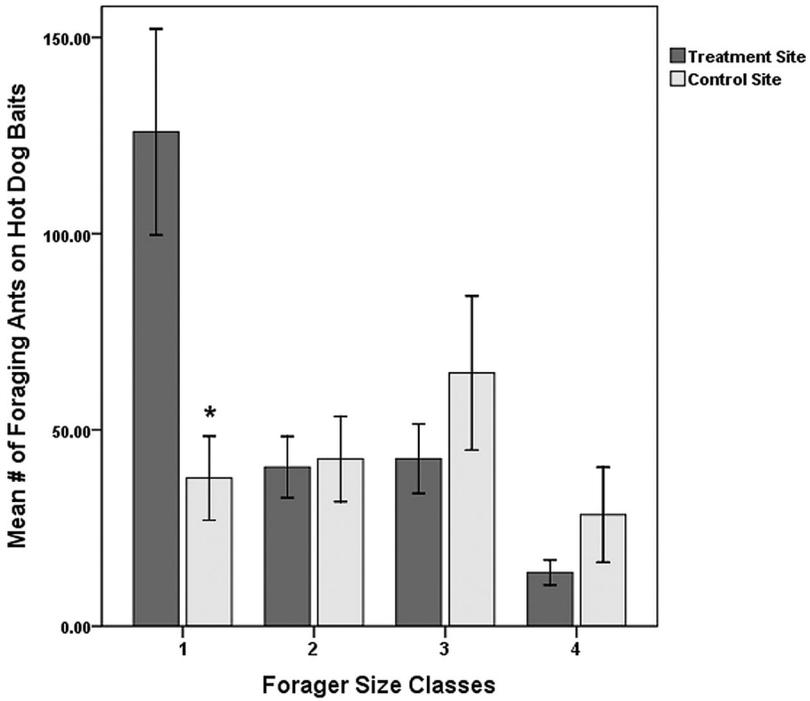


Fig. 5. *S. invicta* forager size class differentials during PM sampling periods only (*, indicates significant difference between sites; $P < 0.05$).

study sites during the PM ($t = 0.79$; $df = 1,16$; $P = 0.44$) or AM ($t = 0.74$; $df = 1,16$; $P = 0.47$) sampling periods. Likewise, there was no significant difference in rela-

tive humidity between the study sites during the PM ($t = 0.97$; $df = 1,16$; $P = 0.35$) or AM ($t = 0.70$; $df = 1,16$; $P = 0.50$) sampling periods. Temperature ranges,

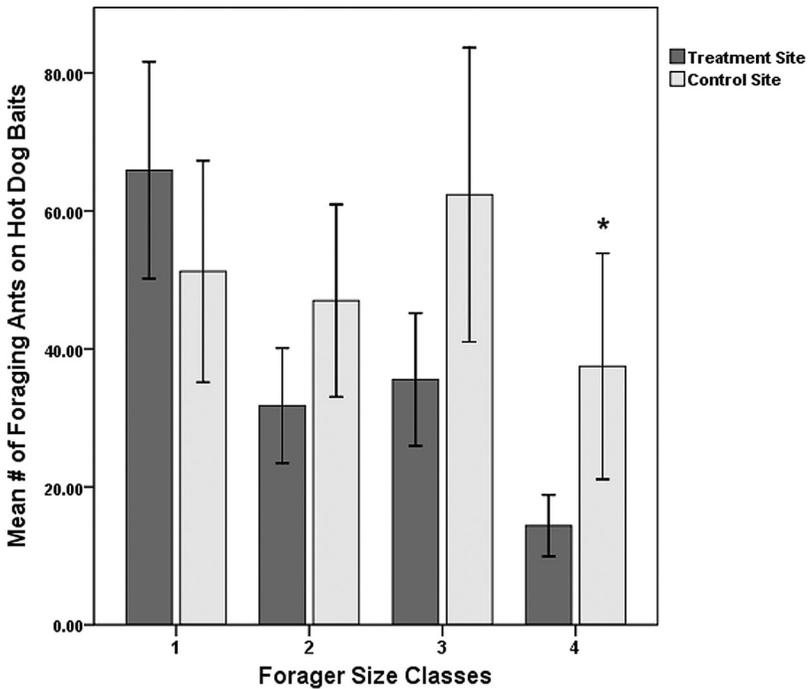


Fig. 6. *S. invicta* forager size class differentials during AM sampling periods only (*, indicates significant difference between sites; $P < 0.05$).

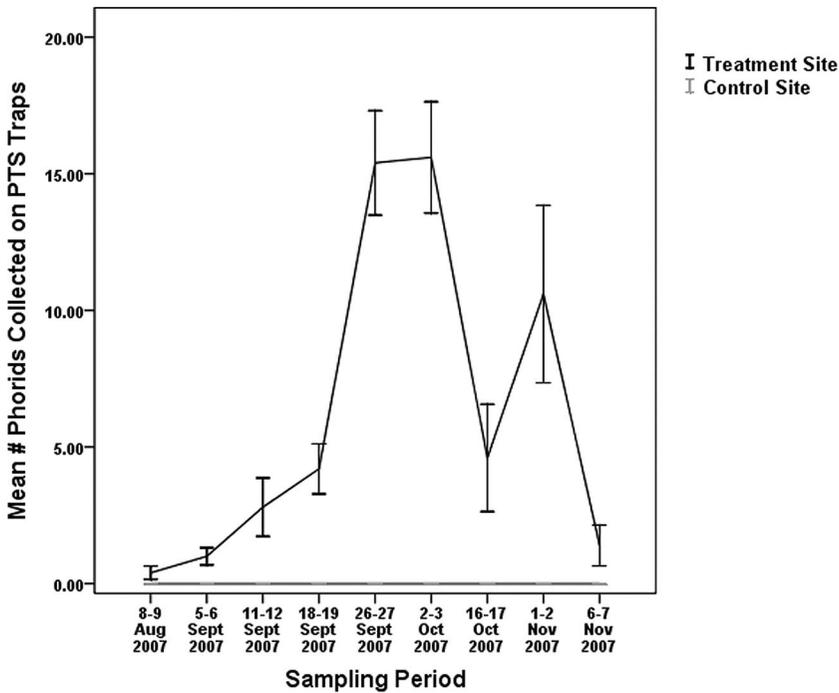


Fig. 7. Mean number of phorids collected on PTS-Traps during all sampling periods. No flies were collected on traps at the control site.

relative humidity ranges, as well as the mean differential of each are presented in Table 1.

Discussion

Worker size polymorphism is important to task allocation in *S. invicta* colonies, and experimental manipulation of the composition of *S. invicta* worker sizes within colonies can have measurable effects on colony success (Porter and Tschinkel 1985). Smaller workers (size classes 1 and 2) are very important to brood production, but are able to perform any colony task required of them (Mirenda and Vinson 1981), whereas larger workers (size classes 3 and 4) are important for such tasks as foraging, mound maintenance, brood moving, defense, and predation (Calabi and Porter 1989, Cassill and Tschinkel 1999, Mirenda and Vinson

1981, O’Neal and Markin 1973, Porter and Tschinkel 1985, Wilson 1978, Wilson et al. 1971). The latter tasks involve exposure to a higher risk of parasitism by phorids. A current strategy in biocontrol efforts on *S. invicta* is to target matching host requirements of the flies to maximize adverse effects of phorid-mediated manipulation of *S. invicta* in the field (Morrison and Porter 1998). Our results contribute to the evaluation of that strategy.

Pseudacteon tricuspis was first released at the treatment site (5-Eagle Ranch) in spring 2002 and recovered during fall 2002. *P. tricuspis* preferentially parasitizes large *S. invicta* workers (Morrison 1999) and was the only field-released phorid species operating in this system until the release of *P. curvatus* at this site in spring 2004; the latter were first recovered in spring 2005 (Puckett 2008) and prefer to parasitize small *S. invicta* workers (Morrison and Porter 1998). These two phorid species had thus interacted with *S. invicta* sympatrically for a 2-yr period before this study; we note this period of interaction is less than the known longevity of *S. invicta* queens with recently established ant colonies present when the parasites were introduced. Therefore, we expect that the population dynamics being expressed among species interacting in this study will, at best, reflect ongoing dynamics that may identify trends toward some level of homeostasis.

The mean number of foraging *S. invicta* at the treatment site and control site is essentially the same (means = 185.2 versus 185.6, respectively). However, the size distribution of all foragers, irrespective of time of sampling, differs within and between these sites.

Table 1. Temperature and relative humidity ranges and mean differentials at the treatment site and control site

Location and sampling period	Temp (°C) range	Temp (°C) differential: mean/SEM	RH range	RH differential: mean/SEM
Treatment site PM	16.00°–28.50°	1.64°C/0.30	42–94	6.88/3.14
Control site PM	15.55°–30.05°		37–87	
Treatment site AM	10.99°–24.00°	1.54°C/0.25	51–100	5.33/1.49
Control site AM	12.77°–23.27°		45–100	

RH, relative humidity.

The four size classes of *S. invicta*, arranged from small to large, occur at frequencies of 52, 20, 20, and 8%, respectively, at the treatment site, whereas they occur at 24, 24, 34, and 18%, respectively, at the control site (Fig. 4). The treatment site consists primarily of small foragers, which may be a result of increased phorid-mediated mortality consistent with the known preference *P. tricuspsis* has for parasitizing large *S. invicta* (Morrison 1999).

The PM and AM foraging intensity data (Figs. 2 and 3) show that fewer ants are foraging in the cooler AM period at the treatment site when phorids are inactive compared with the warmer PM period when phorids are present. This difference is primarily because of significantly fewer small (size class 1) ants foraging in the AM, although reductions are also observed in classes 2 and 3, and there is a slight increase in class 4 (Figs. 5 and 6); this is consistent with class 1 being least able to maintain foraging efficiency when exposed to cooler temperatures, resulting from their higher surface/volume ratio as compared with larger ants (Schmidt-Nielsen 1984). Conversely, there is a slight (not significant) increase in foragers of classes 1 and 4, and little change in classes 2 and 3 at the control site in the AM sampling period. The AM temperature lows (Table 1) at the treatment site are nearing the reported minimum foraging activity threshold of 10°C (Drees et al. 2007) and a few degrees lower than those at the control site, which may account for this difference in small ants (size class 1). More importantly, ants in class 4 at the treatment site that are in peril from phorids and are less vulnerable to temperature effects in the PM remain active at low densities in the AM, but do not (or cannot) exploit this temporary phorid inactive period by increasing numbers to capitalize on their greater foraging efficiency compared with ants in class 1. This suggests the relative densities of size class 4 ants at the phorid-infested treatment site are lower than those at the phorid-free control site, ostensibly because of phorid-induced mortality. We also note that large fire ant workers live longer than small workers and that one large ant is ergonomically comparable to four small ants (Calabi and Porter 1989). A short-term solution to phorid-induced mortality by a mature colony then, would be to deploy 4× more small workers to replace each large worker lost to parasitism. There are ≈2× more small workers and 0.5× less large workers observed foraging at the treatment site compared with the control site; this suggests ants at the treatment site may be ergonomically stressed as a result of an inability to replace parasitized large workers with small workers at a 4× rate.

The processes described above may also affect *P. curvatus*. These flies are physically smaller than *P. tricuspsis* and were selected for their ability to attack smaller workers (Morrison and Porter 1998) in polygyne *S. invicta* colonies; this social form predominates in most of Texas and is characterized by greater mound density with a larger proportion of small worker ants relative to monogyne colonies. *P. curvatus* density was initially below that of *P. tricuspsis* through 2006 and then observed to have increased by June

2007, to ≈5-fold that of *P. tricuspsis* at the treatment site (Puckett 2008). This scenario has also been noted at other sites where *P. curvatus* was released after *P. tricuspsis* had become established (LeBrun et al. 2009). These results are consistent with the view that a reduction in large workers by parasitism from *P. tricuspsis* results in increased foraging by small workers, which in turn are increasingly exposed to parasitism by *P. curvatus*. The addition of *P. curvatus* at 5-Eagle Ranch appears to complement the effects of *P. tricuspsis*, and we anticipate a further reduction in overall *S. invicta* fitness at dually infested sites as additional interactions occur through time.

Although it is clear from these studies that similar numbers of *S. invicta* are foraging regardless of the presence of phorids, there is a difference in the size structure of the foragers at the treatment versus control sites. Whether or not a shift to a small forager-dominated system will allow differential success of native ants remains to be seen. However, we propose that it could via two mechanisms, as follows: 1) increased small *S. invicta* foraging could potentially result in a decrease in brood production as these ants typically perform the duty of brood maintenance, and 2) small workers may not forage as efficiently as typical large workers, resulting in downstream energetic stress on the colony. Each of these scenarios would result in deleterious effects on *S. invicta* colonies, which would secondarily enhance the competitive abilities of native ants within the ever-expanding field-released phorid range in the United States.

Management programs in the field have just begun to establish diverse species of phorids at the same site, and additional time will need to elapse before the full ecological consequences of these parasitoid introductions can be ascertained. Our initial findings and that of others (i.e., LeBrun et al. 2009) indicate the strategy articulated by Morrison and Porter (1998) to release phorid species with different host requirements so as to maximize adverse effects on worker sizes is having a positive effect in the field.

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