

MUTUALISMS, COMMENSALISMS, AND PREDATION: THE DIRECT AND  
INDIRECT EFFECTS OF FIRE ANTS ON ARTHROPODS AND PLANTS

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MUTUALISMS, COMMENSALISMS, AND PREDATION: THE DIRECT AND  
INDIRECT EFFECTS OF FIRE ANTS ON ARTHROPODS AND PLANTS

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THESIS ABSTRACT

MUTUALISMS, COMMENSALISMS, AND PREDATION: THE DIRECT AND  
INDIRECT EFFECTS OF FIRE ANTS ON ARTHROPODS AND PLANTS

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The red imported fire ant, *Solenopsis invicta*, is a voracious generalist predator that has dramatically affected the native arthropod community since its introduction approximately 75 years ago. Most research suggests *S. invicta* negatively affects most native arthropods by consumption or displacement. However several studies have found that *S. invicta* forms mutualisms (positive species interactions) with honeydew-producing insects such as aphids. In field and greenhouse experiments we found evidence that *S. invicta* also forms a positive interaction with spittlebug nymphs. The presence of *S. invicta* has a significant negative effect on spittlebug predators such as spiders which in turn increases spittlebug nymph

abundance. Therefore spittlebug nymphs indirectly benefit from the presence of *S. invicta* and thus fire ants and spittlebug nymphs form a commensalistic relationship. We hypothesize that the impact of red imported fire ants on arthropod communities varies due to the formation of these positive species interactions.

Additionally we quantify the direct benefits that the cotton aphid, *Aphis gossypii*, and the red imported fire ant, *Solenopsis invicta*, receive from their mutualistic relationship in a series of greenhouse experiments. We compared the growth of aphid populations, alate production, and the composition of honeydew of ant attended and unattended colonies in the absence of natural enemies. In addition, we examined worker and brood survival among ant colonies with and without access to aphid colonies. We found strong evidence that both aphids and ants receive direct benefits from the mutualism. Aphid population growth was significantly higher in the presence of fire ants. The presence of fire ants also decreased the proportion of aphids that developed wings (alates) and increased honeydew production by aphids. Survival of fire ant workers and larvae (brood) was significantly higher when fire ant colonies had access to aphids than when they did not. This suggests that honeydew is a high quality food source for fire ants and honeydew consumption directly affects colony survival and growth.

Style manual or journal used: *Insectus Socialis* (Chapter 1), *Oecologia* (Chapter 2)

Computer software used: Microsoft Excel, Microsoft Word, SigmaPlot, SAS 9.1

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## CHAPTER 1: ASSESSING THE DIRECT BENEFITS IN AN ANT-APHID MUTUALISM

### Summary

Honeydew is a carbohydrate rich solution excreted by phloem-feeding insects such as aphids. Ants often consume this substance and, in return, protect aphids from natural enemies. This indirect benefit of ant–aphid mutualisms (i.e. reduced aphid predation) has been examined extensively. Surprisingly few studies, however, have quantified the direct benefits that aphids may gain from the mutualism such as increased performance due to an increase in feeding rates or increased survival due to a reduction in sooty mold. Even less research has focused on the direct benefits that ants receive from this supposedly mutualistic relationship. We conducted a series of greenhouse experiments to quantify the direct benefits that the cotton aphid, *Aphis gossypii* Glover, and the red imported fire ant, *Solenopsis invicta* (Buren), receive from their mutualistic relationships. We compared the growth of aphid colonies and alate production of ant-attended and unattended aphid colonies in the absence of natural enemies. In addition, we quantified survival of ant workers in ant colonies with and without access to aphids. We found strong evidence that both aphids and ants receive direct benefits from the mutualism. Aphid colonies with tending fire ants were 44% larger than their non-tended counterparts. Survival of ant workers was six fold higher when ant colonies had access to aphids than

when they did not. This suggests that honeydew is a high quality food source for ants and honeydew consumption directly affects ant colony survival and growth. Furthermore, this study suggests that there may be constant selection for this mutualism even in the absence of natural enemies since both participants gain direct benefits.

### **Introduction**

Numerous studies have examined mutualistic interactions between aphids and ants. Most of this research has focused on the indirect benefits aphids receive from ants such as protection from natural enemies (Tilles and Wood 1982, Bristow 1984, Buckley 1987, Bach 1991, Volkl 1992, Kaplan and Eubanks 2002, Kaplan and Eubanks 2005). Ants presumably receive energy from aphids by consuming honeydew, a carbohydrate- rich aphid excrement (Carroll and Janzen 1973, Hölldobler and Wilson 1990, Flatt and Weisser 2000). Very few studies, however, have quantified the potential direct benefits aphids receive from tending ants and fewer studies have quantified the benefits of aphid-tending for ants.

Although protection from predators is likely to be the most important benefit aphids receive from ants (Tilles and Wood 1982, Bishop and Bristow 2003), aphids may also gain benefits in the absence of natural enemies. One direct benefit provided by ant attendance may be a reduction in fungal infections. Several studies have suggested that excess honeydew can lead to an increase in sooty mold which in turn decreases hemipteran fitness (Way 1963, Buckley 1987a,b, Gullan and Koszturab 1997, Queiroz and Oliveira 2001). Bach (1991) observed that plants with foraging ants had significantly less honeydew accumulation and sooty mold compared to plants without ants. Thus, the removal of honeydew by ants may directly benefit aphids.

The performance of aphids tended by ants may be increased via other mechanisms as well. For instance, Flatt and Weisser (2000) found that when aphid predators were excluded, the aphid *Metopeurum fuscoviride* lived significantly longer and matured faster when tended by the ant *Lasius niger*. Furthermore, tended aphids produced on average 63 more offspring than unattended aphids. Flatt and Weisser (2000) hypothesized that these aphids benefited from ant tending because of an increased reproduction rate and a reduction in developmental time.

More research has concentrated on the direct benefits that lycaenid butterfly larvae receive from their mutualistic relationship with ants. Like aphids, these larvae secrete a carbohydrate-rich substance, which ants consume, and receive protection from natural enemies via tending ants (Pierce et al. 1987). Therefore lycaenid-ant mutualisms are analogous to aphid-ant mutualisms (Pierce et al. 1991). Like aphids, variation occurs in benefits and costs to lycaenid larvae from their mutualism with ants. For instance, Cushman et al. (1994) observed that tended larvae were 32% heavier than unattended larvae when natural enemies were excluded. Also, tended larvae had fewer instars and spent significantly less time in each instar than unattended counterparts. Furthermore, tended larvae pupated faster, were heavier at pupation, and had a shorter pupal stage. Shorter developmental times can be beneficial because of a reduction in time exposed to natural enemies (Feeny 1976, Price et al. 1980).

Other studies suggest lycaenids incur a cost from their association with ants. For instance, Pierce et al. (1987) found that ant-tended pupae developed slower and eclosed into smaller adults than unattended pupae. Similarly, Robbins (1992) found that tended lycaenid larvae took longer to develop. The lack of sufficient research and the variable

results of the studies that have been conducted to date suggests that more research is needed before we can begin to generalize about the direct benefits of ants to honeydew-producing insects.

Even more surprising is the lack of studies quantifying the benefits that ants receive from tending aphids. Ants form many mutualisms with fungi, plants, and animals, yet very few studies have examined how important these relationships are to ant fitness. Many studies have assumed that ants benefit from honeydew (Carroll and Janzen 1973, Janzen 1974, Degen et al. 1986, Buckley 1987, Fielder and Maschwitz 1988), yet very few studies have demonstrated this experimentally. Furthermore the benefits provided to ants from honeydew may be underestimated. For instance, honeydew is a renewable food source (Carroll and Janzen 1973, Bristow 1983, 1984) and unlike prey has no cost associated with pursuit or capture (MacArthur and Pianka 1966). Also the cost of collecting honeydew is usually low (Bristow 1991). However, ants must often defend honeydew sources from other ant colonies and this may incur a cost (Dreisig 1988).

Although honeydew appears to be an extremely important factor in ant diets there are several likely reasons why very little research has focused on ant benefits, such as their complex social structure (Cushman et al. 1994). Previous studies examining beneficial affects of mutualistic relationships have primarily focused on increases in reproductive success (Flatt and Weisser 2000, Stadler and Dixon 1998). However ants are eusocial insects and worker ants collecting honeydew do not reproduce. However, neglecting to study the benefits gained by each participant in a mutualism may mask the possibility that one species is really exploiting the other (Cushman and Beattie 1991).

A few studies have examined the benefits that ants gain from mutualisms with lycaenids. For instance, Cushman et al. (1994) observed that workers of *Iridomyrmex nitidiceps* with access to lycaenid larvae increased in mass compared to ants without lycaenids. Furthermore, workers with access to larvae had a significantly higher survival rate than those without access. Cushman et al. (1994) argues that this could benefit the entire ant colony because ant workers with more energy could forage more, thereby increasing benefits to the queen and brood. Likewise, Pierce et al. (1987) found that ant workers weighed significantly more after consuming lycaenid secretions. Researchers have estimated that the energetic gain from consuming lycaenid secretions exceeds the energy required to collect them (Pierce et al. 1987, Fielder and Maschwitz 1988). Other research suggests that lycaenids can provide ants with sufficient energy to meet their metabolic requirements (Cushman et al. 1994). Some studies have suggested that ants receive a greater benefit from tending hemipterans than lycaenids (Nash 1989). For example, Helms and Vinson (2002) estimate that hemipterans could provide ant colonies with 45% of their daily energy requirements. The lack of empirical research on the benefits that ants receive from consuming honeydew suggests the need for further research.

This study examines the direct effects of a cotton aphid-fire ant mutualism in the absence of natural enemies. The effect of fire ants on cotton aphid population growth and the effect of honeydew on fire ant worker survival were quantified using greenhouse experiments.

## Materials and Methods

We conducted a series of greenhouse experiments to test the direct effects of fire ant, *Solenopsis invicta*, tending on cotton aphids, *Aphis gossypii*, and the effect of cotton aphid honeydew on the survival of fire ant workers. All experiments were performed in the absence of natural enemies (e.g., ladybeetles) under ambient greenhouse conditions. To test the direct effect of ants on aphids, 40 cotton plants were grown from seed in individual pots. Once plants had 5-6 true leaves (~ 1 m tall) 100 aphids from a greenhouse colony were transferred to each plant. Plants were placed in individual cages containing potting soil and water (see Kaplan and Eubanks 2002 for cage design) and aphids allowed to acclimate for 24 hours. Approximately 500 field collected red imported fire ant workers were added directly to half the cages. Fire ant workers began to tend cotton aphids within 24 hours. We recorded the abundance of apterous and alate aphids on each plant every other day for 12 days. Repeated measures, one-way analysis of variance (ANOVA) was used to compare aphid colony growth and alate production among ant tended and unattended aphids.

In a second greenhouse experiment, a single, large red imported fire ant colony was collected from the field. Worker ants were separated from the colony by raking a stick through the soil and placing one end of a paper bag directly into the colony. Agitated ants immediately climbed onto the bag, and the bag was quickly moved over an empty plastic tray, lined with liquid teflon to prevent ant escape. The top of the bag was tapped causing ants to fall into the empty tray. Using a hand-held aspirator, 500 worker ants were collected from the tray and placed into a second tray, also lined with



liquid teflon, containing potting soil and water. This process was repeated until 40 trays contained 500 ants. A single potted cotton plant with an established colony of *A. gossypii* (approximately 250 aphids) was placed directly into half the ant filled trays. A cotton plant without aphids was placed in the remaining 20 trays. Two weeks later surviving ants were separated and counted from each tray using the technique described above. The survival of ant workers provided with aphids was compared to the survival of workers not exposed to aphids with one-way analysis of variance (ANOVA).

## **Results and Discussion**

### Direct Benefits for Aphids

In a greenhouse experiment we found strong evidence that cotton aphids receive direct benefits from their mutualistic relationship with fire ants in the absence of natural enemies ( $F_{3, 158} = 11.06, P < 0.0001$ ). After seven days, aphids tended by fire ants were significantly more abundant than unattended aphids (Fig 1) and this trend continued throughout the remaining five days of the experiment. After 12 days, aphid colonies exposed to fire ants were 44% larger than aphid colonies without ants. There are several factors that may explain our results. For instance, tended aphids may develop faster (Flatt and Weisser 2000). A second possibility is that like some ant-tended lycaenid larvae (Cushman et al. 1994) tended aphids have an increase in body mass. This could result in an increase in population because body mass is strongly correlated with insect fecundity (Elgar and Pierce 1987).

Several studies have suggested that the presence of ants cause aphids to feed above their optimal levels for nutrient assimilation (Yao and Akimoto 2001) thereby incurring a cost to aphids (Stadler and Dixon 1999, Yao et al. 2000). However our

results did not detect any evidence of a cost to cotton aphids from their association with fire ants. Rauch et al. (2002) argues that ants may increase the efficiency at which aphid's uptake nutrients, thereby incurring a benefit.

Our study found no differences in alate production between the two treatments ( $F = ?? P < 0.05$ ). In fact, overall alate production was very low. Previous studies have observed a reduction in alates when ants were present (Tilles and Wood 1982, Kleinjan and Mittler 1975). However, there is also evidence that alate production is correlated with host plant quality (Dixon 1998). Since all plants used in this experiment were healthy and void of herbivores or other plant predators, aphids may not have produced alates regardless of the presence or absence of ants. Furthermore this experiment may not have allotted enough time to surpass for aphids to reach such a density to produce alates.

#### Direct Benefits for Ants

The presence of cotton aphids significantly increased the survival of fire ant workers in a greenhouse experiment ( $P < 0.0001$ ). Ants with access to aphids were six times as likely to survive as ants without access to aphids (Fig. 2). This suggests that honeydew is an important food resource for fire ants. Ants in this study received honeydew from approximately 200 aphids, however in nature aphid colonies are often much larger. Therefore honeydew may provide more energy to ant colonies than previously estimated. Davidson et al. (2003) suggests honeydew provides worker ants with energy needed to forage for protein, which in turn supplies the colony with energy for growth and reproduction. Future studies should examine whether the brood and or queen benefits from honeydew.

Future research should also consider variation in mutualistic partners. Different aphid species often produce different quantities and varying qualities of honeydew (Volk et al. 1999). Therefore different species of aphids may provide ants with different levels of direct benefits. Likewise, different species of ants have been shown to provide different levels of protection to aphids (Messina 1981). Therefore it is reasonable to suggest that different ant species will also have differential direct effects on aphids when natural enemies are excluded.

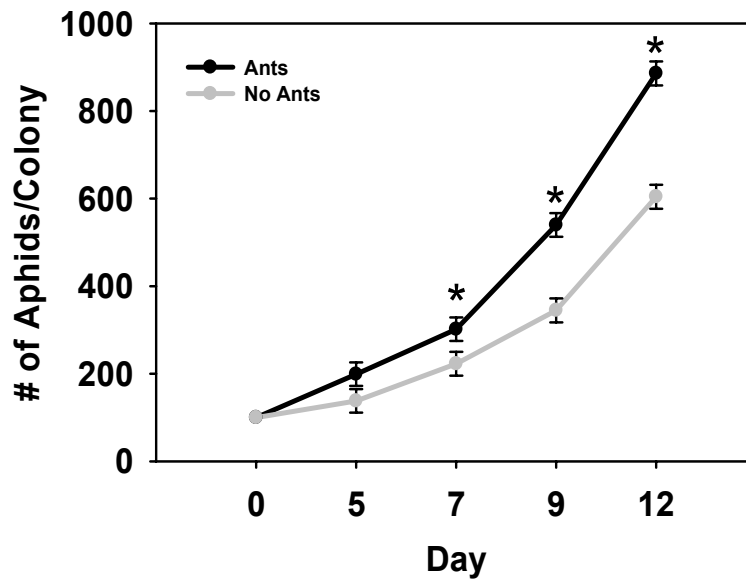


Fig. 1. The number of aphids per plant exposed to fire ants (black line) and not exposed to fire ants (gray line). Colonies exposed to ants were significantly larger after day seven ( $P < 0.05$ ) as indicated by asterisks.

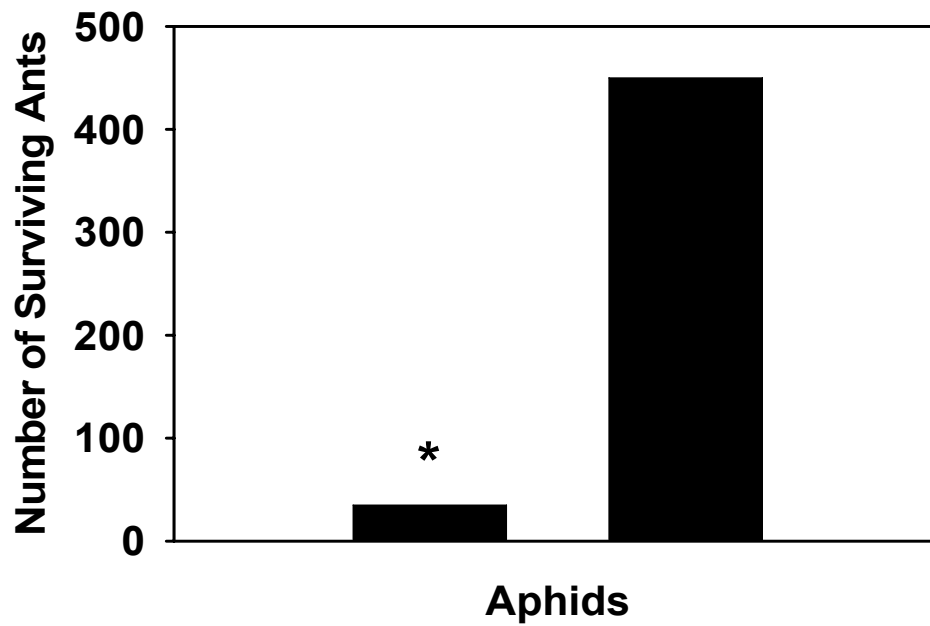


Fig. 2. The mean number of surviving worker ants after 14 days with and without access to aphid colonies. The presence of aphids significantly increased worker ant survival ( $P < 0.005$ ).

## CHAPTER 2: VARIATION IN POSITIVE SPECIES INTERACTIONS: THE EFFECTS OF FIRE ANTS ON OLD FIELD ARTHROPOD COMMUNITIES AND PLANTS

### Introduction

Negative species interactions (e.g., predation and competition) and positive species interaction (e.g., mutualisms and commensalisms) can dramatically alter community population dynamics (Wooten 1994). Invasive species tend to exacerbate these effects due to a lack of natural enemies (Buren 1983, Porter et al. 1997). In this study we examine the direct and indirect effects of an introduced predatory ant on a native arthropod community through predation and the formation of mutualisms and commensalisms

The red imported fire ant, *Solenopsis invicta*, was unintentionally introduced to Mobile, Alabama approximately 75 years ago and has spread across the entire Southern United States (Vinson 1997). Fire ants are voracious generalist predators that are capable of altering population abundances of vertebrate and invertebrate animals. For instance, several studies have concluded that the presence of fire ants has a detrimental effect on several species of birds (Ridleyhuber 1982, Allen et al. 1995, Lockley 1995, Legare and Eddleman 2001), reptiles (Mount et al. 1981, Freed and Neltman 1988, Montgomery 1996, Allen et al. 1997, Moulis 1997), and small mammals (Killion and Grant 1993, Ferris et al. 1998).

The impact of *S. invicta* on arthropods is even more dramatic. Fire ants negatively affect several arthropod guilds including herbivores (Eubanks 2001, Forsy et al. 2001, Harvey and Eubanks 2004), predators (Tedders et al. 1990, Kaplan and Eubanks 2002, Kaplan and Eubanks 2005), and decomposers (Summerlin et al. 1984, Vinson 1991). However one group of insects that benefit from the presence of fire ants are the phloem feeders such as aphids, scales and whiteflies, due to their ability to form facultative mutualistic relationships with ants (Kaplan and Eubanks 2002). The foundation of this mutualism lies on the production of honeydew, a carbohydrate-rich excrement of a phloem-feeding insect. Ants consume honeydew and in return for the nutritious meal protect the phloem-feeder from natural enemies (Buckley 1987, Hölldobler and Wilson 1990).

Previous studies have examined fire ant-aphid mutualisms (Kaakeh and Dutcher 1992, Kaplan and Eubanks 2002, 2005, Diaz et al. 2004, Persad and Hoy 2004), however, a majority of this research has focused on agroecosystems and far fewer studies have examined these relationships in natural settings (Holway et al. 2002). Furthermore, most research has focused on the negative effects of fire ants (e.g., predation and competition) and less research has examined the ecological consequences of possible positive species interactions involving fire ants (e.g., mutualisms and commensalisms).

*S. invicta* can dramatically affect arthropod abundance, therefore fire ants may indirectly affect herbivore host plants. Several studies have recently examined this topic. For instance Styrsky and Eubanks (2007) found the mutualistic relationship between fire ants and cotton aphids, *Aphis gossypii*, indirectly benefited cotton plants. They observed that plants infested with honeydew-producing aphids attracted foraging ants onto the

plant. The presence of fire ants resulted in a reduction in leaf damage due to the consumption of leaf chewing herbivores by ants. Likewise cotton plants hosting aphids increased seed and boll numbers, and received less boll damage compared to plants without aphids.

However a similar study in tomato fields found a different effect of fire ants on host plants (Cooper 2005). The presence of fire ant-aphid mutualisms had an indirect negative affect on tomato plants. In this system, aphids transmit *Cucumber mosaic virus* (CMV), and virus infection leads to plant necrosis, stunting, and lesions (Cooper 2005). Therefore as fire ants tend and protect aphids that transmit CMV they indirectly increase the spread of the virus.

Only relatively few studies have focused on the indirect effects of fire ants on plants (Cooper 2005, Styrsky 2006). Furthermore the majority of these studies have focused primarily on agroecosystems and relatively few studies have quantified the effects of fire ants on arthropods in natural systems. Therefore we conducted a two year field experiment to determine the effects of *S. invicta* on arthropods in a natural setting. We also examined the indirect effect of fire ants on goldenrod. Additionally, we quantify positive fire ant interactions such as mutualisms and commensalisms using greenhouse experiments.

## **Materials and Methods**

*Effect of red imported fire ants on the arthropod community in a natural field setting: 2005*

To quantify the effects of fire ants on the arthropod community in a natural system we conducted a field experiment at Auburn University, Lee County, Alabama. In the spring



and summer of 2005, 30 2x3 meter plots dominated by goldenrod, *Solidago altissima*, were sectioned off in an old field (~ one acre). All plots were separated by 10 to 15 meters. We manipulated fire ant abundance by applying a commercially available, ant-specific bait (Amdro®, American Cyanamid, Wayne, New Jersey, USA) to half the plots. Hydramethylnon is the active ingredient in Amdro which interrupts ATP production thereby killing the fire ant (Valles and Koehler 1997). Amdro was applied every three weeks throughout the experiment to preserve the suppression of ants. Amdro treated plots (suppressed fire ants) were separated from control plots (high fire ants) by 100 meters. Visual surveys of each plant within a plot were conducted weekly and arthropods identified and recorded. The abundance of arthropods in suppressed fire ant and control plots was compared using a repeated measures, one-way analysis of variance (ANOVA) (Proc Mixed, SAS, version 9.1; SAS Institute 1995).

*Effect of red imported fire ants on arthropod host plants*

The effect of fire ants on the above ground biomass of goldenrod was determined by harvesting each plant within a plot. Leaves, flowers and stems were separated, dried to a constant weight in a drying oven, then weighed. Dry mass of plants was compared in suppressed fire ant plots and control plots using a one-way analysis of variance (ANOVA).

*Effect of red imported fire ants on the arthropod community and host plants in a natural field setting: 2006*

To determine the effects of red imported fire ants on the arthropod community in old fields we repeated and expanded our 2005 field experiment. In the spring and summer of 2006, two field experiments were conducted. In addition to our 2005 field site, a second field site (Approximately 40 miles from Lee Co.) was used at E.V. Smith Research Center, in Macon County, Alabama.

Ten 2X3 meter plots were established at our Lee County field site and 20 plots at our Macon county site as previously described. The Macon Co. field site was approximately four acres and each plot was separated by at least 60m. Again Amdro was applied to half the plots to suppress fire ants. In addition to visually surveying plants, a pitfall trap was positioned in each plot for 24 hours once weekly (see Harvey and Eubanks 2004 for pitfall design). A D-Vac suction sampler with a 0.093-m<sup>2</sup> sampling head was also used to survey a square meter section of each plot once a week. D-Vac collection bags were returned to the lab and arthropods identified and recorded. The abundance of arthropods in control and fire ant suppressed plots was compared using a repeated measures, one-way analysis of variance (ANOVA).

Above ground biomass of goldenrod was quantified using the same procedure as 2005. However due to the increased density of plants at the Macon County field site only a randomly selected square meter of plants was harvested from each plot.

*Effect of red imported fire ants on two species of Uroleucon aphids: Greenhouse experiment*

We observed two species of aphids on goldenrod during our field experiments, *Uroleucon luteolum* and *U. nigrotuberculatum*, however, we never observed honeydew

production or ant tending. Therefore we conducted a series of greenhouse experiments to determine the effects of red imported fire ants on *U. luteolum* and *U. nigrotuberculatum* aphids and whether fire ants formed a facultative mutualism with these aphids.

In our first experiment 40 goldenrod, possessing 4-6 true leaves, were harvested from the field and transplanted to individual pots containing potting soil and water. Plants were transported to a greenhouse, caged with mesh netting (see Kaplan and Eubanks 2002 for cage design) and allowed to acclimate for 72 hours. Twenty field collected *U. luteolum* were transferred to each plant and allowed to acclimate for 24 hours. Approximately 250 fire ant workers were placed directly into half the cages. The number of aphids on each plant was recorded 24 and 48 hours after the experiment began. This experiment was repeated using *U. luteolum*. Aphid densities were compared between those with ants and those without ants using a one-way analysis of variance (ANOVA).

#### *Effect of red imported fire ants on spittlebugs and spittlebug predators: Greenhouse experiment*

To determine the effects of red imported fire ants on the survival of spittlebugs and spittlebug predators, we conducted a 2x2 factorial greenhouse experiment using spittlebug nymphs as the independent variable and the presence or absence of *S. invicta* and green lynx spiders (*Peucetia viridans*) as dependant variables. Forty field-grown goldenrod plants were clipped at the base and placed into individual Erlenmeyer flasks containing water. Plants chosen for the experiment possessed 4-6 true leaves and one spittlebug nymph. Plants were transported to a greenhouse and caged as previously

described. Spittlebugs continued to feed and produce spittle during the experiment. Plants and spittlebugs were allowed to acclimate to greenhouse conditions for 24 hours at which point one of four treatments was randomly assigned to each cage: 1) spittlebug; 2) spittlebug and fire ants (~250); 3) spittlebug and two spiders; 4) spittlebug, fire ants, and spiders. The number of surviving spittlebugs, spiders and the number of ants on each plant was recorded 24 and 48 hours after the initiation of the experiment. This experiment was replicated three times and statistical analysis for spittlebug and predator survival was performed using a Wald Chi-Square.

## **Results**

### *Effect of red imported fire ants on the arthropod community in a natural field setting: 2005*

In our 2005 field experiment, Amdro successfully suppressed fire ants. The number of fire ants foraging on plants was significantly higher in control plots compared to ant suppressed plots on six out of eight sampling dates. ( $F_{1,8} = 42.85$ ;  $P < 0.0001$ ) (Figure 1). We found significant differences in the abundance of several arthropods among control and fire ant suppressed plots. Leafhoppers (Cicadellidae) were significantly less abundant in control plots than suppressed plots on three out of eight sampling dates ( $F_{1,8} = 24.21$ ;  $P < 0.0001$ ) (Figure 2). Likewise, fire ants decreased the abundance of other insects such as hymenopterans and dipterans. Dipterans in fire ant plots were significantly less abundant on all but one sampling date ( $F_{1,8} = 57.22$ ;  $P < 0.0001$ ) (Figure 3) and hymenopterans were significantly less abundant (Figure 4) on every sampling date throughout the experiment ( $F_{1,8} = 9.97$ ;  $P = 0.0038$ ).

Fire ants also negatively affected several predator taxa such as spiders and assassin bugs (Reduviidae). Spiders were significantly less abundant in control plots on six out of eight survey dates ( $F_{1,8} = 68.61$ ;  $P < 0.0001$ ) (Figure 5) and assassin bugs on two out of eight dates ( $F_{1,8} = 11.43$ ;  $P = 0.002$ ) (Figure 6). Fire ants reduced the abundance of aphid predators such as ladybird beetles (Coccinellidae) (Figure 7) on three of the dates surveyed ( $F_{1,8} = 15.59$ ;  $P = 0.0005$ ). However, the presence of fire ants did not affect the abundance of aphids. For instance, there was no difference in the number of alate ( $F_{1,8} = 0.32$ ;  $P = 0.5775$ ) or apterous aphids ( $F_{1,8} = 1.2$ ;  $P = 0.2820$ ) (Figure 8) between the two treatments. Likewise, fire ants had no effect on treehoppers (Membracidae). However, a surprising, positive fire ant-arthropod interaction was observed. Spittlebug nymphs were more abundant in control plots than in fire ant suppressed plots on more than half of the dates surveyed (Figure 9) ( $F_{1,8} = 22.36$ ;  $P < 0.0001$ ).

#### *Effect of red imported fire ants on arthropod host plants*

The presence of fire ants had a significant indirect, negative, effect on goldenrod, the dominant host plant. The dry mass of stems in control plots was significantly lower than in suppressed ant plots ( $F_{1,328} = 13.19$ ;  $P = 0.0003$ ). The dry mass of stems in control plots was 35% higher than in fire ant suppressed plots. Fire ants, however, did not significantly affect leaf ( $F_{1,325} = 1.15$ ;  $P = 0.284$ ) or flower ( $F_{1,128} = 2.6$ ;  $P = 0.109$ ) dry mass (Figure 10).

*Effect of red imported fire ants on the arthropod community and host plants in a natural field setting: 2006*

Lee county Field site:

Amdro was successful in suppressing fire ants in 2006. (Table 1, Figure 11). Fire ants had no effect on alate production on *U. luteolum* ( $F_{1,7} = 0.0$ ;  $P = 0.976$ ) and *U. nigrotuberculatum* ( $F_{1,7} = 0.08$ ;  $P = 0.7842$ ) (Figure 12) aphids. Likewise, the presence of fire ants did not affect apterous aphids of *U. luteolum* ( $F_{1,7} = 2.28$ ;  $P = 0.1693$ ) and *U. nigrotuberculatum* ( $F_{1,7} = 0.10$ ;  $P = 0.7586$ ) (Figure 13). D-Vac sampling, however, revealed that fire ants significantly decreased leafhopper ( $F_{1,8} = 5.27$ ;  $P = 0.050$ ) (Figure 14) and spider abundances ( $F_{1,8} = 10.74$ ;  $P = 0.011$ ) (Figure 15). Visual observations also showed a reduction in spiders ( $F_{1,7} = 7.7$ ;  $P = 0.024$ ) (Figure 16). No statistically significant effect of ants was observed on spittlebugs ( $F_{1,7} = 2.29$ ;  $P = 0.168$ ). Spittlebugs, however, were twice as abundant in control plots compared to fire ant suppressed plots (Figure 17).

Macon County Field Site:

Amdro was successful in reducing fire ant densities ( $F_{1,8} = 11.71$ ;  $P = 0.003$ ) (Table 1, Figure 18). Fire ants did not affect alate production in either *Uroleucon* aphid (*U. luteolum*  $F_{1,8} = 2.11$ ;  $P = 0.163$  and *U. nigrotuberculatum*  $F_{1,8} = 1.11$ ;  $P = 0.3068$ ) (Figure 20). Likewise, fire ants had no effect on apterous *U. nigrotuberculatum* ( $F_{1,8} = 2.25$ ;  $P = 0.151$ ) (Figure 21). Fire ants did, however, negatively affect apterous *U. luteolum* ( $F_{1,8} = 9.78$ ;  $P = 0.005$ ) on half of the sampling dates (Figure 22).

Fire ants negatively affected four out of 16 taxa surveyed at E.V. Smith in 2006. For instance, plots with fire ants had significantly fewer katydids than fire ant suppressed plots ( $F_{1,9} = 6.48$ ;  $P = 0.020$ ) (Figure 23). Plant bugs ( $F_{1,9} = 4.20$ ;  $P = 0.055$ ) (Figure 24), assassin bugs ( $F_{1,9} = 5.27$ ;  $P = 0.034$ ) (Figure 25), and dipterans ( $F_{1,9} = 9.43$ ;  $P = 0.006$ ) (Figure 26) were all negatively affected by fire ants, however, no significant differences between treatments were observed for spittlebugs ( $F_{1,8} = 0.64$ ;  $P = 0.435$ ) (Figure 27).

#### *Effect of red imported fire ants on arthropod host plants 2006*

Fire ants had an indirect, positive effect on goldenrod plants at both field sites in 2006. The dry mass of stems ( $F_{1,309} = 21.08$ ;  $P = <0.0001$ ) and leaves ( $F_{1,309} = 34.71$ ;  $P = <0.0001$ ) weighed significantly more in plots with ants at the Lee Co. site (Figure 31). Likewise, stem ( $F_{1,1085} = 29.44$ ;  $P = <0.0001$ ) and leaf ( $F_{1,1085} = 26.94$ ;  $P = <0.0001$ ) dry mass were significantly higher in plots with ants at the Macon Co. site (Figure 30). There was no significant difference in flower mass between the treatments at Macon Co. ( $F_{1,6} = 0.10$ ;  $P = 0.757$ ). No flower data was recorded for the Lee Co. site in 2006.

#### *Effect of red imported fire ants on two species of Uroleucon aphids: Greenhouse experiment*

We conducted a series of greenhouse experiments to determine the effect of fire ants on two species of *Uroleucon* aphids. Fire ants had a significant, negative effect on both species of aphid when no alternative food source was available. The presence of fire ants resulted in a four-fold reduction in the number of *U. luteolum* aphids ( $F_{1,20} = 79.81$ ;  $P < 0.0001$ ) and *U. nigrotuberculatum* aphids ( $F_{1,20} = 45.25$ ;  $P < 0.0001$ ) (Figure 28).

*Effect of red imported fire ants on spittlebugs and spittlebug predators: Greenhouse experiment*

In a greenhouse experiment we found strong evidence of a fire ant-spittlebug commensalism. The survival of spittlebugs in ant only treatments did not statistically differ from survival of spittlebugs alone ( $X^2 = 0.5376$ ;  $P = 0.4634$ ), suggesting that fire ants were not significant predators of spittlebugs. However spittlebug survival decreased significantly in the spider only treatment ( $X^2 = 7.5599$ ;  $P = 0.0060$ ). Survival of spittlebugs increased when ants and spiders were present compared to spider only treatments ( $X^2 = 5.2918$ ;  $P = 0.0214$ ) (Figure 29).

## **Discussion**

This study finds evidence that the red imported fire ant has dramatic effects on arthropods in natural fields dominated by goldenrod plants. Fire ants had a significant negative affect on six out of the 20 arthropod taxa recorded in our 2005 field experiment and seven out of 23 in our 2006 field experiment. Surprisingly fire ants did not appear to form mutualistic interaction with aphids found in this system, however, fire ants did form a positive interaction with spittlebug nymphs (Table 2). We found evidence of a fire ant-spittlebug commensalism where spittlebugs benefit from the presence of fire ants due to their negative impact on spittlebug predators such as spiders and assassin bugs (Table 2). This positive effect on spittlebugs results in a negative affect on spittlebug host plants.

We found fire ants had no effect on *Uroleucon* aphids at Lee Co. in 2006 (Table 3). At our Macon Co. field site, however, fire ants appear to have a negative impact on apterous *U. luteolum* aphids. No effect was observed on *U. nigrotuberculatum* aphids



(Table 6). These results suggest that fire ants do not form mutualistic relationships with either species of *Uroleucon* aphids. Our greenhouse experiments provide further evidence that fire ants negatively affect these aphids. *U. luteolum* aphids in cages with fire ants had a 90% reduction in abundance compared to those without ants in less than 48 hours. Likewise, fire ants reduced *U. nigrotuberculatum* aphids by 90% (Figure 28).

We believe the absence of a mutualistic relationship between these aphids and ants results from inadequate honeydew production. Fire ants form facultative mutualisms with a variety of honeydew producing aphids (Kaplan and Eubanks 2002, 2005, Tedders et al. 1990), however, we observed no direct or indirect signs of honeydew production by either *U. luteolum* or *U. nigrotuberculatum* aphids in our field and greenhouse studies. Other studies on *Uroleucon* aphids have found similar results. For instance, Woodring et al. (2004) observed that *Uroleucon tanaceti* produced extremely small quantities of honeydew. Without honeydew fire ants have no incentive to protect aphids and may, instead, prey upon them (Whittaker 1991, Stadler and Dixon 2005).

In our 2006 study spittlebug predators were negatively affected by the presence of fire ants. Sampling at our Lee Co. site revealed a significant negative affect of fire ants on spiders (Table 3, 4). Likewise, spiders and assassin bugs were negatively affected by fire ants at our Macon Co. site (Table 7). However our 2006 study failed to produce any positive interaction between fire ants and spittlebugs at either location (Table 3, 6). Our greenhouse experiment, however, did reveal a commensalistic relationship between fire ants and spittlebug nymphs. For instance, green lynx spiders had a significant negative effect on spittlebug nymphs. Spittlebugs were 50% less abundant in cages with spiders than those without spiders, suggesting strong predation of spittlebug nymphs by spiders.

However when fire ants and spiders were present there was no significant affect on spittlebugs (Figure 29), suggesting that fire ant predation and/or harassment of spiders reduced their consumption of spittlebug nymphs. Our results from two years of field experiments showed that fire ants negatively affected spiders including green lynx spiders (Table 7). Previous studies have found similar results. For instance Eubanks (2001) and Eubanks et al. (2002) found that fire ants negatively affected spiders. In our greenhouse experiments fire ants had no significant affect on spittlebugs, therefore this suggest a commensalistic relationship. That is, spittlebugs indirectly benefit from fire ants due to a reduction of spittlebug predators by fire ants, but fire ants presumably do not benefit from spittlebugs.

The positive fire ant-spittlebug interaction can adversely affect host plant quality due to the xylem-feeding of spittlebugs. Our field data from 2005 suggests that the increase in spittlebug abundance from fire ant predation on spittlebug predators has a negative impact on goldenrod. Goldenrod in plots with fire ants had a significant lower dried stem mass after harvest compared to goldenrod without fire ants present (Figure10). We suggest this results from the increase in spittlebugs in fire ant plots (Figure 9). Previous studies have demonstrated significant damage to goldenrod from spittlebug herbivory (Cronin and Abrahamson 1999, Meyer and Whithow 1992, Meyer 1993, Meyer and Root 1993).

We found no evidence of fire ant-spittlebug commensalisms in our 2006 field season, therefore we did not observe an indirect negative affect on plant quality. In fact goldenrod plants in plots with fire ants had significantly greater leaf and stem mass at both field sites (Figure 30,31). We suggest that this results from a reduction in

herbivores due to fire ant predation. For instance, fire ants reduced leafhoppers (Table 4) at our Lee Co. site and reduced plant bug and katydid abundances at our Macon Co. site (Table 7). Therefore fire ants had an indirect positive effect on host plants in 2006. Previous studies have found fire ants to be beneficial to host plant fitness. For instance, Styrsky (2006) observed an increase in cotton yield due to fire ant predation on damaging herbivores.

We suggest the absence of fire ant-spittlebug commensalisms in 2006 field experiments result from a reduction of foraging fire ants on plants. Visual sampling suggests fire ants spent less time on plants at both field sites during 2006. In 2005 at our Lee Co. site we observed a significant difference in fire ant abundance between fire ant suppressed plots and control plots on six out of the eight visual sampling dates (Figure 1), however, in 2006 only two visual sampling dates show a significant difference in fire ant abundance (Figure 33). Likewise, at Macon Co. only two out of seven visual sampling dates show a significant difference in fire ant abundance between the two treatments (Figure 32). The lack of foraging fire ants on plants may explain why we observed no evidence of a commensalism between ants and spittlebugs during the 2006 field season. The reduction of foraging ants found on plants in 2006 may result from increased prey abundances on the ground. Fire ants typically ground foragers, unless honeydew producing insects encourage them onto plants (Styrsky 2006). Therefore if prey on the ground was less abundant in 2005 fire ants may have increased foraging on plants.

This study is one of the first to examine the impact fire ants have on arthropods in natural systems. In addition our study is the first to suggest a positive interaction between fire ants and spittlebugs. Future studies should not only focus on the effect of

fire ant predation on arthropods but look for possible positive species interactions such as commensalisms. Furthermore many studies have examined the role fire ants play in agroecosystems, however far less research has focused on the affect they have in natural systems. Fire ants are important predators that can dramatically affect native arthropods negatively and/or positively thereby indirectly affecting plant fitness. Therefore future work should continue to examine the effect fire ants have on systems they invade.

Ant	Field Site	Year	Method	Effect	P-Value	F Stat
<i>S. invicta</i>	Lee	2005	Visual	-	<0.0001	42.85
<i>S. invicta</i>	Lee	2006	Visual	-	0.0228	7.90
<i>S. invicta</i>	Lee	2006	D-Vac	-	0.0006	29.83
<i>S. invicta</i>	Lee	2006	Pitfalls	-	<0.0001	69.14
<i>S. invicta</i>	Macon	2006	Visual	-	0.0019	13.26
<i>Crematogaster</i>	Macon	2006	Visual	-	0.0740	3.60
Other Ants	Macon	2006	Visual	0	0.2469	1.43
<i>S. invicta</i>	Macon	2006	D-Vac	0	0.0654	3.85
<i>Crematogaster</i>	Macon	2006	D-Vac	-	0.0520	4.33
<i>Pheidole</i>	Macon	2006	D-Vac	0	0.1745	2.00
<i>Pseudomyrmex</i>	Macon	2006	D-Vac	0	0.9715	0.00
<i>Monomorium</i>	Macon	2006	D-Vac	0	0.4191	0.68
<i>Dolichoderus</i>	Macon	2006	D-Vac	0	0.1510	2.25
<i>Tetrumorium</i>	Macon	2006	D-Vac	0	0.3306	1.00
<i>S. invicta</i>	Macon	2006	Pitfalls	-	0.0030	11.71
<i>Crematogaster</i>	Macon	2006	Pitfalls	0	0.9071	0.01
<i>Dolichoderus</i>	Macon	2006	Pitfalls	0	0.6250	0.25
<i>Monomorium</i>	Macon	2006	Pitfalls	0	0.5016	0.47
<i>Pheidole</i>	Macon	2006	Pitfalls	0	0.3018	1.13
<i>Camponotus</i>	Macon	2006	Pitfalls	0	0.2170	1.64

**Table 1.** The effect of Amdro on ants surveyed at two field sites over the course of two field seasons. Ant abundance was collected using D-Vac suction samplers, pitfall traps and visually scouting plants. Ants significantly negatively affected by Amdro are indicated by (-), and ants not affected by Amdro indicated by (0).

<b>Arthropod</b>	<b>Effect</b>	<b>P-Value</b>	<b>F Stat</b>
<i>Uroleucon spp. (Alates)</i>	0	0.5775	0.32
<i>Uroleucon spp. (Apterous)</i>	0	0.2820	1.20
Orthoptera	0	0.4098	0.70
Mantidae	0	0.2379	1.45
Spittle Mass	+	<0.0001	22.36
Cercopidae	0	0.1412	2.29
Cicadellidae	-	<0.0001	24.21
Membracidae	0	0.3440	0.93
Miridae	0	0.1888	1.81
Reduviidae	-	0.0021	11.43
Pentatomidae	0	0.4681	0.54
Coreidae	0	0.6439	0.22
Chrysomelidae	0	0.9822	0.00
Coccinellidae	-	0.0005	15.59
Scarabaeidae	0	0.7490	0.10
Lampyridae	0	0.1054	2.80
Hymenoptera	-	0.0038	9.97
Lepidoptera Larvae	0	0.7156	0.14
Diptera	-	<0.0001	57.22
Spiders	-	<0.0001	68.61

**Table 2.** The effect red imported fire ants have on arthropod abundances at our Lee Co. field site in 2005. Results obtained by visually scouting goldenrod plants within plots. Taxa benefiting from the presence of fire ants indicated by (+), taxa negatively affected by fire ant indicated by (-). Taxa not significantly affected by fire ants indicated by (0).

Arthropod	Effect	P-Value	F Stat
Orthoptera	0	0.8586	0.03
<i>U. luteolum</i> (Alates)	0	0.9764	0.00
<i>U. luteolum</i> (Apteros)	0	0.1693	2.28
<i>U. nigrotuberculatum</i> (Apteros)	0	0.7586	0.10
Spittle Mass	0	0.1683	2.29
Cercopidae	0	0.3466	1.00
Cicadellidae	0	0.1026	3.39
Membracidae	0	0.5796	0.33
Miridae	0	0.3466	1.00
Reduviidae	0	0.8089	0.06
Pentatomidae	0	0.3466	1.00
Coccinellidae	0	0.6491	0.22
Hymenoptera	0	0.8760	0.03
Diptera	0	0.4169	0.73
Spider	-	0.0241	7.70

**Table 3.** The effect of fire ants on visually surveyed arthropod abundances at the Lee Co. field in 2006. Arthropods significantly negatively affected by fire ants indicated by (-) and arthropods unaffected by fire ants indicated by (0).

Arthropod	Effect	P-Value	F Stat
Gryllidae	0	0.5893	0.32
Cicadellidae	-	0.0509	5.27
Cercopidae	0	0.9017	0.02
Miridae	0	0.1674	2.31
Reduviidae	0	0.4059	0.77
Tingidae	0	0.2327	1.67
Thysanoptera	0	0.2573	1.49
Chrysomelidae	0	0.6659	0.20
Curculionidae	0	0.7563	0.10
Hymenoptera	0	0.8571	0.03
Diptera	0	0.2959	1.25
Spider	-	0.0112	10.74
Green Lynx	0	0.8501	0.04

**Table 4.** The effect of fire ants on arthropods collected from D-Vac suction sampling in Lee Co. in 2006. Arthropods significantly negatively affected by fire ants indicated by (-) and arthropods unaffected by fire ants indicated by (0)

Arthropod	Effect	P-Value	F Stat
Isopod	0	0.0902	3.71
Gryllidae	0	0.3616	0.94
Acrididae	0	0.8370	0.05
Cercopidae	0	0.4780	0.55
Scarabaeidae	0	0.2094	1.86
Carabidae	0	0.2825	1.33
Chrysomelidae	0	0.9837	0.00
Diptera	0	0.1976	1.97
Spider	0	0.8759	0.03

**Table 5.** The effect of fire at on arthropods collected from pitfall traps in Lee Co. in 2006. Arthropods not significantly affected by fire ants indicated by (0).

Arthropod	Effect	P-Value	F Stat
Orthoptera	0	0.7302	0.12
<i>Uroleucon luteolum</i> (Alates)	0	0.1634	2.11
<i>Uroleucon luteolum</i> (Apteros)	-	0.0058	9.78
<i>Uroleucon nigrotuberculatum</i> (Alates)	0	0.3068	1.11
<i>Uroleucon nigrotuberculatum</i> (Apteros)	0	0.1507	2.25
Spittle Mass	0	0.4357	0.64
Cercopidae	0	0.4084	0.72
Cicadellidae	0	0.7532	0.10
Membracidae	0	0.9287	0.01
Miridae	0	0.7092	0.14
Reduviidae	0	0.4316	0.65
Pentatomidae	0	0.3553	0.90
Coccinellidae	0	0.1444	2.33
Scarabaeidae	0	0.6958	0.16
Chrysomelidae	0	0.8839	0.02
Lacewing Larvae	0	1.00	0.00
Hymenoptera	0	0.2683	1.31
Lepidoptera Larvae	0	0.2069	1.71
Diptera	0	0.2261	1.57
Spider	0	0.1513	2.25

**Table 6.** The effect of fire ants on visually sampled arthropods in Macon Co. in 2006. . Arthropods significantly negatively affected by fire ants indicated by (-) and arthropods unaffected by fire ants indicated by (0).



Arthropod	Effect	P-Value	F Stat
Gryllidae	0	0.6377	0.23
Acrididae	0	0.7405	0.11
Tettigoniidae	-	0.0203	6.48
<i>Uroleucon spp.</i>	0	0.3113	1.09
Cercopidae	0	0.1499	2.26
Cicadellidae	0	0.0707	3.69
Membracidae	0	0.2516	1.40
Miridae	-	0.0554	4.20
Reduviidae	-	0.0340	5.26
Pentatomidae	0	0.2076	1.71
Tingidae	0	0.5318	0.41
Thysanoptera	-	0.0350	5.20
Coccinellidae	0	1.00	0.00
Curculionidae	0	0.7669	0.09
Scarabaeidae	0	0.2025	1.75
Chrysomelidae	0	0.0950	3.10
Lacewing larvae	0	0.1510	2.25
Lepidoptera	0	0.2643	1.33
Diptera	-	0.0066	9.43
Spiders	-	<0.0001	23.77
Green Lynx	-	0.0126	7.67

**Table 7.** The effect of fire ants on arthropods collected by D-Vac sampling in Macon Co. in 2006. Arthropods significantly negatively affected by fire ants indicated by (-) and arthropods unaffected by fire ants indicated by (0).

Arthropod	Effect	P-Value	F Stat
Gryllidae	-	0.0193	6.60
Acrididae	0	0.7246	0.13
Reduviidae	0	0.7054	0.15
Scarabaeidae	0	0.3844	0.79
Chrysomelidae	0	0.2405	1.47
Carabidae	0	0.8150	0.06
Hymenoptera	0	0.8086	0.06
Lepidoptera	0	0.8675	0.03
Diptera	0	0.1080	2.86
Opiliones	0	0.3805	0.81
Spiders	0	0.2464	1.44

**Table 8.** The effect of fire ants on arthropods collected from pitfall traps in Macon Co. in 2006. Arthropods significantly negatively affected by fire ants indicated by (-) and arthropods unaffected by fire ants indicated by (0).

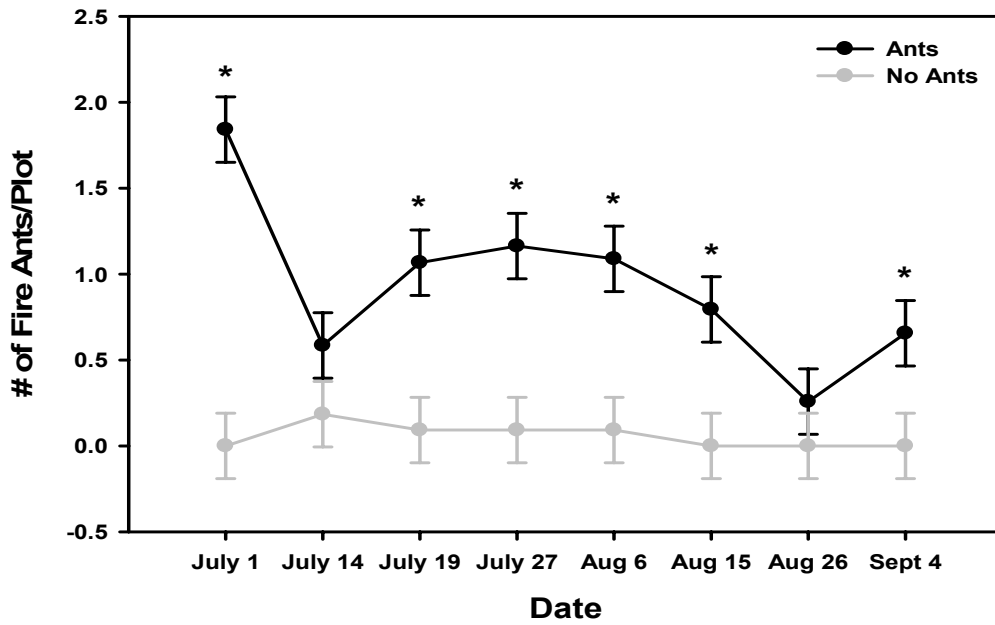


Figure 1. Amdro successfully suppressed fire ants at Lee Co. in 2005. Ants were significantly less abundant in Amdro treated plots (gray line) compared to control plots (black line) ( $F_{1,8} = 42.85$ ;  $P < 0.0001$ ).

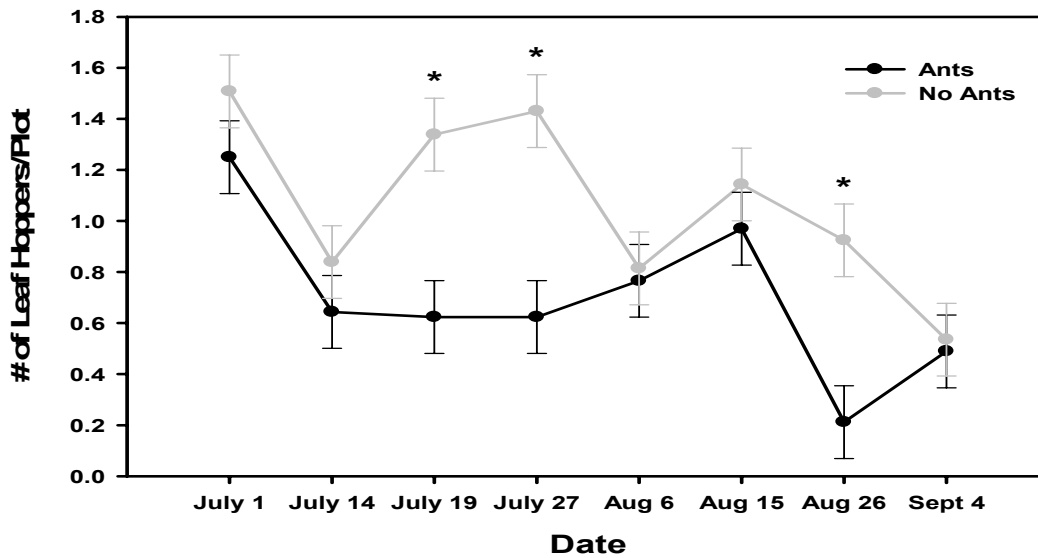


Figure 2. Fire ants reduced the abundance of leaf hoppers (black line) at Lee Co. in 2005. Leaf hoppers were significantly reduced on three of the eight sampling dates ( $F_{1,8} = 24.21$ ;  $P < 0.0001$ ).

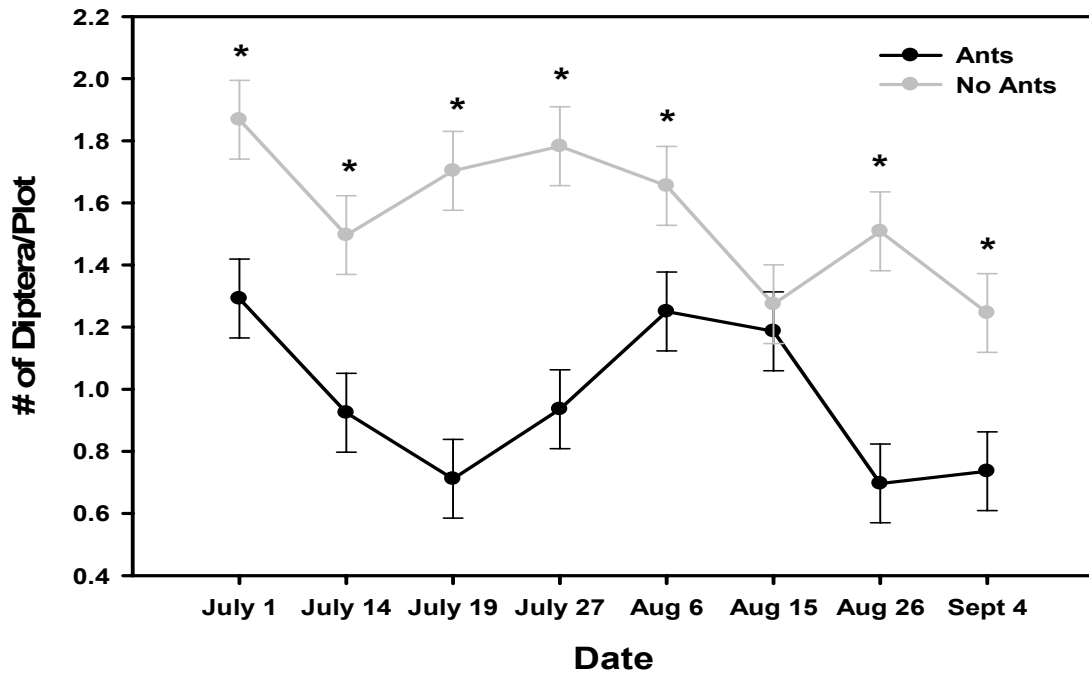


Figure 3. Fire ants reduced diptera abundance at Lee Co. in 2005. The presence of ants significantly reduced dipterans (black line) on nine out of eight sampling dates ( $F_{1,8} = 57.22$ ;  $P < 0.0001$ ).

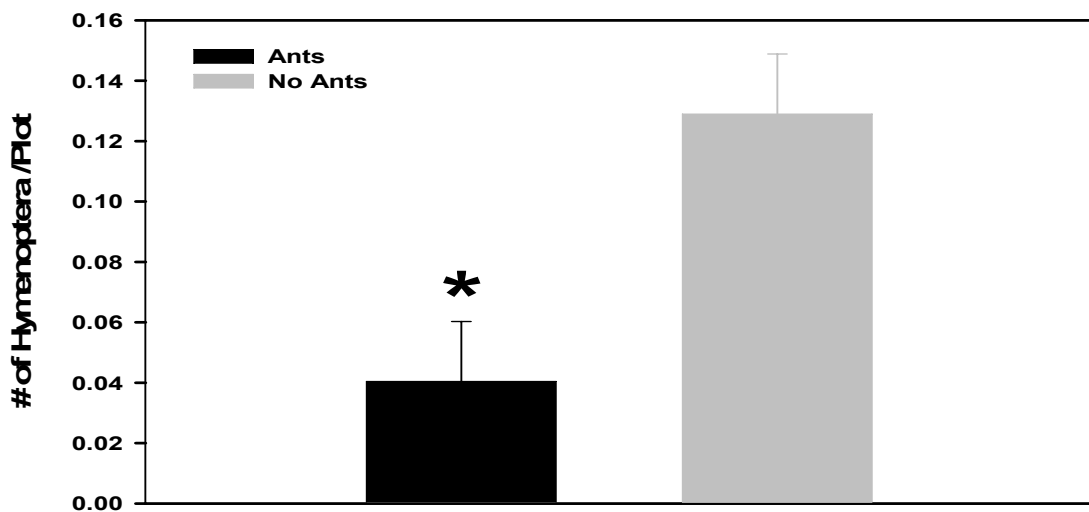


Figure 4. The presence of fire ants had a negative affect on hymenopterans at Lee Co. in 2005. ( $F_{1,8} = 9.97$ ;  $P = 0.0038$ ).

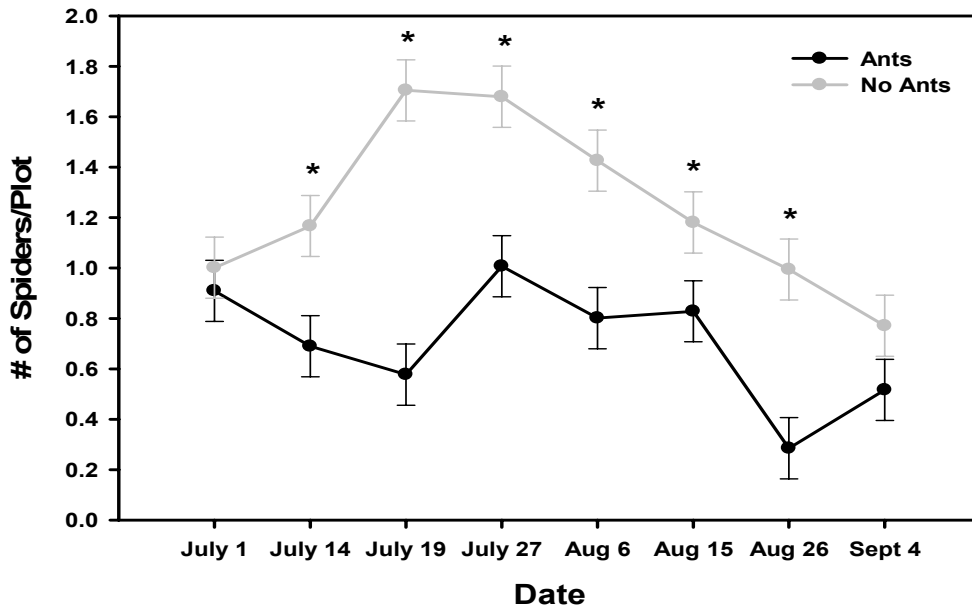


Figure 5. Fire ants decreased spider abundance at Lee Co. in 2005. Spiders were less abundant in control plots (black line) on six out of eight dates sampled ( $F_{1,8} = 68.61$ ;  $P < 0.0001$ ).

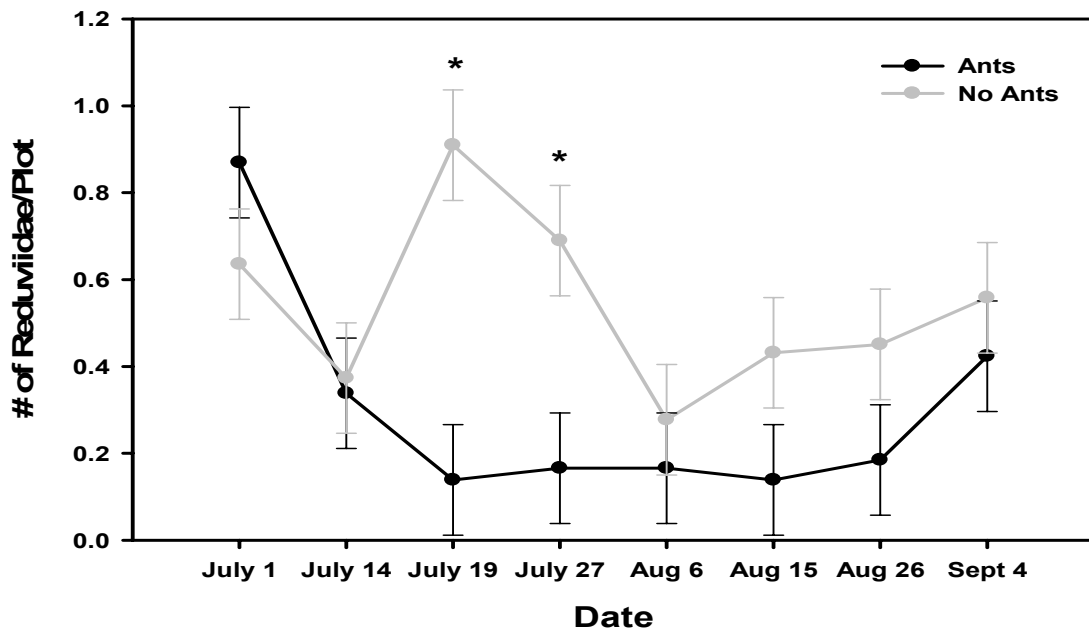


Figure 6. Fire ants had a negative affect on reduviids at Lee Co. in 2005. Reduviids were significantly less abundant in fire ant plots (black line) on two of eight sampling dates ( $F_{1,8} = 11.43$ ;  $P = 0.002$ ).

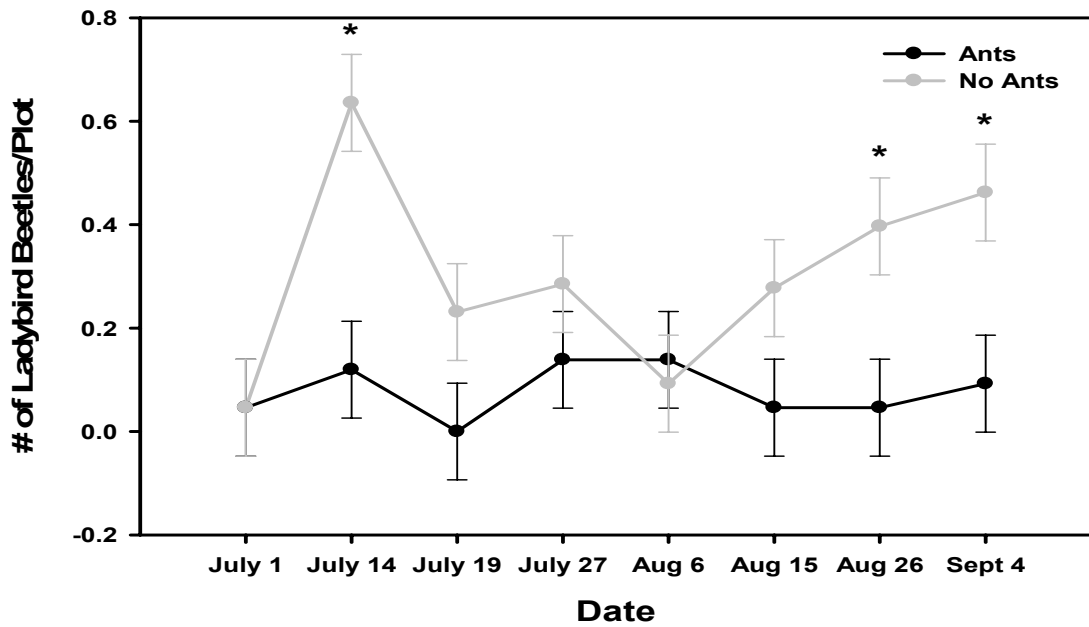


Figure 7. The presence of fire ants reduced ladybird beetle densities at Lee Co. in 2005. Ladybirds were significantly less abundant in plots with ants (black line) on three of eight sampling dates ( $F_{1,8} = 15.59$ ;  $P = 0.0005$ ).

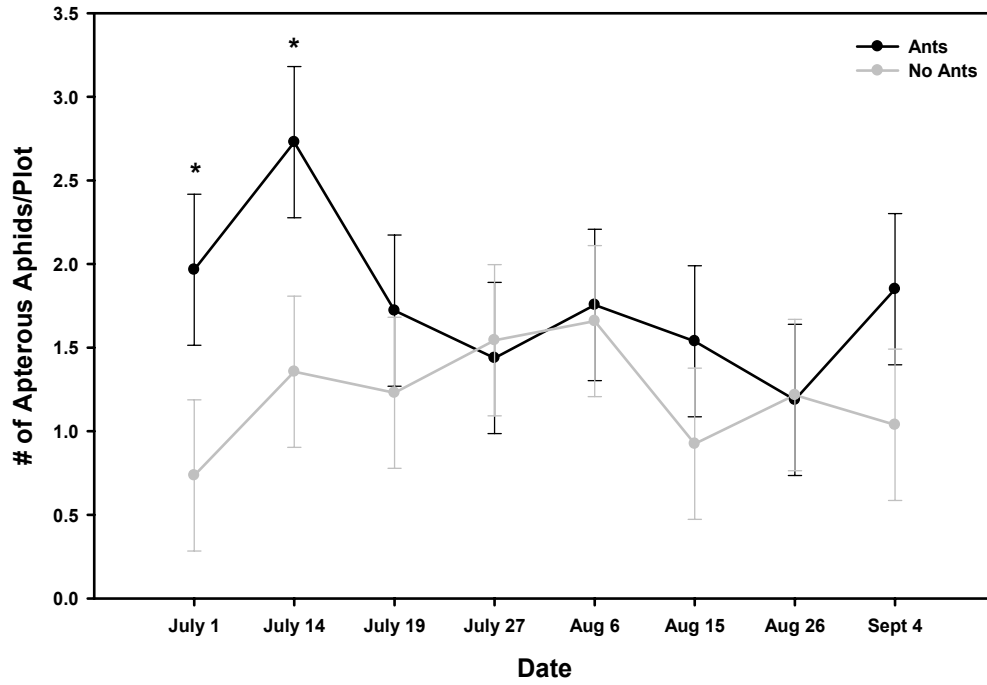


Figure 8. Fire ants had no consistent affect on aphid densities at Lee Co. in 2005 ( $F_{1,8} = 1.2$ ;  $P = 0.282$ ).



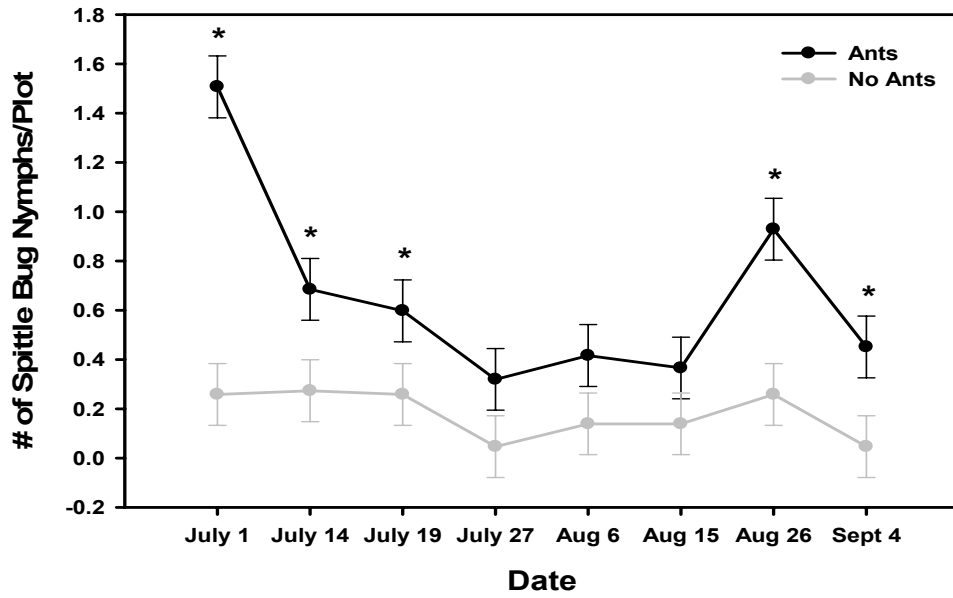


Figure 9. Fire ants increased spittlebug densities at Lee Co. in 2005. Spittlebugs were significantly more abundant in fire ant plots (black line) on five of eight sampling dates ( $F_{1,8} = 22.36$ ;  $P < 0.0001$ ).

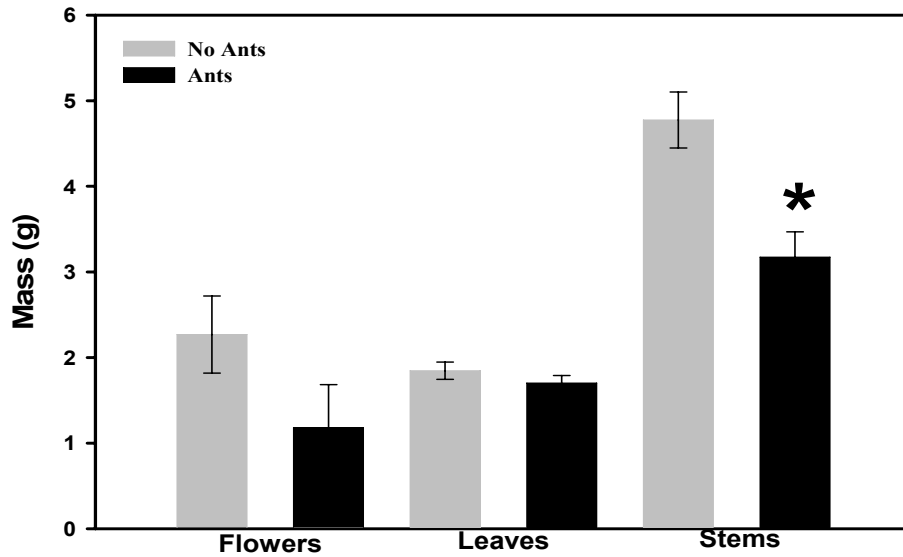


Figure 10. Fire ants had an indirect negative affect on arthropod hosts plants in Lee Co. in 2005. The dry mass of goldenrod stems was significantly lower in plots with ants (black bar) compared to ant suppressed plots (gray bar) ( $F_{1,328} = 13.19$ ;  $P = 0.0003$ ). Fire ants had no significant affect on the dry mass of flowers ( $F_{1,128} = 2.6$ ;  $P = 0.109$ ) and leaves ( $F_{1,325} = 1.15$ ;  $P = 0.284$ ).

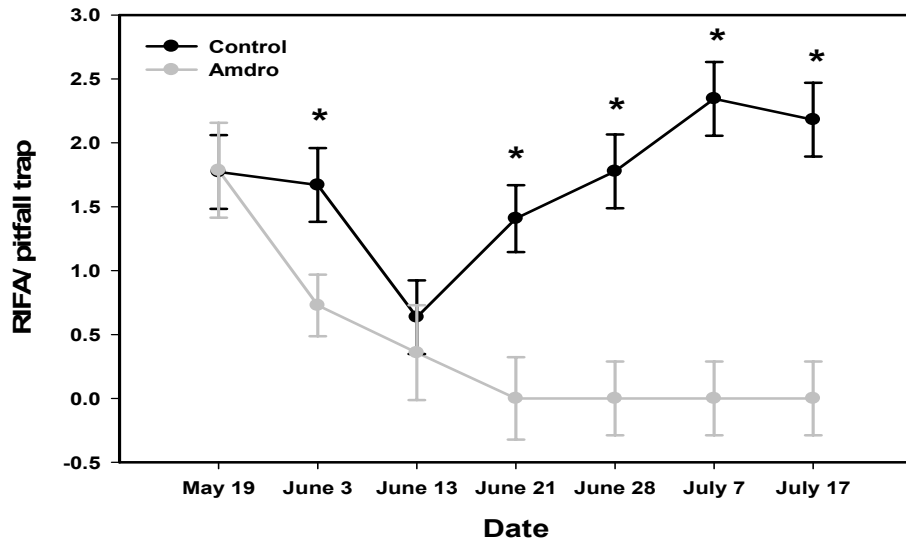


Figure 11. Amdro applications successfully reduced fire ant densities at Lee Co in 2006. Significantly less fire ants were captured in pitfall traps in Amdro treated plots (gray line) compared to control plots (black line) ( $F_{1,7} = 69.14$ ;  $P < 0.0001$ ).

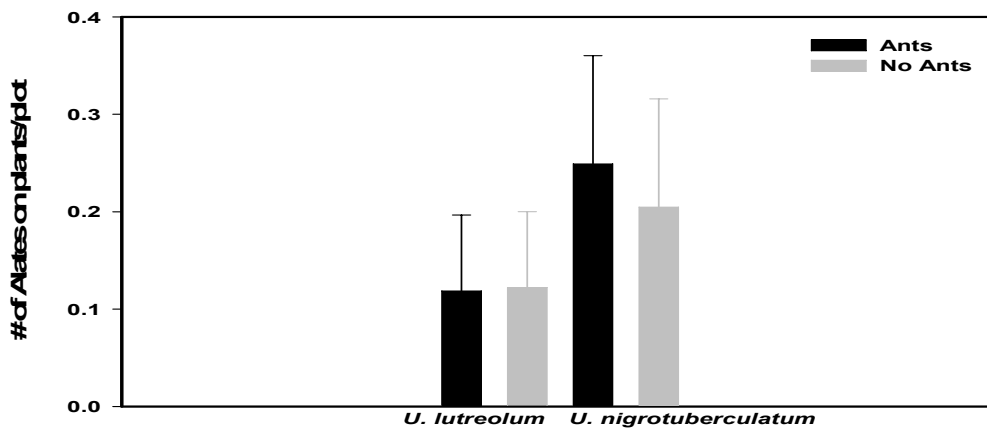


Figure 12. The presence of fire ants had no significant affect on alate production in Lee Co. in 2006. *U. luteolum* ( $F_{1,7} = 0$ ;  $P = 0.976$ ) and *U. nigrotuberculatum* ( $F_{1,7} = 0.08$ ;  $P = 0.7842$ ).

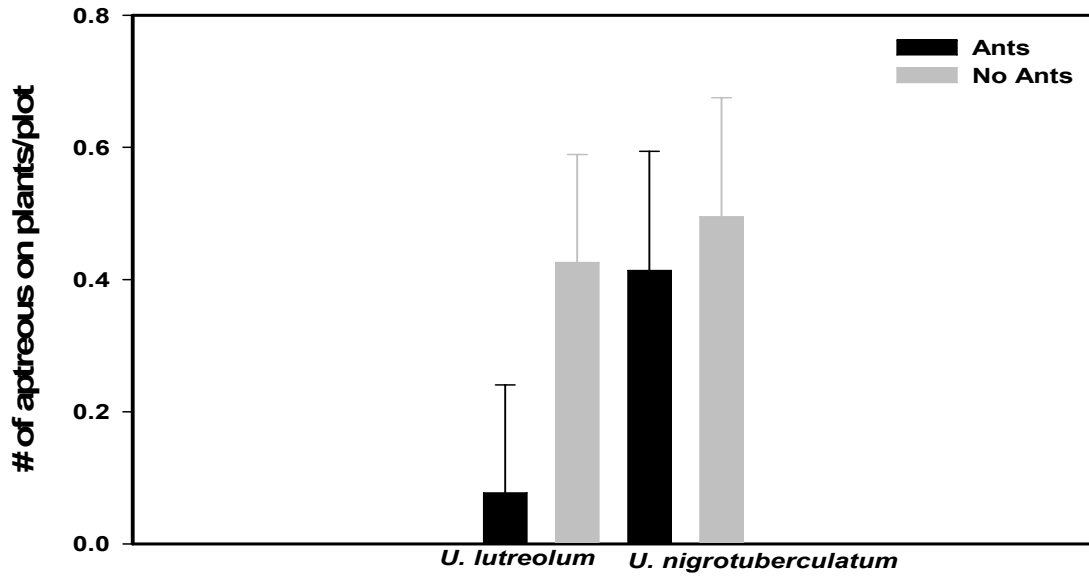


Figure 13. Fire ants did not significantly affect apterous aphid densities at Lee Co. in 2006 *U. luteolum* ( $F_{1,7} = 2.28$ ;  $P = 0.1693$ ) *U. nigrotuberculatum* ( $F_{1,7} = 0.10$ ;  $P = 0.7586$ ).

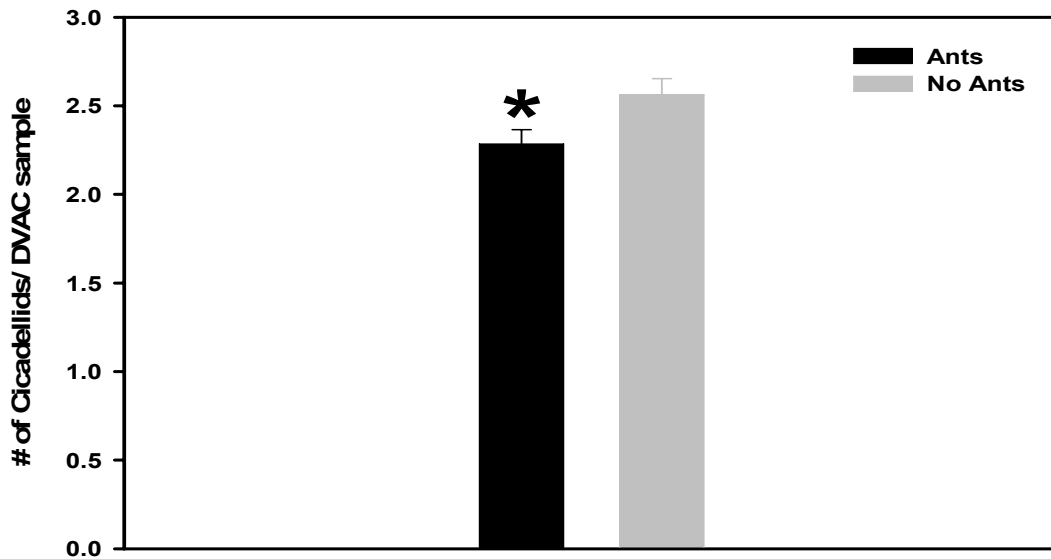


Figure 14. Fire ants decreased leaf hopper abundances at Lee Co. in 2006. D-Vac samples in fire ant plots (black bar) contained significantly less leaf hoppers than suppressed fire ant plots (gray bar) ( $F_{1,8} = 5.27$ ;  $P = 0.050$ ).

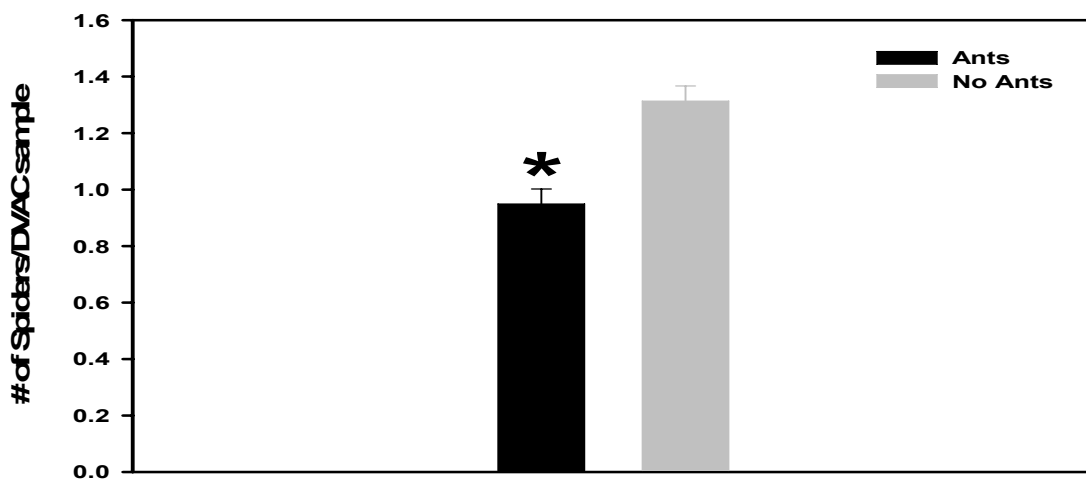


Figure 15. Fire ants significantly reduced spider densities at Lee Co. in 2006. D-Vac samples collected in fire ant plots (black bar) contained significantly less spiders than fire ant suppressed plots (gray bar) ( $F_{1,8} = 10.74$ ;  $P = 0.011$ ).

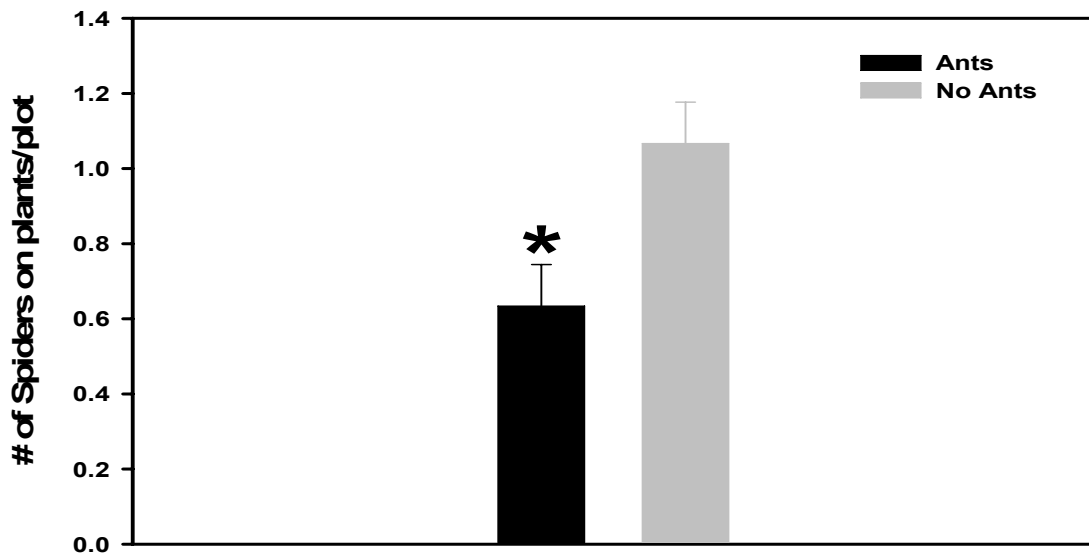


Figure 16. Visual surveys of plots at Lee Co. in 2006 revealed fire ants negatively affect spiders. Significantly fewer spiders were observed in plots with ants (black bar) compared to plots without ant (gray bar) ( $F_{1,7} = 7.7$ ;  $P = 0.024$ ).

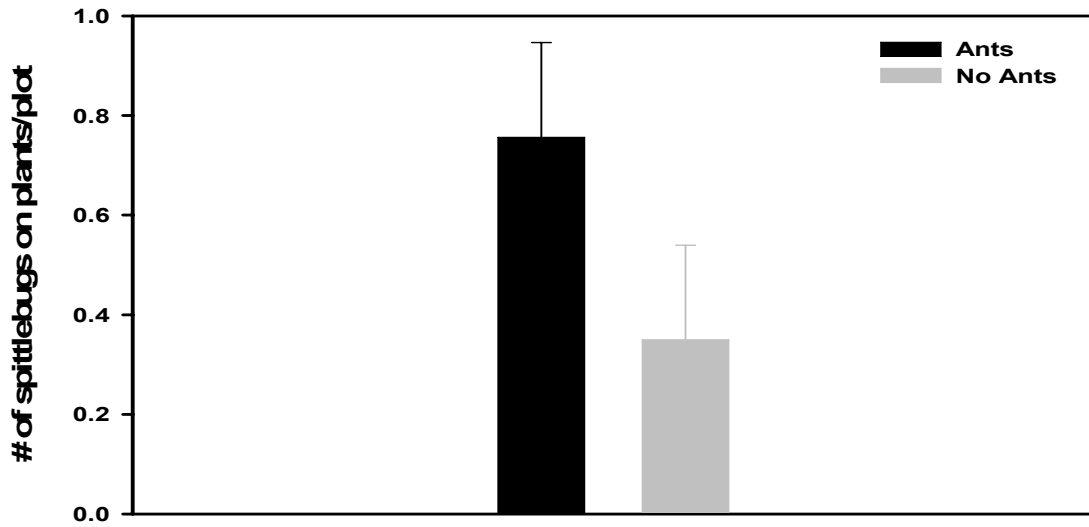


Figure 17. Fire ants did not significantly affect spittlebugs at the Lee County field site in 2006 ( $F_{1,7} = 2.29$ ;  $P = 0.168$ ). However spittlebugs were two times more abundant in plots with fire ants (black bar).

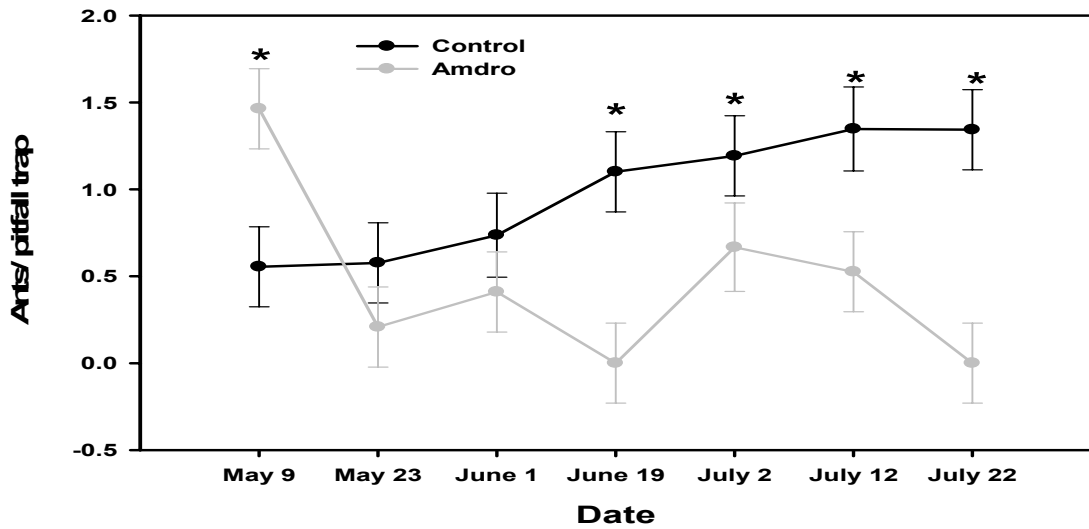


Figure 18. Amdro successfully reduced fire ant densities at Macon Co. in 2006. Plots with Amdro application (gray line) capture significantly less fire ants in pitfall traps compare to control plots (black line) ( $F_{1,8} = 11.71$ ;  $P = 0.003$ ).

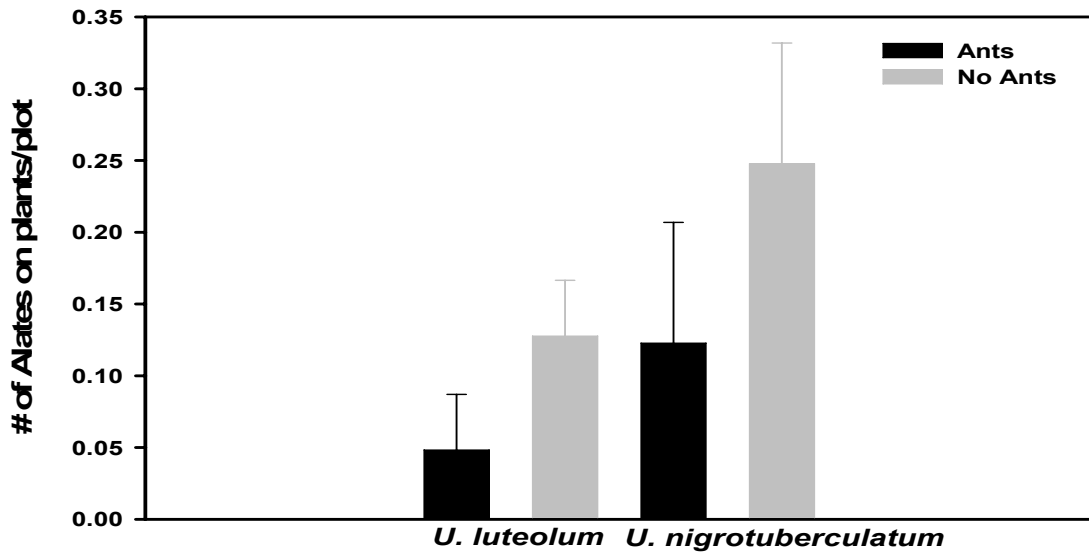


Figure 20. The presence of ants did not affect alate production in *U. luteolum* ( $F_{1,8} = 2.11$ ;  $P = 0.163$ ) or *U. nigrotuberculatum* ( $F_{1,8} = 1.11$ ;  $P = 0.3068$ ) at Macon Co. in 2006.

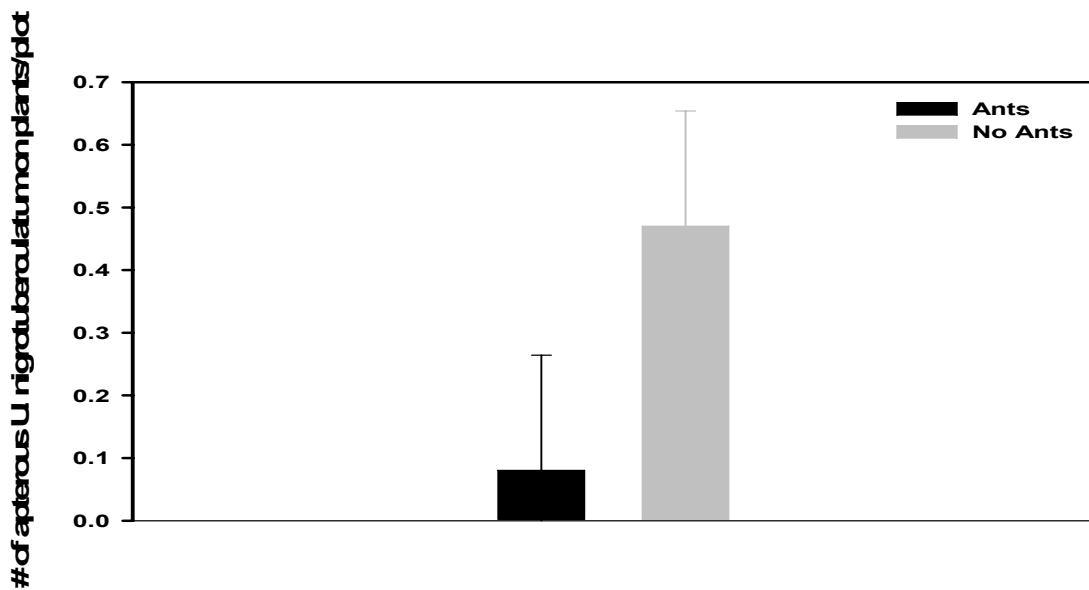


Figure 21. Fire ants had no significant affect on apterous *U. nigrotuberculatum* densities ( $F_{1,8} = 2.25$ ;  $P = 0.151$ ) at Macon Co. in 2006.



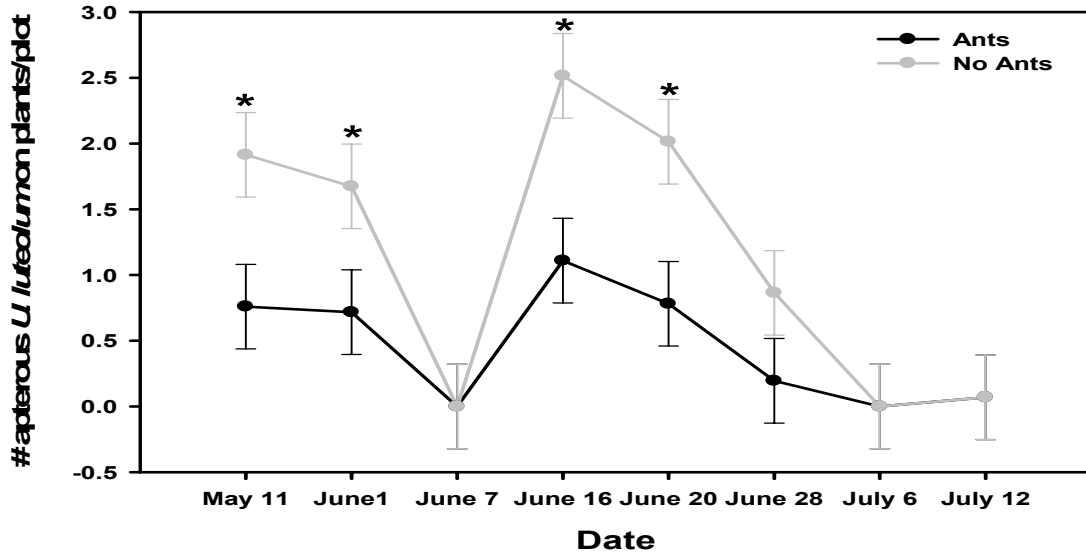


Figure 22. Fire ants had a negative affect on apterous *U. luteolum* at Macon Co. in 2006. Fire ant plots (black bar) had significantly less apterous *U. luteolum* on four of eight dates sampled ( $F_{1,8} = 9.78$ ;  $P = 0.005$ ).

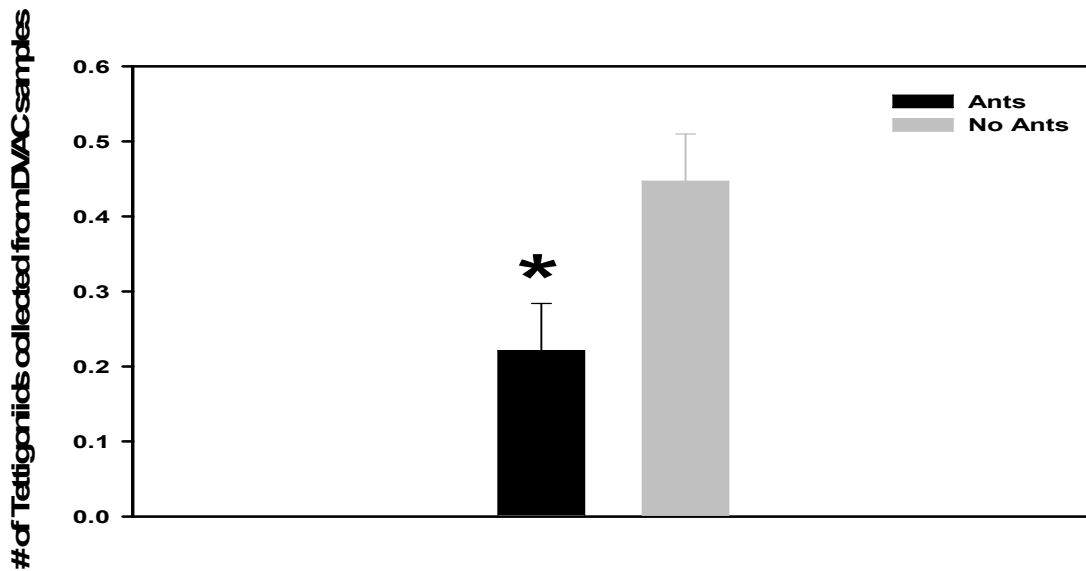


Figure 23. Fire ants decreased tettigoniid abundances at Macon Co. in 2006. Significantly less tettigoniids were collected from D-Vac samples in fire ant plots (black bar) compared to plots without fire ants (gray bar) ( $F_{1,9} = 6.48$ ;  $P = 0.020$ ).

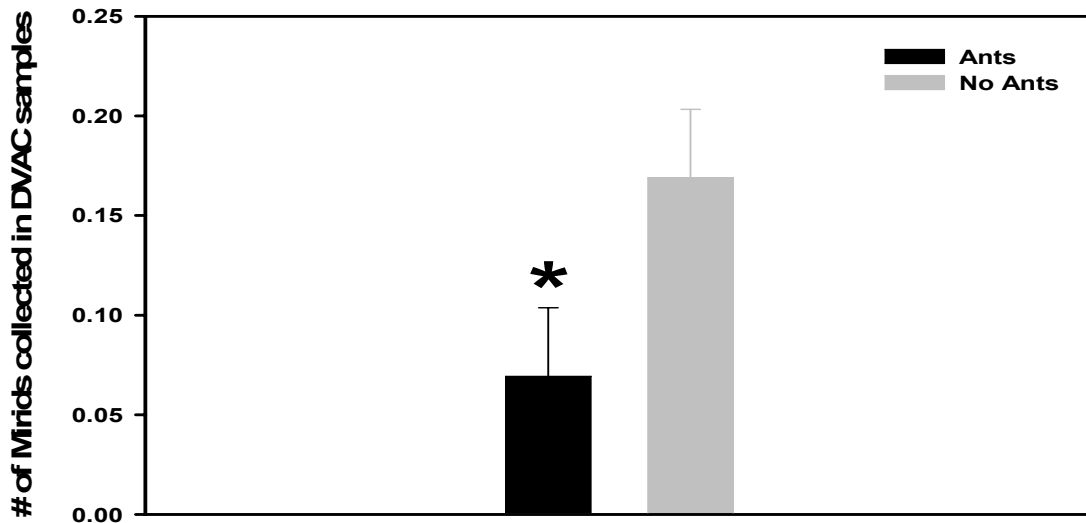


Figure 24. Fire ants negatively affect mirids at Macon Co. in 2006. Significantly less mirids were collected from D-Vac samples in plots with fire ants (black bar) ( $F_{1,9} = 4.20$ ;  $P = 0.055$ ).

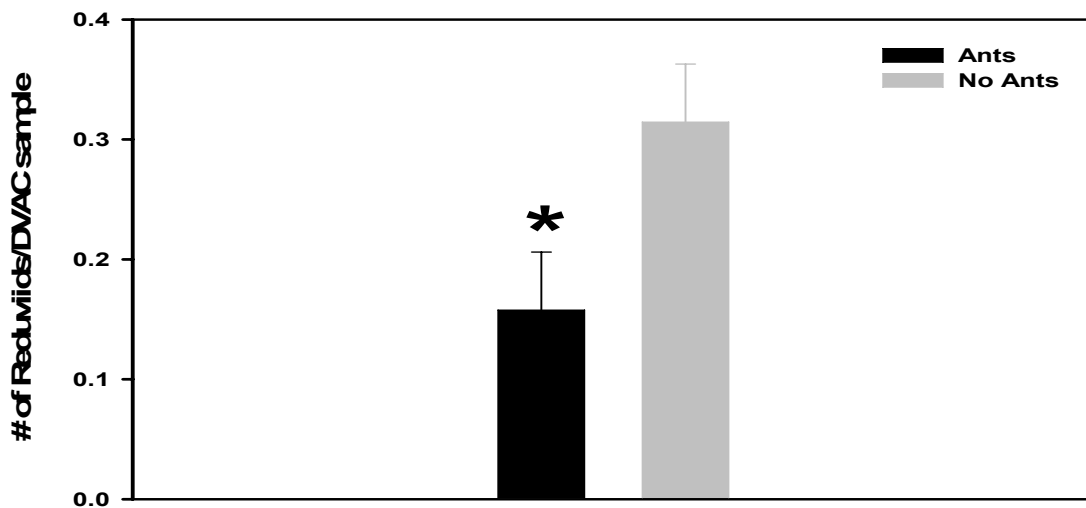


Figure 25. Reduviid densities decreased in the presence of fire ants at Macon Co. in 2006. Plots with fire ants (black bar) had significantly fewer reduviids collected from D-Vac samples ( $F_{1,9} = 5.27$ ;  $P = 0.034$ ).

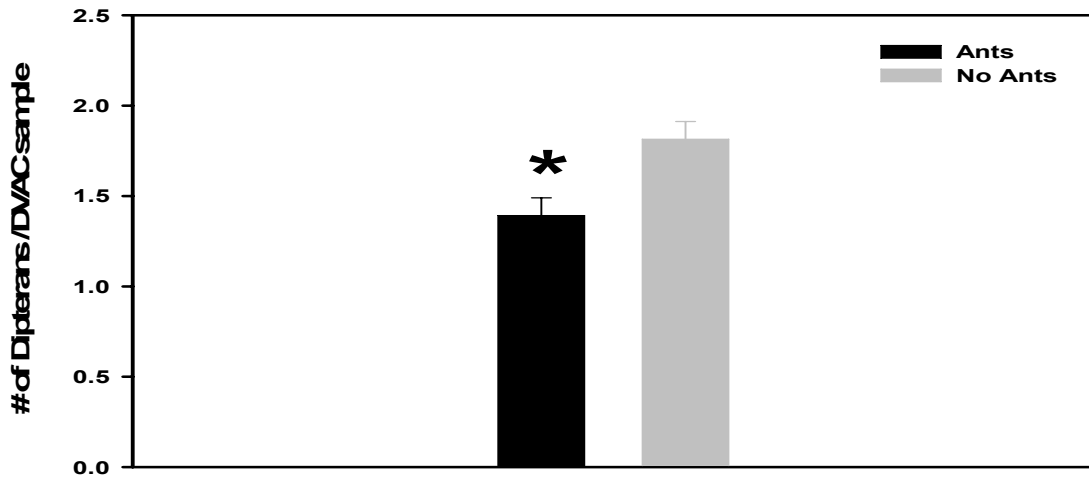


Figure 26. Fire ants decreased diptera abundance. Plots with fire ants (black bar) had significantly less dipterans collected in D-Vac samples ( $F_{1,9} = 9.43$ ;  $P = 0.006$ ) at Macon Co. in 2006.

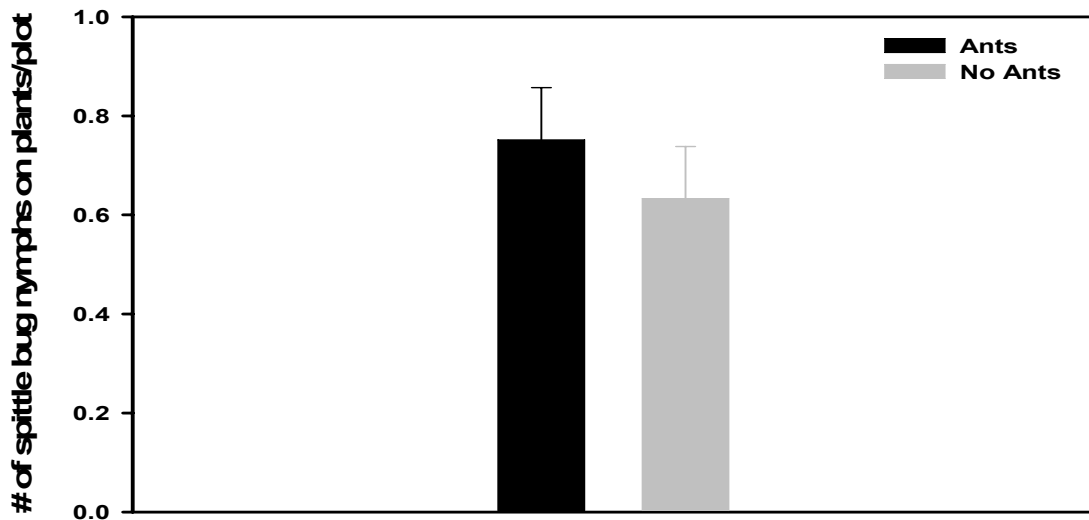


Figure 27. No significant difference was observed in spittlebug abundance in plots with fire ants (black bar) compare to plots with no ants (gray bar) ( $F_{1,8} = 0.64$ ;  $P = 0.435$ ) at Macon Co. in 2006.

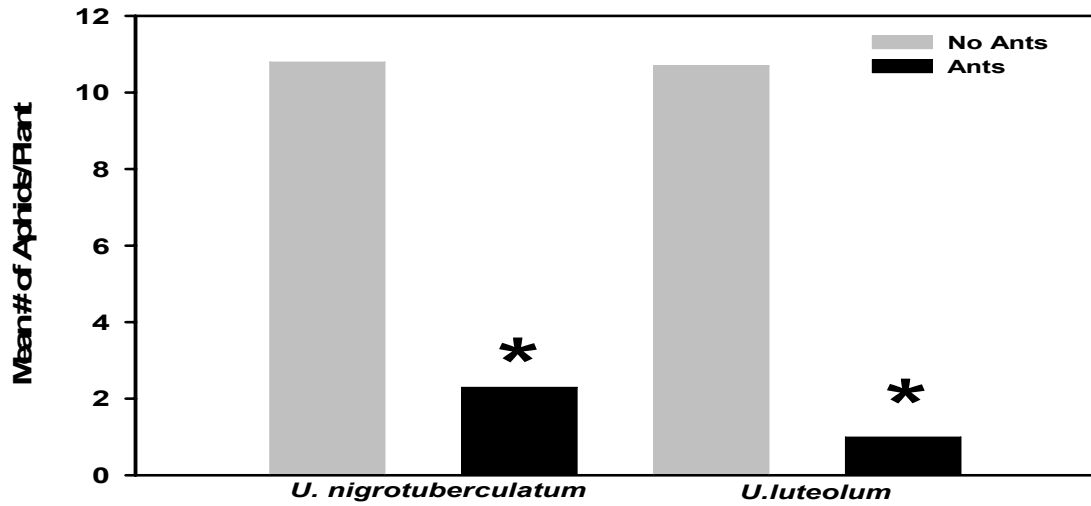


Figure 28. In a greenhouse experiment we found strong evidence that fire ants negatively affect two species of *Uroleucon* aphids. Aphids exposed to fire ants had a significant reduction in density. *U. luteolum* ( $F_{1,20} = 79.81$ ;  $P < 0.0001$ ), *U. nigrotuberculatum* ( $F_{1,20} = 45.25$ ;  $P < 0.0001$ ).

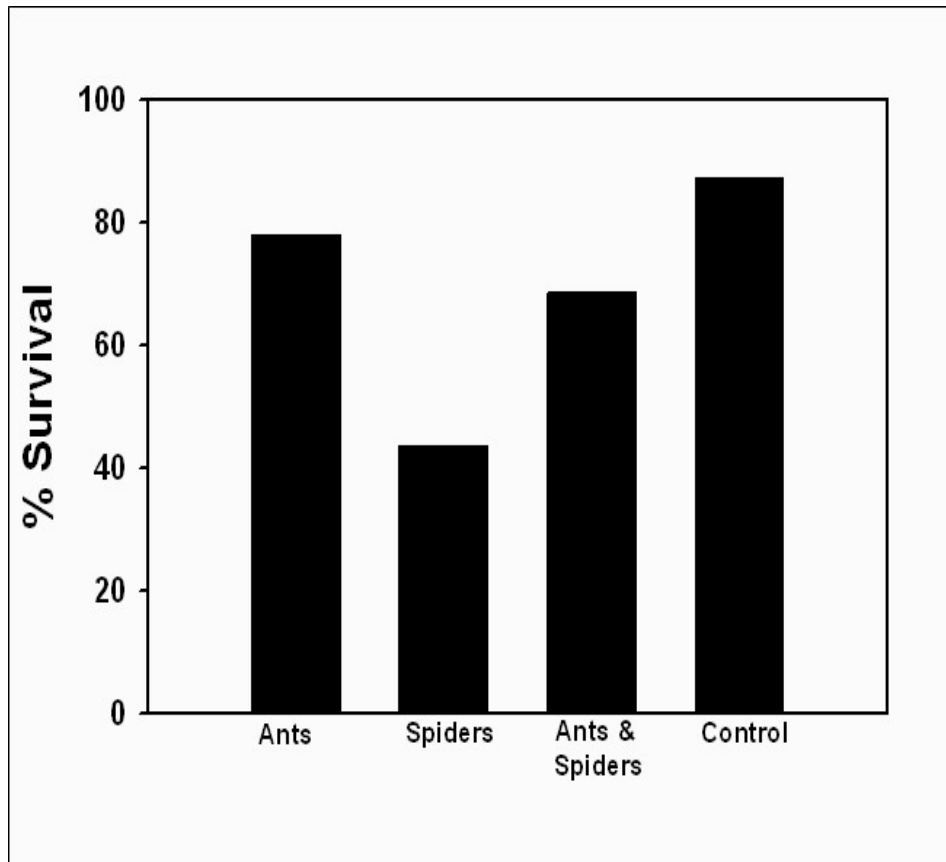


Figure 29. Greenhouse experiments indicate a fire ant-spittlebug commensalism. Ants do not significantly affect spittlebug survival( $X^2 = 0.5376$ ;  $P = 0.4634$ ). However spiders have a significant negative affect on spittlebug survival( $X^2 = 7.5599$ ;  $P = 0.0060$ ). The presence of fire ants reduces the negative affect spiders have on spittle bug survival( $X^2 = 5.2918$   $P = 0.0214$ ).

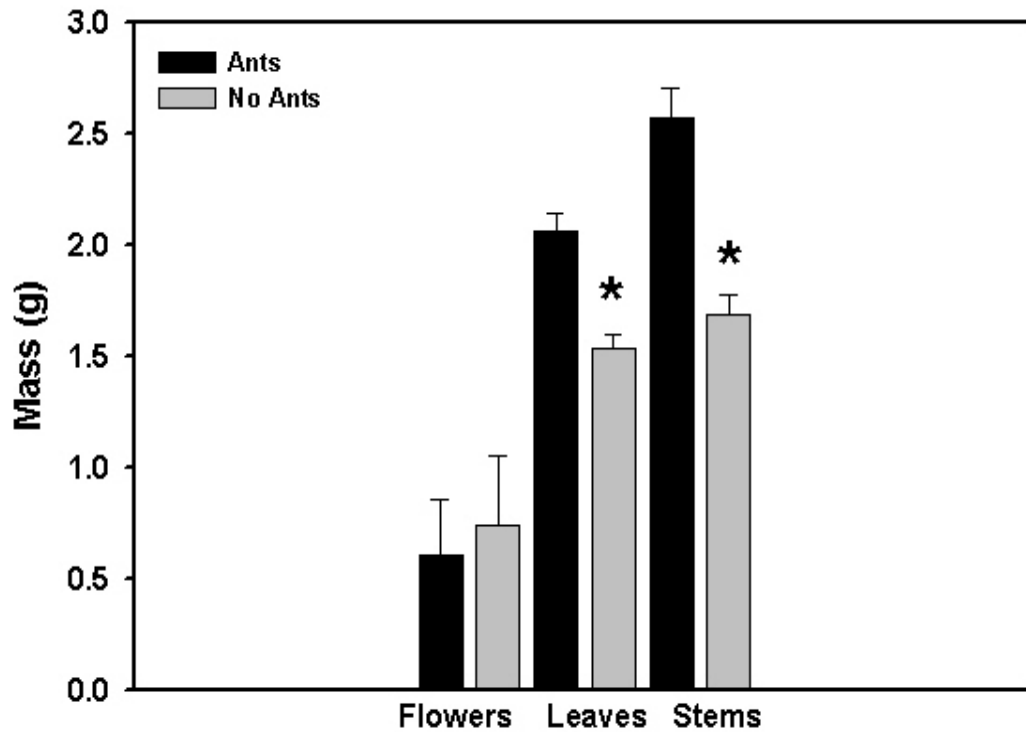


Figure 30. The indirect effect of fire ants on goldenrod plants in Macon Co. in 2006. Plants in plots with fire ants had significantly higher leaf ( $F_{1,1085} = 26.94$ ;  $P < 0.0001$ ) and stem ( $F_{1,1085} = 29.44$ ;  $P < 0.0001$ ) mass. Flower mass did not significantly differ between the treatments ( $F_{1,6} = 10$ ;  $P = 0.757$ ).

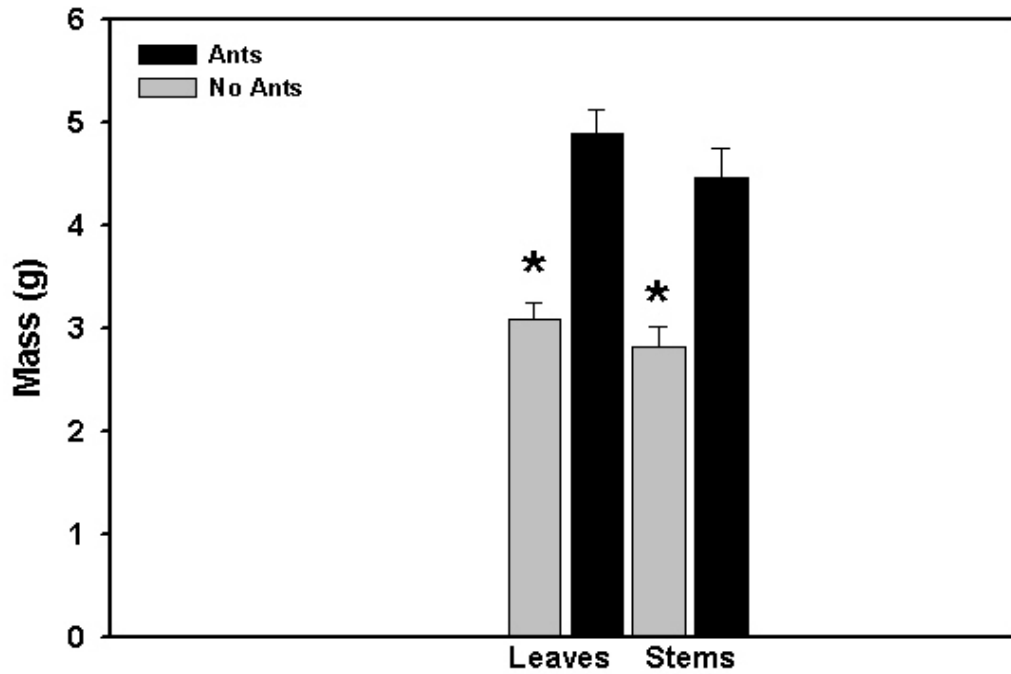


Figure 31. The indirect effect of fire ants on goldenrod plants In Lee Co. in 2006. Plants in plots with fire ants has higher leaf ( $F_{1,309} = 34.71$ ;  $P = <0.0001$ ) and stem ( $F_{1,309} = 21.08$ ;  $P = <0.0001$ ) mass. No flower data was collected from Lee Co. in 2006.

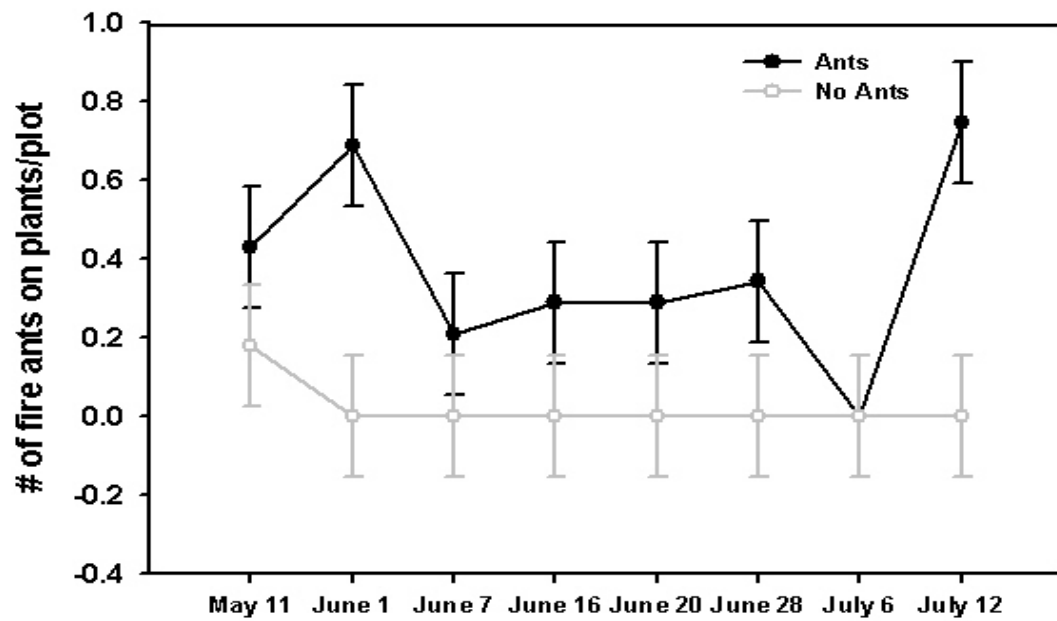


Figure 32. The number of fire ants found on plants in suppressed ant plots (gray line) and control plots (black line) from visual surveys conducted in Macon Co. in 2006.



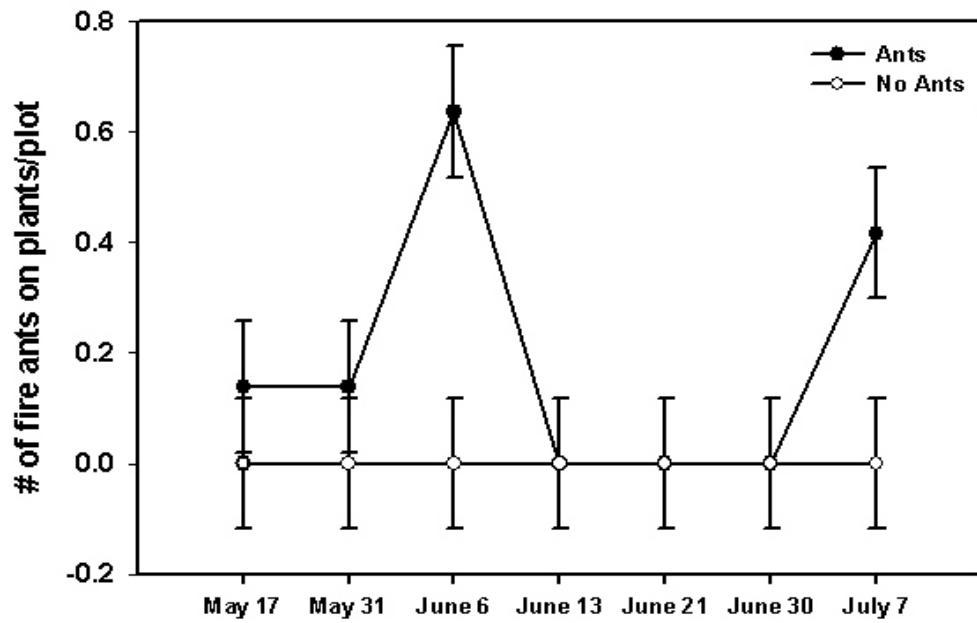


Figure 33. The number of fire ants found on plants by visual surveys in Lee Co. in 2006. Fire ants were significantly more abundant in control plots (black line) than suppressed ant plots (gray line) on two out of seven sampling dates.

## OVERALL CONCLUSION

This study is one of the first to examine the impact of fire ants on arthropods in natural systems. In addition our study is the first to suggest a positive interaction between fire ants and spittlebugs. Future studies should not only focus on the effect of fire ant predation on arthropods but look for possible positive species interactions such as commensalisms. Furthermore, many studies have examined the role fire ants play in agroecosystems, however far less research has focused on the effect they have in natural systems. Fire ants are important predators that can dramatically affect native arthropods negatively and/or positively thereby indirectly affecting plant fitness. Future work should continue to examine the effect fire ants have on systems they invade.

Future research should also focus on direct effects of positive interactions. For instance research should also consider variation in mutualistic partners. Different aphid species often produce different quantities and varying qualities of honeydew (Volkl et al. 1999). Therefore different species of aphids may provide ants with different levels of direct benefits. Likewise, different species of ants have been shown to provide different levels of protection to aphids (Messina 1981). Therefore it is reasonable to suggest that different ant species will also have differential direct effects on aphids when natural enemies are excluded.

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