To the Graduate Council:

I am submitting herewithin a thesis written by Leah V. Gibbons entitled "Assessment of Competition Between Hybrid Imported Fire Ants, *Solenopsis invicta* x *S. richteri*, and Native Ants in Southeastern Tennessee." I have examined the final paper of this thesis for form and content and recommend that it be accepted in partial fulfillment of the requirements for the degree of Master of Science, with a major in Ecology and Evolutionary Biology.

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and recommend its acceptance:

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Accepted for the Council:

Vice Provost and Dean of Graduate Studies

ASSESSMENT OF COMPETITION BETWEEN HYBRID IMPORTED FIRE ANTS, *SOLENOPSIS INVICTA* x *S. RICHTERI*, AND NATIVE ANTS IN SOUTHEASTERN TENNESSEE

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Abstract

Interspecific competition between invasive hybrid imported fire ants, *Solenopsis invicta* x *S. richteri*, and native ants and the role of fire ant population density on competitive ability were quantified in two different habitat types, field and pasture, in southeastern Tennessee. To quantify the effects of competition indirectly, diversity values for ant communities were calculated in sites invaded and not invaded by fire ants within the field and pasture habitats. Sites invaded by fire ants had lower ant species diversity than sites not invaded. Further, sites invaded by fire ants had up to 6.75 times more individuals than sites not invaded, but fire ants accounted for as much as 93% of these individuals.

Baiting experiments were performed in invaded sites to observe competition directly and to quantify it. Species composition and interactions at a total of 60 baits in each habitat were recorded every 15 minutes over a three-hour period. Competitive ability was described by the number of baits a species discovered first, recruited to first, and numerically controlled at the end of the three-hour observation period. Fire ants performed better than all native ant genera combined for all of these variables. Fire ants discovered and recruited to baits more quickly than all native ant genera except for *Monomorium*. Fire ants also recruited to a higher portion of baits discovered except for *Monomorium* in the pasture habitat. In addition, fire ants were present at baits in much higher densities than native ants. Very few baits were recruited to by more than one genus at the same time. When more than one genus did co-occur at a bait, the genera always spatially partitioned the bait, thus avoiding interspecific interactions. Dietary preferences were shown in this partitioning. Fire ants preferred to feed upon the hot dog

(lipid and protein source) portion of the bait while other genera preferred the sugar-sodium hydroxide portion of the bait (carbohydrate source). When interspecific interactions did occur, they were rarely aggressive. In fact, of 120 baits and 72 hours of observation time, only 2 aggressive interactions were observed. Despite the lack of co-occurrence of genera at baits and the lack of aggressive encounters, control of some baits did switch throughout the course of the observation period. When a switch occurred, the density of the numerically dominant genus slowly decreased while the density of the other genus at the bait slowly increased until it dominated at the bait.

To examine the role of fire ant population density on competitive performance, half of all fire ant mounds in a one hectare area in each habitat were poisoned with Ortho^{R} Orthene^{R} Fire Ant Killer and the same baiting experiment as described above was performed. After fire ant population density had been reduced, native ant genera discovered and recruited to more baits first than did fire ants. In fact, after fire ant nest poisoning, native ants discovered first, recruited to first, and controlled more than twice as many baits as they did before poisoning. Additionally, after fire ants were poisoned, native ants recruited to a higher portion of baits discovered and recruited to baits more quickly once they had been discovered than they did before poisoning. The reduction in fire ant population density negatively affected its competitive ability. After poisoning, fire ants discovered first and recruited first to approximately half as many baits as they did before poisoning, but they controlled the same number of baits that they did before poisoning. Fire ants recruited to fewer baits discovered in the field habitat, and their recruitment time after discovery of a bait was longer in the pasture habitat. Importantly, native ants and fire ants controlled equal numbers of baits after poisoning. Even after

poisoning, fire ants were present at baits in higher densities than native ants. As occurred before poisoning, few baits were recruited to by more than one genus at the same time, very few aggressive interactions occurred, baits were spatially partitioned, dietary preferences were shown, and control of baits changed slowly over time.

These results support the hypothesis that invasive fire ants are superior competitors to native ants in invaded habitats. In contrast to what other studies have reported, aggressive interactions at baits played an insignificant role in competitive outcome for resources while exploitation competition appeared to be the dominant mode of competition. Fire ant population density played a pivotal role in their competitive superiority and may be the proximate reason why introduced fire ants have had such a high level of success invading native ant communities.

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Chapter I

Introduction

Two forms of fire ants have invaded North America. The black imported fire ant, *Solenopsis richteri*, is native to southernmost Brazil (Rio Grande do Sul), Uruguay, and Argentina (Fig. 1). The red imported fire ant, *Solenopsis invicta*, is native to Paraguay and Mato Grasso, Brazil, specifically the Pantanal (Fig. 1) (Buren 1972). Both species were first detected in Mobile, Alabama, *S. richteri* in 1918 and *S. invicta* in the late 1930's. They were probably carried in nursery stock imported from South America (Buren 1972, Buren et al. 1974). Since their introduction, these fire ants have spread rapidly. By 1999 they occupied 121 million hectares of land in the southeastern United States and Puerto Rico. They have recently infested California and are present in isolated areas in Arizona, Maryland, Nevada, New Mexico, and Virginia, though they are not yet quarantined in most of these states (Fig. 2) (Wojcik et al. 2001). Red imported fire ants are found throughout most of the Southeast, black imported fire ants are found (mostly) to the north of the red imported fire ants' range, and hybrid forms (*S. invicta* x *S. richteri*) are found between the two and interspersed among them. In Tennessee, all three forms exist, *S. invicta*, *S. richteri*, and *S. invicta* x *S. richteri* (*Karen Vail, personal communication*) (Fig. 3).

Fire ants are important economic pests in the southern United States, exacting a cost in excess of $1 billion annually (Thompson et al. 1995). They feed on crops, girdle young citrus trees, tend aphids and mealy bugs on plants, sting livestock and humans, damage farm machinery that strikes mounds, and cause the loss of hay and grazing areas

Figure 1. Native range of the red fire ant, *Solenopsis invicta*, and the black fire ant, *S. richteri*. From Buren et al. 1974.

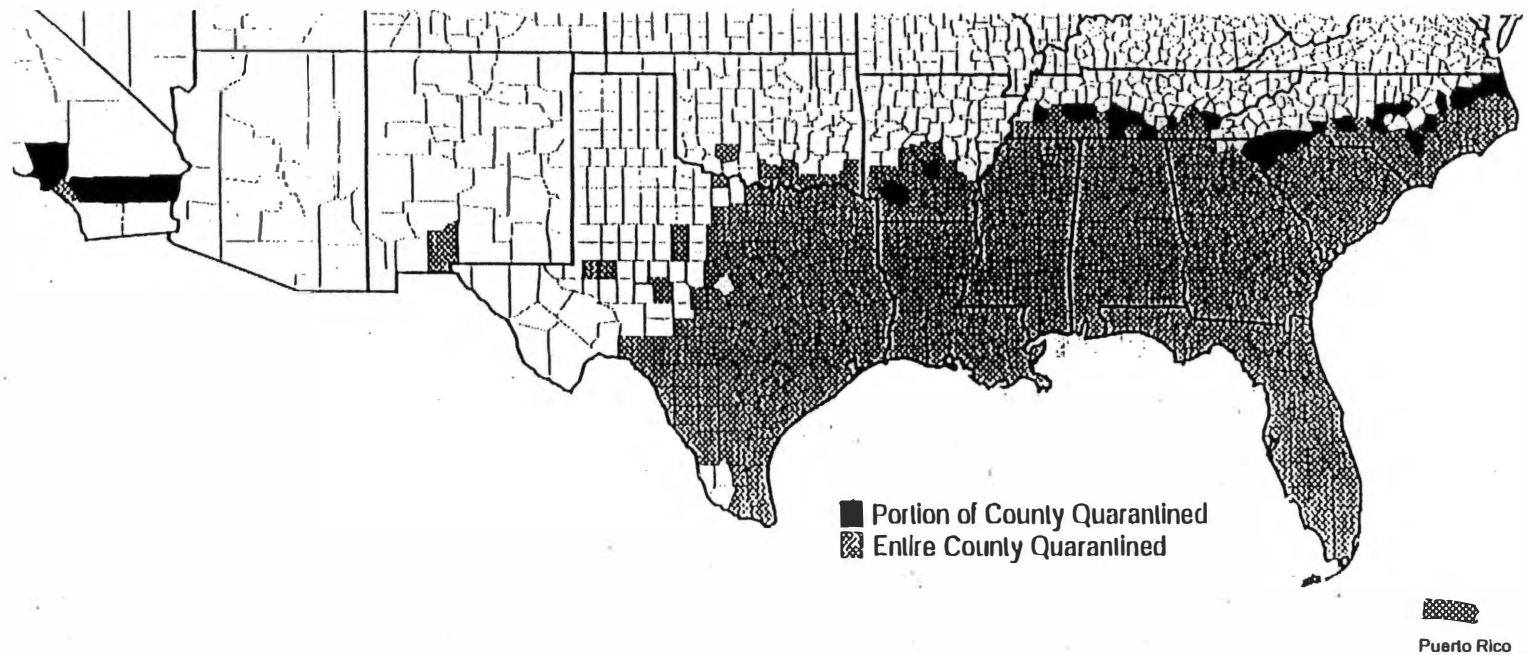


Figure 2. Imported fire ant quarantine areas of the United States. Reported by the United States Department of Agriculture-Animal and Plant Health Inspection Service (USDA-APHIS) November 6, 2000.

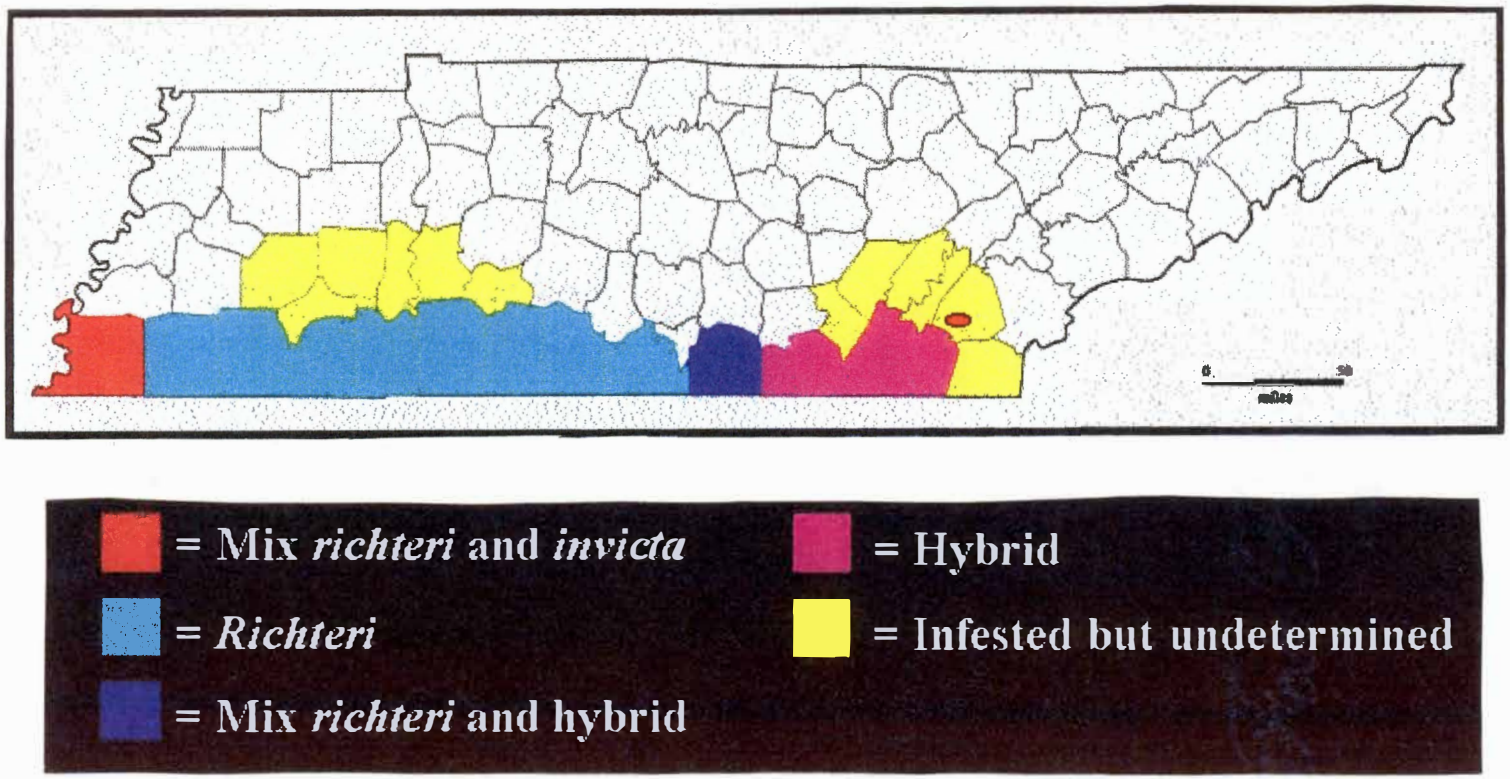


Figure 3. Fire ant diversity in Tennessee. All three forms of fire ants—*Solenopsis invicta*, *S. richteri*, and *S. invicta* x *S. richteri*—occupy areas in Tennessee (*Bob Milam, Jason Oliver, and Karen Vail, personal communication*).

(USDA 1958, Oliver 1960, Crance 1965, Green 1967, Adkins 1970). Fire ants can kill small mammals, reptiles, amphibians, and birds (Travis 1938, Kroll et al. 1973, Parker 1977, Mount et al. 1981, Ridlehuber 1982, Sikes and Arnold 1986, Allen et al. 2001). They may chew through electrical wires, causing short circuits and blackouts (Lofgren et al. 1975). Additionally, fire ants are a public health hazard. They administer a painful sting that is often accompanied by swelling, blistering, and itching of the skin. In 1% of the population, fire ant stings cause anaphylactic shock and may lead to death (Vinson 1997).

There are few barriers, most of them abiotic, to fire ants' spread (Buren et al. 1974, Morrill 1974, Calcott et al. 2000). They are transported easily by man through nursery stock and crops (Culpepper 1953). Their characteristics as tramp species greatly facilitate their successful spread. As tramp species, fire ants tolerate a wide range of climatic conditions and prefer ecologically disturbed habitats (Vinson and Greenberg 1986, Tschinkel 1988), have a generalized diet, (Wilson and Oliver 1969, Harris and Burns 1972, Howard and Oliver 1978, Sterling 1978, Vinson 1994), reproduce and grow very rapidly with a potential dispersal distance, by mating flights, of up to five miles (Markin et al. 1971, Lofgren et al. 1975, Tschinkel 1986). Under field conditions, mature colonies (approximately three years old) may contain as many as 230,000 workers (Markin et al. 1971) and population densities of polygynous (multiple-queen) colonies (*S. invicta* only), which occupy most invaded areas in North America, are two times as great as those of monogynous (single-queen) colonies (Glancey et al. 1976, Porter et al. 1991, Macom and Porter 1996).

There is evidence suggesting that fire ants are superior competitors to native ant species, which would allow fire ants to spread more easily. Fire ants prefer disturbed areas, where native ants may already be weakened (Tschinkel 1986, Vinson 1997). Fire ants are efficient foragers-recruiters and can dominate most available food resources (Horton et al. 1975, Kidd and Aperson 1984, Phillips et al. 1986). Also, fire ants replace native ant species and reduce species abundance and diversity (Wilson 1951, Wilson and Brown 1958, Whitcomb et al. 1972, Glancey et al. 1976, Camilo and Phillips 1990, Porter and Savignano 1990, Gotelli and Arnett 2000).

Controlling fire ants is of primary concern for economic, health, and environmental reasons. Chemical methods are the most widely used and are currently the most effective method of control. However, they are difficult to develop. Since 1958, more than 7,100 chemicals have been evaluated by the USDA, but fewer than 10 have been commercially developed (Williams 1983, Collins 1992, *Karen Vail, personal communication*). Ultimately, chemical control of fire ants is an ongoing and losing battle, as new queens may continue establishing new colonies and fire ants can reinvade an area after treatment. Additionally, chemicals may actually precondition an area to invasion by fire ants (Summerlin et al. 1977).

Biocontrol of fire ants offers hope as a way to control permanently invasive fire ant populations. In their native range, infection/parasitism of fire ants is negatively correlated with population density, mound density, number of worker brood and queens, speed of production of sexual brood, and foraging rate (Briano et al. 1995, Orr et al. 1995, Porter et al. 1997, Calcaterra et al. 1999). Also, parasitic flies alter the competitive outcome between ant species, allowing non-parasitized ant species to compete better

against parasitized ant species (Feener 1981). In their introduced range in North America, no native predators, parasites, or pathogens of fire ants exist, and this may be an important factor contributing to their invasion success (Jouvenaz et al. 1977). One hopes that by establishing one or more biocontrol agents, fire ant populations will decrease and cease to spread. Another effect of introducing biocontrol agents of fire ants may be to decrease fire ants' competitive ability, allowing native ants to compete better against them and offer another biotic constraint on fire ant populations.

Although hypothesized as important to their establishment, the role of competition in the invasion success of fire ants is unclear and has seldom been documented in the field. The objectives of this study were: 1) to assess quantitatively competition between hybrid imported fire ants and native ants using the indirect method of analyzing abundance and diversity in invaded and uninvaded sites, 2) to assess quantitatively competition between hybrid fire ants and native ants using the direct method of observing competition at baits, 3) to assess quantitatively the role of population density on competitive outcome between hybrid fire ants and native ants at baits, and 4) to assess the role of habitat type on the effects that fire ants have on native ants.

Chapter II

The Effect of Hybrid Imported Fire Ants on Native Ant Abundance and Diversity

Introduction

Importance of ants in the ecosystem

Ants are important in an ecosystem because they directly and indirectly affect the flow of energy and materials, as well as the habitats of other species. They consume a significant portion of resources in an ecosystem but also offer microhabitats used by myrmecophiles, plants, fungi, and bacteria. Ants have bioturbation effects on the topsoil and subsoil, changing the physical and chemical properties of soil. They aid in soil movement, aeration, nutrient immobilization, and humification. Importantly, ants increase the water-holding capacity of soils, organic matter content of soils, rate of decomposition processes, and plant species abundance. They aid in plant dispersal, succession, and productivity. In short, ants may be termed "ecosystem engineers", or "organisms that directly or indirectly control the availability of resources to other organisms by causing physical state changes in biotic or abiotic materials. The ecological effects of engineering on other species occur because the physical state changes directly or indirectly control resources used by other species" (Jones et al. 1997). Many authors (Hacker and Gaines 1997, Jones et al. 1997, Folgarait 1998) predict that landscapes with persistent ant mounds should have greater diversity than those without them. Further, these impacts should vary greatly spatially and temporally (see Folagarait 1998 for a review).

Effect of imported fire ants on the abundance and diversity of other ants

Clearly, ants are important elements in ecosystem function. When ant abundance and diversity is reduced, it follows that ecosystem functions are likely to be impaired. Imported fire ants have been documented to reduce ant species abundance and diversity on both local and regional scales. Wojcik (1994) sampled ant populations in Florida from March 1972 to September 1992, while the red imported fire ant, *Solenopsis invicta*, invasion progressed there. As *S. invicta* populations increased and came to dominate the ant fauna, most native ants species populations decreased, although a few increased (Wojcik 1994). We would expect most species populations to decrease but some to increase owing to direct and indirect effects that imported fire ants may have on a community, defensive mechanisms that native ants may have against imported fire ants, or responses to habitat disturbance that facilitate imported fire ant invasion. Wojcik (1994) found that other introduced species of ants were more likely than natives to increase with increasing *S. invicta* populations, and that this was probably due to habitat disturbance. In Texas, polygyne, or multiple queen, colonies of *S. invicta* reduced ant species richness by up to 70% (Porter and Savignano 1990) and replaced colonies of the native fire ant, *S. geminata*, at a ratio of 6:1 (six colonies of *S. invicta* replaced one colony of *S. geminata*), indicating a radical restructuring of the arthropod community (Porter et al. 1988). Not only do imported fire ants reduce diversity of ground ants, they reduce diversity of arboreal ants as well (Kaspari 2000). Other authors have found similar results (Jusino-Atresino and Phillips 1994, Vinson 1994, Wojcik et al. 2001).

Effect of imported fire ants on the abundance and diversity of non-ant arthropods

The presence of imported fire ants is associated not only with decreased ant abundance and diversity, but also with decreased abundance and diversity of other arthropods. Porter and Savignano (1990) found that isopod, erythraeid mite, and tumblebug scarab abundance declined significantly in the presence of *S. invicta.* Overall, the species richness of non-ant arthropods was 30% lower in infested sites (Porter and Savignano 1990). Other authors report similar impacts (see Wojcik et al. 2001 for a review).

Effect of imported fire ants on the abundance and diversity of non-arthropod organisms

Imported fire ants also affect non-arthropod species. Stoker et al. (1995) found that *S. invicta* can drastically alter community composition and the process of succession within the decomposer community. Similar results were found by Vinson (1991), studying decomposer communities on fruits. In the southeastern United States, population reductions of northern bobwhite quail (*Colinus virginianus*) have been correlated with increases in *S. invicta* (Allen et al. 2000). Other bird species, such as the least tern (*Sterna antillarum*) (Lockley 1995) and cliff swallows (*Hirundo prrrhonota*) (Sikes and Arnold 1986), and altricial young, pipping young, and, rarely, adult vertebrates are vulnerable to imported fire ants. Mammals, for example, can be blinded due to fire ants stings or be forced to change their habitat use, displacing them to suboptimal habitats. Oviparous reptiles and amphibians, such as the peninsular intergrade kingsnake (*Lampropeltis getula floridanus*), the six-lined race runner (*Cnemidophorus sexlineatus*), and the box turtle (*Terrapene carolina triunguis*), among many others, may also be affected by the

imported fire ant (Wojcik et al. 2001). Imported fire ants also alter the dynamics of seed dispersal and germination (Ready and Vinson 1995) (see Wojcik et al. 2001 for a review).

Effect of imported fire ants on a biogeographic scale

Imported fire ants not only affect species locally, they also affect species biogeographically. Gotelli and Arnett (2000) censused ground-foraging ant communities on a 2000 km transect from Florida through New York. They found that the presence of *S. invicta* reduces species density locally and alters co-occurrence patterns of ant species at a biogeographic scale.

Study objectives

I analyzed abundance and diversity data for invaded and uninvaded habitats in southeastern Tennessee to determine the effect of the hybrid imported fire ant invasion at this latitude. Besides Gotelli and Arnett's (2000) work, I know of no other study that has been conducted on the effect of the imported fire ant on native ant species abundance and diversity at a higher latitude. This study is important for assessing the effects of temperature on the imported fire ant's impact on native species. Additionally, this is the first study, to my knowledge, reporting the effect of the hybrid fire ant on native ant species.

Methods

Data collection

I collected samples in two habitats in southeast Tennessee, both invaded by the hybrid imported fire ant, *S. invicta* x *S. richteri*. During this study, these habitats were on the invasion front. A field habitat, located in Bradley County, had been invaded for less than one year at the time of the study. The field habitat's vegetation consisted of grasses. A pasture habitat, located in Hamilton County, had been invaded for less than 5 years. This was a poorly managed pasture with vegetation consisting of grasses, small shrubs, briars, and early successional-stage trees. Study sites were primarily flat but did contain some gently rolling hills (Figs. 4a and 4b). In each habitat on two separate occasions, I randomly placed a 50m transect in an invaded area and in an uninvaded area approximately 500m from the invaded area. Invaded and uninvaded areas, within each habitat type, were alike in vegetation type and differed only in the presence or absence of fire ants. Along each 50m transect, every 5m I buried a 15mm x 45 mm glass vial half filled with ethanol in the ground flush with the ground surface. Thus, 10 pitfall traps were laid out at each sampling period along each transect. In both the field and the pasture habitats, I laid transects on July 9, 2000 and August 8, 2000. It is during the summer months when most ants found in this part of Tennessee are the most active (Creighton 1950). I allowed pitfall traps to remain for two full days before collecting them. During the collection periods, weather was sunny and warm, with temperatures between 19 and 36 degrees Celsius. After collection, I identified all ants to genus level. Voucher specimens have been deposited at the University of Tennessee, Knoxville, Entomology and Plant Pathology Insect Museum.

a. Field habitat, located in Bradley County, Tennessee.

b. Pasture habitat, located in Hamilton County, Tennessee.

Figure 4. Study sites.

Data analysis

For invaded and uninvaded areas in both field and pasture habitats, I calculated the Shannon-Weaver Index. I chose this index because it is influenced by both species richness and the degree of dominance of the dominant species while other indexes may be influenced more by one measure than another (Longino 2000). Within each habitat type, I used a method developed by Hutcheson (1970) to calculate a p-value for the difference between the value of the Shannon-Weaver Index for invaded and uninvaded areas.

Results

In both habitats, there was a marked decrease in native ant species abundance and diversity in invaded areas when compared with uninvaded areas only 500m away. For the field habitat, in the uninvaded area, 9 genera of ants and 72 individuals were collected. In the invaded area, only 4 ant genera were collected. The number of individuals collected was greater, with 486 individuals collected. However, imported fire ants accounted for 93% (452/486) of all individuals collected. Thus, there were less than half as many individuals of all other ant genera combined. Individuals from the genera *Aphaenogaster*, *Forelius, Pheidole, Prenolepis, Pseudomyrmex,* and *Tetramorium* were present in samples from the uninvaded area but completely absent from samples taken in the invaded area (Table 1). The Shannon-Weaver Index was H=1.6697 for the uninvaded area and H=0.3188 for the invaded area. The difference between these values was statistically significant ($p<0.01$) (Table 1).

Table 1. Ant abundance and diversity—field habitat. The Shannon-Weaver Index was calculated to compare diversity between uninvaded and invaded areas.

Uninvaded Area		Invaded Area	
genus	number of individuals	genus	number of individuals
Aphaenogaster	1	*Lasius*	15
Forelius	5	*Monomorium*	3
Lasius	6	*Solenopsis*	452
Monomorium	27	*Solenopsis* (*Diplorhoptrum*)	16
Pheidole	1		
Prenolepis	8		
Pseudomyrmex	1		
Solenopsis (*Diplorhoptrum*)	20		
Tetramorium	3		
Total	72	Total	486
Shannon-Weaver Index	H=1.6697		H=0.3188
Hutcheson's t-test	p<0.01, t=12.0021, v=96.3953		

For the pasture habitat, in the uninvaded area, 295 individuals in 9 different genera of ants were collected. In the invaded area, 1,195 individuals in only 4 different ant genera were collected. Of these 1195 individuals, 91.88% (1098/1195) were imported fire ants. The number of individuals of all other ant genera combined decreased by more than 2/3. In the uninvaded area, individuals from the genera *Crematogaster, Forelius, Lasius, Pheidole, Polyergus,* and *Tetramorium* were present, but these genera were absent from the invaded area (Table 2). The Shannon-Weaver Index was H=1.4496 for the uninvaded area and H=0.3313 for the invaded area. The difference between these values was highly statistically significant (p<0.0001) (Table 2).

Table 2. Ant abundance and diversity—pasture habitat. The Shannon-Weaver Index was calculated to compare diversity between uninvaded and invaded areas.

Uninvaded Area		Invaded Area	
genus	number of individuals	genus	number of individuals
Crematogaster	4	*Monomorium*	72
Forelius	5	*Prenolepis*	1
Lasius	123	*Solenopsis*	1098
Monomorium	89	*Solenopsis* (*Diplorhoptrum*)	24
Pheidole	5		
Polyergus	1		
Prenolepis	26		
Solenopsis (*Diplorhoptrum*)	41		
Tetramorium	1		
Total	295	Total	1195
Shannon-Weaver Index	H=1.4496	H=0.3313	
Hutcheson's t-test	p<0.0001, t=25.7519, v=1168.1529		

Discussion

In both the field and pasture habitats in southeastern Tennessee, the presence of imported fire ants is correlated with a decrease in abundance and diversity of ant genera. In the field and pasture habitats, 6 of the 9 genera present in the uninvaded areas were absent from the invaded areas. It is interesting that in both field and pasture habitats, *Monomorium* and *Solenopsis* (*Diplorhoptrum*) are present in both invaded and uninvaded areas. *Monomorium* abundance in the pasture habitat shows little difference between invaded and uninvaded site; this is also true of *S.* (*Diplorhoptrum*) abundance in field and pasture habitats. These facts suggest that these genera possess characteristics that allow them to coexist with the imported fire ant. *Monomorium* has often been found to coexist

with imported fire ants. Phillips (unpublished data) found *Monomorium minimum* present at high frequencies with *S. invicta* in Kerr and Bandera Counties, Texas. Baroni Urbani and Kannowski (1974) found that *Monomorium minimum* was one of two species besides *S. invicta* common in an invaded pasture in Louisiana. Through baiting experiments, they found evidence that *M. minimum* is a strong competitor of *S. invicta* and is thus able to exist with *S. invicta* in higher densities than other native ant species (Baroni Urbani and Kannowski 1974). Additionally, *Monomorium minimum* secretes a strong chemical repellant that contributes to its defensive abilities (Baroni Urbani and Kannowski 1974, Jones and Phillips 1987) and competitive abilities (Baroni Urbani and Kannowski 1974), helping it to coexist with fire ants. Many species of *Solenopsis (Diplorhoptrum)* are lestobiotic, living in other species' nests (Thompson 1980), and this may be one reason *S. (Diplorhoptrum)* can coexist with fire ants. Alternative explanations for coexistence include shifts in foraging patterns.

Not only is the richness of native ant genera in invaded areas lower than the richness in uninvaded areas, abundance is lower as well. Even though more individuals were collected from invaded areas, the vast majority of those individuals were imported fire ants. In the field habitat, 93% of all individuals collected in invaded areas were imported fire ants; in the pasture habitat, 92% of all individuals collected in invaded areas were fire ants. Total numbers of native ants decreased by one-half and two-thirds in invaded field and pasture habitats, respectively. Shannon-Weaver Index values confirm that there is a decrease in abundance and diversity in invaded areas compared with uninvaded areas. The differences between the Shannon-Weaver Index for invaded and uninvaded areas within habitats are highly statistically significant (field, $p<0.01$; pasture,

$p<0.0001$). To my knowledge, this is the first time that the effect of the hybrid imported fire ant on native ant abundance and diversity has been examined. These results are consistent with results of similar studies pertaining to *S. invicta* (e.g., Porter and Savignano 1990, Jusino-Atresino and Phillips 1994, Wojcik 1994, Porter et al. 1998, Kaspari 2000). It appears as if the higher latitude of my study sites makes little difference in the effect of imported fire ants on native ants.

Other than the presence or absence of the hybrid (*S. invicta* x *S. richteri*) imported fire ant, there is no apparent difference between areas sampled within habitat type. This fact suggests that the hybrid imported fire ant is the cause, directly and/or indirectly, of the decrease in abundance and diversity of native ant genera. In invaded areas, up to 93% of the ants collected were imported fire ants. Up to 675% more ant individuals were collected in invaded areas than in noninvaded areas. However, in the invaded areas, the total number of native ant individuals was as much as 2/3 less than in the uninvaded areas. These statistics suggest that a restructuring of the ecosystem is taking place. The hybrid imported fire ant is largely replacing native ants, and they are occupying the ecosystem with a much higher total ant density than existed before invasion. This type of restructuring can radically alter ecosystem dynamics and affect a wide variety of organisms, not only other ant species (Porter and Savignano 1990, Vinson 1994, Ready and Vinson 1995, Stoker et al. 1995, Folgarait 1998, Allen et al. 2000, Wojcik et al. 2001). Similar results in different habitat types show that negative effects of imported fire ant invasions are widespread and generalized throughout habitat types, although the exact severity of their effects may depend upon habitat type (Tschinkel 1988).

It is unclear exactly how imported fire ants are leading to a decrease in naitve ant abundance and diversity. There is overwhelming evidence that fire ants are superior competitors to native ants and can prevent native ants from obtaining resources. If prevented from obtaining enough resources for a long enough period of time, native ant populations eventually would decline. I discuss this idea more thoroughly in the next chapter (Chapter III). An as yet uninvestigated (to my knowledge) idea is that fire ants prey upon founding queens of native ants, thus leading to declines in their population sizes. Fire ants do prey upon queens intraspecifically (Hölldobler and Wilson 1990), but interspecific queen predation is unreported. Competition with native ants appears to be the primary reason for population declines, as discussed next.

Chapter III

Interspecific Competition and the Effect of Hybrid Imported Fire Ant Population Density on Competitive Outcome

Introduction

Competitive exclusion and its elusive nature

Competitive exclusion occurs when one species in a community completely displaces another through one of two types of competition, exploitative or interference (Hardin 1960). Exploitative competition occurs when one species finds and uses potentially limiting resources more quickly than others, depriving others of those resources (Fellers 1987). For example, Petren and Case (1996) have shown that exploitative competition for insect food resources occurs between two gecko species, Hemidactylus frenatus and Lepidodactylus lugubris. Hemidactylus frenatus is able to consume more insects than L. lugubris and outcompete it. Interference competition occurs when one species prevents others from obtaining resources directly by aggression (Fellers 1987). Bhatkar et al. (1972), for example, documented aggressive interactions between the ants Lasius neoniger and Solenopsis richteri, which was the eventual victor of the competitive interactions, both in the field and in the laboratory. Solenopsis richteri was able to keep L. neoniger from obtaining food resources and thus to procure more food resources itself (Bhatkar et al. 1972).

Competition can lead to particular patterns in community assembly. Under competition theory, species are expected to occupy different functional, spatial, or temporal niches often mediated by character displacement. If species cannot adapt to one

another's presence, the poorer competitor may disappear from the community. Gause and Witt (1935) performed a laboratory experiment with *Paramecium* that showed that two different species lived preferentially in different layers, or different microhabitats, of the same food supply, showing spatial niche separation. Lack (1945) found that the cormorant (*Phalacrocorax carbo*) and the shag (*P. aristrotelis*), on Britain's southwest, west, and north coasts, differed in their specific nesting and feeding habits. Although the two birds occupied similar habitats, their functional niches were different. The snail *Succinea oblonga* was widely distributed over England during the Late-glacial period but is now confined to a few coastal sand dunes. Elton (1958) claims this range reduction was imposed by superior competitors and demonstrates a progressive, long-term niche shift. Character displacement, in which species' morphological characteristics shift in the presence of competition (Lewin 1983), may also occur. Jones (1997), for example, found character displacement among carnivorous marsupials in four characteristics that relate to feeding and killing behavior and skull length, which are presumed to play important roles in competition.

Much theory has rested on the assumption that the patterns of community assembly we currently see are the products of past competitive interactions between species; competitive mechanisms have already resulted in niche differentiation, or partitioning of resources, thus alleviating the need for further competition between species (Brown & Wilson 1956, Udvardy 1959, DeBach 1960, Hardin 1960, Connell 1980). We rely on such evidence because competitive interactions may be transitory and difficult to observe. To confirm that competition is occurring, we must show that resources are limiting (Fretwell 1972, Kingsland 1982). A progressive change in resource

use by a native species after introduction of another species constitutes strong but indirect evidence for competition for a limiting resource (Williamson 1996). Competition may be observed in recently disturbed communities undergoing successional change (Schoener 1983) or in communities into which new species have been introduced (Williamson 1996).

Invasions—An opportunity to document competition directly

Species introductions provide an excellent opportunity to observe not only the results of competition, but also the process itself. When an introduced species enters a community, its interactions with natives can be quantified and the role of competition in structuring the community may be assessed as it progresses. See Table 3 for a summary of some studies documenting the importance of competition in structuring communities and its role in invasion success.

Competition in ant communities

Although the role of competition in structuring communities in general has been debated (Connell 1983; Schoener 1982, 1983; Wiens 1977), there is much indirect evidence that it is important in structuring ant communities (Hölldobler and Wilson 1990). Divergence of foraging patterns, which may imply competitive mechanisms were in operation in the past, appears to be a general pattern that allows species to coexist (Wilson 1971). For example, Perfecto (1994) found that differences in the foraging behavior of *Pheidole radoszkowskii* and *Solenopsis geminata* permit their coexistence;

Table 3. Competition studies. Studies documenting the occurrence of competition between an invasive species and native species. The superior competitor is in bold. These studies show that competition is an important mechanism structuring communities and often plays a role in invasion success.

Organisms		Authors	Mode of Competition
native	invasive		
Lasius neoniger	*Solenopsis richteri*	Bhatakar et al. 1972	interference
native ants	*S. invicta*	Fraelich 1991	exploitative and interference
Hemidactylus frenatus	*Lepidodactylus lugubris*	Petren and Case 1996	exploitative
native ants	*Linepithema humile*	Holway 1999	exploitative and interference

while *P. radoszkowskii* is better at finding food resources, *S. geminata* is better at defending food resources once they are encountered (Perfecto1994). Fellers (1987) found an inverse correlation between exploitative and interference abilities in a woodland ant community, suggesting divergences in foraging behavior enabled less aggressive species to obtain resources. Savolainen and Vepsäläinen (1988) investigated interference competition for food in an ant community and found that species occupied a competitive hierarchy, with aggressive species adept at interference competition towards the top of the hierarchy and submissive species good at exploitative competition towards the bottom. The farther apart two species were in the hierarchy, the more likely they were to coexist (Savolainen & Vepsäläinen 1988).

The importance of competition in structuring ant communities leads one to believe it is an important mechanism enabling invasive ants to displace native ants.

Several studies document competitive interactions between invasive and native ants and show invasive ants to be the superior competitors. Porter and Savignao (1990) found imported fire ants superior to native ants in exploitative competition. Bhatkar et al. (1972) and Bhatkar (1988) found imported fire ants better at interference competition than native ants. Fraelich (1991) documented exploitative and interference competition between the imported fire ants and native ants in a Florida pasture. Fire ants were superior competitors in terms of first arrival, domination, and displacement at food resources (Fraelich 1991). Holway (1999) documented exploitative and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ants in California riparian woodlands. *Linepithema humile* recruited to and obtained food resources faster than natives, outcompeting them exploitatively. Additionally, *L. humile* individuals won more aggressive encounters than natives, demonstrating superior interference competitive ability (Holway 1999).

Escape from predators—Do higher population densities of invaders lead to a competitive advantage?

There is experimental evidence that larger population sizes result when invasive species escape their native parasites and predators in their introduced ranges. Extensive sampling of the red imported fire ant, *Solenopsis invicta,* in both its native and introduced ranges shows that the greatest environmental difference between the two populations is a low to nonexistent parasite load in its introduced range, compared to a high parasite load in its native range. Additionally, *S. invicta* population levels in its introduced range are 4-7 times higher than in its native range (Porter et al. 1997). A study of *Solenopsis richteri*

in its native range showed that with a 13.3% decrease in percent of colonies infected with the parasitic microsporidium, *Thelohania solenopsae*, the colony density per hectare increased by 82.7% (Briano et al. 1995). A similar study examined *S. richteri* colonies parasitized and not parasitized by the parasitic ant *Solenopsis daguerrei*. Parasite-free sites had higher mound densities, a higher proportion of mounds with worker brood present, more queens, more worker brood, and quicker production of sexual brood. All of these features would result in higher population densities (Calcaterra et al. 1999).

There is also evidence that higher population densities result in a higher level of competitive ability. In ants, competitive outcome frequently depends upon colony size, with the advantage going to the colony with the larger worker force (Hölldobler and Wilson 1990). Porter and Savignano (1990) found that *S. invicta*'s foraging rate is superior to that of native ants, and Fraelich (1991) found that *S. invicta* is superior both at exploitative and interference competition in its introduced range. Morrison's (2000a) study of aggressive interactions among *S. invicta*, *S. geminata*, and *S. geminata* x *xyloni* showed that *S. invicta*'s superior interference ability depends at least partially upon population density. Given that *S. invicta* population densities in its introduced range are much higher than are native ant population densities (Porter and Savignano 1990, Porter et al. 1997) and that its densities are 4-7 times higher in its introduced range than in its native range, the hypothesis that escape from natural enemies leads to greater population densities and increased competitive ability seems likely. Holway (1999) observed interference interactions between invasive Argentine ants and native ants. He found that, in its introduced range, the Argentine ant's numerical advantage was key to its superior interference ability. Indeed, invasive ants typically arrive in higher numbers than natives

at bait (food) items and may outcompete native species by recruiting many workers, which engage in interference competition (Haskins & Haskins 1965, Clark et al. 1982, Majer et al. 1984, Porter & Savignano 1990, Human & Gordon 1996, Holway 1999).

Parasitoids may stress ant colonies and render them less able to compete with natives (Jouvenaz et al. 1981, Feener 2000). Anti-parasitoid behavior exacts indirect costs on ant colonies in the forms of resource abandonment (Feener 1988, Orr et al. 1995, Orr and Seike 1998), reduction of the ability to defend resources against other ant species (Feener 1981), or a reduction in foraging rate (Feener and Brown 1992, Porter et al. 1995) or efficiency (Feener and Moss 1990, Orr 1992, Morrison 2000b). Thus, the presence of parasitoids and anti-parasitoid behavior may alter competitive outcomes. Orr et al. (1995) found that parasitic phorid flies diminished the competitive dominance of *S. invicta* at baits in its native range. In *S. geminata*'s native range in the United States, phorid flies reduced food retrieval by as much as 50%, putting it at a distinct disadvantage in exploitative competition against its congener, *S. invicta* (Morrison 2000b).

Escape from parasitoids and the reduction in competitive ability that they exact on their hosts may contribute importantly to the success of invasive ants. It seems likely that this is an important mechanism responsible for the success of the Argentine ant, *Linepithema humile* (Holway 1999, Feener 2000), as it is likely an important mechanism responsible for the success of the imported fire ant. It is apparent that *S. invicta* is superior at both exploitative and interference competition to most native ants (Bhatkar et al.1972, Bhatkar1988; Fraelich 1991; Porter and Savignano 1990; Morrison 2000a), although some native ants do seem to affect imported fire ants negatively (Nichols and

Sites 1991, King and Phillips 1992). As biocontrol agents of *S. invicta* are being introduced into the United States more frequently in an effort to control this pest, it is not only scientifically intriguing but economically important to postulate what effects biocontrol agents may have on imported fire ants.

Study objectives

My objectives in this study were to use populations of the hybrid imported fire ant, *Solenopsis invicta* x *S. richteri*, located on the invasion front to 1) test the competitive exclusion hypothesis and 2) determine the effect of imported fire ants at different densities on the competitive ability of native ants. The two portions of my study are not mutually exclusive and lend credibility to one another. By observing competition among ant genera in the field at food resources, I was able to quantify and compare their competitive abilities. Because parasitoids, particularly phorid flies, can reduce the number of fire ants actively foraging in an area (Feener 1981, Orr et al. 1995, Morrison 1999), manipulating fire ant population density may simulate the effects that parasitoids can have on fire ant populations and foraging ability. Thus, manipulating fire ant population density allowed me to quantify changes in competitive outcome that parasitoids may induce in fire ant populations in North America. These are the first data of which I am aware documenting competitive abilities of the hybrid imported fire ant and it is one of the relatively few studies to quantify competitive interactions of fire ants and native ants in the field (see Bhatkar et al. 1972, Baroni Urbani and Kannowski 1974, Porter and Savignano 1990, Fraelich 1991).

Methods

Field sites

I conducted all research in two different habitat types, both located in southeast Tennessee. A field habitat, with vegetation consisting of grasses, was located in Bradley County, Tennessee (Fig. 4a). At the time of this study, the field habitat had been infested with the hybrid imported fire ant (*Solenopsis invicta* x *S. richteri*) for less than one year. A pasture habitat, with vegetation consisting of grasses, small shrubs, early successional-stage trees, briars, and forbs, was located in Hamilton County, Tennessee (Fig. 4b). This habitat had been infested with the hybrid imported fire ant (hereafter referred to as "imported fire ant" or "fire ant") for less than five years.

Baits

I used food baits to induce and observe easily competitive interactions between ant genera. Food baits have been used effectively in many studies of ants (Fellers 1987, Savolainen and Vepsäläinen 1988, Fraelich 1991, Perfecto 1994, Human and Gordon 1996, Holway 1999). Baits consisted of an eighth of an Oscar-Meyer brand all-beef wiener and a standard-size cosmetic pad saturated with a sugar-sodium hydroxide mixture (Vail et al. 1999). Food items presented offered proteins, lipids, and carbohydrates, essential dietary components for ants (Hölldobler and Wilson 1990). These food items were placed in a 100x15mm clear petri dish that was then placed on a white notecard, facilitating observation of ants at the bait. All ant individuals were identified to genus level. Voucher specimens have been deposited at the University of Tennessee, Knoxville, Entomology and Plant Pathology Insect Museum.

Interspecific competition

I marked off a one hectare area in the infested portion of both field and pasture habitats. I counted all fire ant mounds in the study areas and grouped them according to size in three classes: small, medium, and large. Small mounds occupied less than 0.125 m^3 above ground; medium mounds occupied between 0.125 m^3 and 1 m^3 above ground; large mounds occupied more than 1 m^3 above ground. In each habitat, on alternating days, I laid out a randomly-chosen 50m transect within the study area. I placed a bait every 10m along the transect, beginning at the 10m mark and ending at the 50m mark, for a total of 5 baits along a transect. Every 15 minutes, for 3 hours, I watched each bait for 3 minutes. For each time step, I recorded the number of individuals of each genus present at the bait, any interactions occurring among individuals, and the spatial organization of individuals. I laid out 12 transects in each habitat, for a total of 60 baits in each habitat. I conducted baiting experiments only if weather conditions were sunny, without significant cloud cover or rain.

For each habitat, I calculated the number of baits discovered first by each genus, the number of baits recruited to first by each genus, and the number of baits controlled by each genus. I define "discover first" as the first individual to find a bait. I define "recruit to first" as the first genus that has 10 individuals at a bait at the same time. I define "controlled" as the genus that has the most individuals at a bait at the end of the observation period. I recorded all switches in numerical dominance between genera at a bait during an observation period. I used a binomial test to compare the performance of native ants and fire ants for each of these three variables. For these analyses, I grouped all native ant genera to maintain statistical integrity. For each genus, I calculated the number

of baits that were recruited to out of the total number of baits discovered by that genus. I will refer to data and results from this portion of the study as "pre-poison" data and results. I compared the average number of individuals present at a bait for each genus using the Wilcoxon Rank Sum test. Averages were calculated across all time steps for each habitat. I also calculated the average time into an observation period that each genus discovered and recruited to baits and the time from discovery to recruitment for each genus for each habitat.

Effect of population density on competitive outcome

After completing the interspecific competition (pre-poison) portion of the study, I poisoned half of the imported fire ant mounds in each size class in the study area in each habitat. I used Ortho^{R} Orthene^{R} Fire Ant Killer, whose active ingredient is acephate, O,S-dimethylacetylphosphoramidothioate. This poison is a powder that is applied directly to the mound. After applying the poison to half of the fire ant mounds in each size class in each area, I waited one week, then I checked the mounds to be certain that all fire ants within the mound were gone. I also checked the study area to be certain that poisoned mounds had not simply moved and established elsewhere within the area. I then conducted baiting experiments in the same manner as described above. I described and analyzed the data in the same way as in the interspecific competition (pre-poison) portion of the study. I also compared data from the pre-poison portion of the study to what I will refer to as the "post-posion" data from this portion of the study. I used binomial tests to compare number of baits discovered first, recruited to first, and controlled for native ant genera and fire ants pre-poison and post-poison.

Research was conducted June 2000 through the beginning of August 2000, between the temperatures of 21.1 and 32.2 degrees Celsius. It is between these temperatures that ants found in my study areas are active (Hölldobler and Wilson 1990) (Table 4).

Results

Interspecific competition (pre-poison)

The number of mounds in each size class for each habitat is shown in Table 5. The field habitat had only small mounds. The pasture habitat had mounds in all size classes, but mounds in the medium size class ($0.125m^3$-$1m^3$) occurred most frequently. The total number of mounds in the pasture habitat (83) was much greater than that in the field habitat (46).

In the field habitat, pre-poison, imported fire ants performed better than native ants on all variables measuring competitive outcome. Fire ants discovered more baits first, recruited to more baits first, and controlled more baits than did native ants (Table 6). I obtained similar results in the pasture habitat. Again, fire ants discovered more baits first, recruited to more baits first, and controlled more baits than did native ants (Table 6). Fire ants discovered and recruited to baits more quickly than most native ant genera, in both field (Table 7) and pasture (Table 8) habitats. It is interesting that *Monomorium* discovered and recruited to baits more quickly than did *Solenopsis* in both habitat types. Out of all baits discovered, fire ants recruited to a higher portion than most other genera (Tables 7 and 8). Only *Monomorium*, in the pasture habitat, recruited to a higher portion of baits discovered. Further, fire ants recruited to baits more quickly once they had been

Table 4. Temperature range within which ant workers forage. (From Hölldobler and Wilson 1990, pp. 380-381.)

Species	Study location	Temperature (°C) at which foraging . . . Begins	Peaks	Ends
Monomorium minimum	Massachusetts	32	32	40
M. (= *Chelaner*) sp.	Semi-arid Australia	12	22	33
Solenopsis invicta	Florida	15	22-36	43
Forelius pruinosis	Desert, western United States	19	---	52
Lasius neoniger	Massachusetts	29	29	36
Prenolepis imparis	Maryland	5	15-19	26
Prenolepis imparis	Missouri	0	7-18	18.5

Table 5. Imported fire ant mound densities in field and pasture habitats.Small mounds occupied less than $0.125m^3$ aboveground, medium mounds occupied between $0.125m^3$ and $1m^3$ aboveground, and large mounds occupied more than $1m^3$ aboveground.

Number of mounds/ha, field habitat	mound class	Number of mounds/ha, pasture habitat
46	small	23
	medium	47
	large	13
46	total	83

Table 6. Pre-poison competitive performance of fire ants and native ants in field and pasture habitats. Binomial tests were performed on all variables.

	fire ants	native ants	Z-value	p-value
Field Habitat				
# baits discovered first	36.5	17.5	2.6099	<0.01
# baits recruited to first	36	15	2.9406	<0.01
# baits controlled	31	11	3.0861	=0.001
Pasture Habitat				
# baits discovered first	39	15	3.2600	<0.001
# baits recruited to first	31	15	2.3591	<0.01
# baits controlled	30	15	2.2361	=0.01

Table 7. Average time to discover and recruit to baits—field habitat. Pre-poison (pre) and post-poison (post) values are reported in average minutes ± standard deviation. Sample size, or number of baits, is reported in parentheses. For entries of "NA", individuals discovered one or more baits but did not recruit to any baits or recruited to too few baits to allow calculation of a difference between the two variables.

Genus	Time to discover baits		Time to recruit to baits		% baits recruited to of those discovered	
	pre	post	pre	post	pre	post
Forelius	absent	15 (1)	absent	15 (1)	absent	100
Lasius	80±43.3 (3)	52.2±29.4 (29)	112.5±10.6 (2)	73.0±37.7 (23)	66.7	79.3
Monomorium	30±18.4 (5)	79.4±42.7 (17)	52.5±15 (4)	89.1±47.6 (16)	80.0	94.1
Pheidole	30 (1)	absent	NA	absent	NA	absent
Prenolepis	48.2±39.2 (19)	48.2±35.2 (33)	78.8±56.9 (12)	58.5±35.3 (30)	63.2	90.9
Solenopsis (Diplorhoptrum)	absent	120 (1)	absent	NA	absent	NA
Solenopsis	44.8±44.7 (43)	44.6±37.2 (34)	61.1±58.6 (39)	57.4±39.1 (29)	90.2	85.3

Table 8. Average time to discover and recruit to baits—pasture habitat. Pre-poison (pre) and post-poison (post) values are reported in average minutes ± standard deviation. Sample size, or number of baits, is reported in parentheses.

Genus	Time to discover baits		Time to recruit to baits		% baits recruited to of those discovered	
	pre	post	pre	post	pre	post
Forelius	126.3±33.5 (12)	absent	140±39.6 (8)	absent	66.7	absent
Lasius	84.4±67.1 (8)	78.8±47.9 (8)	180 (1)	126±56.7 (5)	12.5	62.5
Monomorium	43.9±42.6 (14)	72.3±43.6 (22)	50.8±40.9 (13)	83.8±39.0 (17)	92.9	77.3
Prenolepis	absent	65±45.4 (12)	absent	79.1±39.2 (11)	absent	91.7
Solenopsis (Diplorhoptrum)	93.8±75.9 (4)	52.5±35.7 (4)	30 (1)	85±43.3 (3)	25.0	75.0
Solenopsis	52.5±43.6 (50)	49.8±38.8 (31)	53.8±35.4 (34)	57.4±44.0 (23)	68.0	74.2

discovered than did native ant genera (Table 9). Importantly, fire ants were present at baits in higher densities, on average, than were native ants in both field and pasture habitats (Figures 5a and 5b) (Table 10).

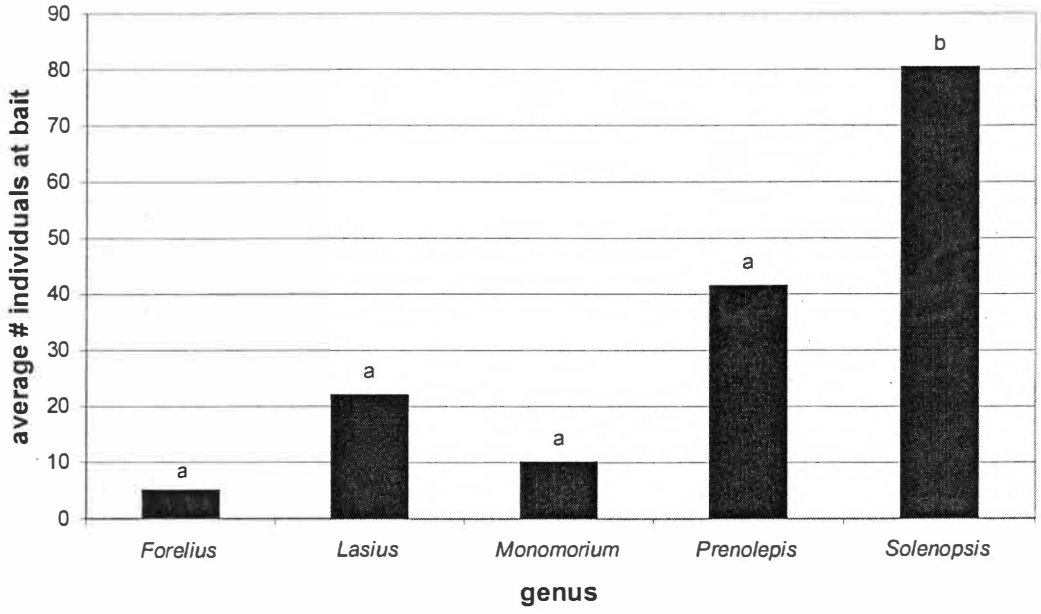
Of 120 baits and 72 hours of observation time, only two aggressive interactions between ants were observed. In the pasture habitat, I observed a *Monomorium* individual touch a *Lasius* individual with its antenna, and the *Lasius* individual fled the bait. Also in the pasture habitat, I observed an instance in which several *Monomorium* individuals gaster-flagged several *Solenopsis* individuals, and the *Solenopsis* individuals retreated.

Usually, only one ant genus was present at a bait at a given time. In the field habitat, only 5 baits were recruited to by more than one genus at a time (Table 10). *Solenopsis* and *Prenolepis* individuals successfully recruited to baits while individuals of the other genus were present. In the pasture habitat, 7 baits were recruited to by more than one genus at a time (Table 11). *Forelius* (3 out of 60 baits), *Lasius* (1 out of 60

Table 9. Average time from discovery of a bait to recruitment to a bait. Pre-poison (pre) and post-poison (post) times listed are listed and are the difference between the averages reported in tables 8 and 9 and are reported in minutes. For entries of "NA", individuals discovered one or more baits but did not recruit to any baits or recruited to too few baits to allow calculation of a difference between the two variables.

Genus	Field habitat		Pasture habitat	
	pre	post	pre	post
Forelius	absent	0	13.8	absent
Lasius	32.5	20.8	95.6	47.3
Monomorium	22.5	9.9	6.8	11.6
Prenolepis	30.6	10.3	absent	14.1
Solenopsis (Diplorhoptrum)	absent	NA	NA	32.5
Solenopsis	16.2	12.9	1.3	7.6

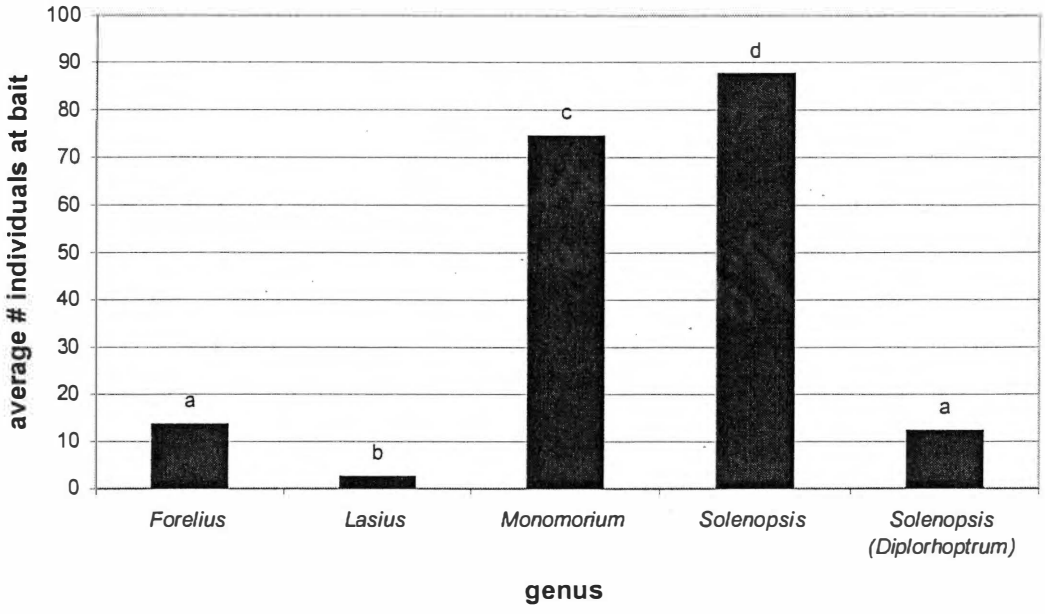
Field Habitat



a. Average number of individuals at a bait, pre-poison, in a field habitat.

Figure 5. Average number of individuals at a bait, pre-poison. Number of individuals was averaged across all time steps. All differences are significant below the 0.05 level using the Wilcoxon Rank Sum test (continued on next page).

Pasture Habitat



b. Average number of individuals at a bait, pre-poison, in a pasture habitat.

Figure 5. (continued)
Average number of individuals at a bait, pre-poison. Number of individuals was averaged across all time steps. All differences are significant below the 0.05 level using the Wilcoxon Rank Sum test.

Table 10. Results of the Wilcoxon Rank Sum test for average number of individuals of each genus at baits. Data above the diagonals represent pre-poison conditions. Data below the diagonals represent post-poison conditions.

Field Habitat

	Forelius	*Lasius*	*Monomorium*	*Prenolepis*	*Solenopsis*
Forelius	-----	-----	-----	-----	-----
Lasius	Z= 0.94 p=0.35	-----	Z=1.64 p=0.11	Z=0.26 p=0.79	Z=1.99 p<0.05
Monomorium	Z=2.08 p<0.05	Z=4.71 p<0.0001	-----	Z=1.80 p=0.07	Z=4.86 p<0.0001
Prenolepis	Z=2.70 p<0.01	Z=9.57 p<0.0001	Z=2.58 p=0.01	-----	Z=4.49 p<0.0001
Solenopsis	Z=3.10 p=0.001	Z=12.85 p<0.0001	Z=8.24 p<0.0001	Z=9.87	-----

Pasture Habitat

	Forelius	*Lasius*	*Monomorium*	*Prenolepis*	*Solenopsis*	*Solenopsis (Diplorhoptrum)*
Forelius	-----	Z=4.21 p<0.0001	Z=5.85 p<0.0001	-----	Z=5.29 p<0.0001	Z=1.02 p=0.31
Lasius	-----	-----	Z=6.93 p<0.0001	-----	Z=6.82 p<0.0001	Z=2.08 p<0.05
Monomorium	-----	Z=7.10 p<0.0001	-----	-----	Z=2.16 p<0.05	Z=4.33 p<0.0001
Prenolepis	-----	Z=7.40 p<0.0001	Z=0.30 p=0.77	-----	-----	-----
Solenopsis	-----	Z=7.77 p<0.0001	Z=6.57 p<0.0001	Z=6.31 p<0.0001	-----	Z=3.85 p<0.0001
Solenopsis (Diplorhoptrum)	-----	Z=4.16 p<0.0001	Z=3.79 p<0.001	Z=4.18 p<0.001	Z=5.23 p<0.0001	-----

Table 11. Number of baits recruited to by more than one genus at the same time and genera that successfully recruited to those baits. Data above the diagonals represent pre-poison conditions. Data below the diagonals represent post-poison conditions.

Field Habitat

	Forelius	*Lasius*	*Monomorium*	*Prenolepis*	*Solenopsis*	*Solenopsis (Diplorhoptrum)*
Forelius	-----	0	0	0	0	0
Lasius	0	-----	0	0	0	0
Monomorium	0	1	-----	0	0	0
Prenolepis	0	13	1	-----	5	0
Solenopsis	0	4	8	6	-----	0
Solenopsis (Diplorhoptrum)	0	0	0	0	0	-----

Pasture Habitat

	Forelius	*Lasius*	*Monomorium*	*Prenolepis*	*Solenopsis*	*Solenopsis (Diplorhoptrum)*
Forelius	-----	0	0	0	2	0
Lasius	0	-----	0	0	1	0
Monomorium	0	0	-----	0	3	0
Prenolepis	0	0	0	-----	0	0
Solenopsis	0	1	2	0	-----	1*
Solenopsis (Diplorhoptrum)	0	0	0	0	1	-----

**Forelius* also recruited to this bait at the same time as *Solenopsis* and *Solenopsis* (*Diplorhoptrum*), for a total of three genera recruiting to this bait at the same time.

baits), *Monomorium* (3 out of 60 baits), and *Solenopsis* (*Diplorhoptrum*) (1 out of 60 baits) all recruited to baits while *Solenopsis* was present. At one bait, *Forelius*, *Solensopsis*, and *Solenopsis* (*Diplorhoptrum*) all recruited at the same time. When more than one genus of ant was present at a bait, individuals always spatially partitioned the bait. Fire ants usually arrived at a bait first and quickly covered the hotdog piece, then spread out from the hot dog along the edges of the sugar-sodium hydroxide saturated cosmetic pad. *Monomorium* individuals also recruited to the hotdog on a few occasions. If other genera, besides *Solenopsis* and *Monomorium*, were the first to recruit to a bait, they would recruit to the sugar-sodium hydroxide saturated cosmetic pad and ignore the hotdog. Native ant genera, when they arrived at a bait after fire ants already occupied it, would position themselves 180° away from the center of the fire ant spatial organization, which was usually 180° away from the hotdog. Rarely, *Monomorium* individuals would be the first to recruit to a bait and would cover and control the hot dog. If this was the case, when fire ants arrived at the bait, they fed on the sugar-sodium hydroxide mixture, but they initially positioned themselves about 90° away from the center of *Monomorium*'s spatial position, the hotdog. If fire ant individuals did not discover and recruit to a bait first, they more frequently positioned themselves closer to individuals of the genus already present at the bait than did native ant genera. It appeared as if ant genera spatially partitioned the bait in order to avoid interaction with other genera present. If an individual of one genus traveled to an area of the bait numerically dominated by another genus, it very quickly moved back to the area dominated by its congeners.

Sometimes, control of a bait switched during the observation period, with numerical dominance of the bait changing from one ant genus to another (Table 12). In

Table 12. Baits that changed control (i.e., numerical dominance) during observation periods. The genus with initial control was the first genus to recruit to a bait that maintained numerical dominance for two or more observation periods. The genus that took over replaced the genus with initial control and became the genus with numerical dominance. In all instances, the genus that took over the bait maintained numerical dominance and thus maintained control of the bait (continued on next page).

	genus with initial control	genus that took over	time into observation period when change occurred
Pre-poison			
Field Habitat			
	Lasius	*Prenolepis*	45 minutes
		Prenolepis	45 minutes
	Monomorium	*Solenopsis*	30 minutes
	Prenolepis	*Solenopsis*	75 minutes
		Solenopsis	15 minutes
		Solenopsis	15 minutes
	Solenopsis	*Prenolepis*	120 minutes
		Prenolepis	75 minutes
		Prenolepis	75 minutes
		Prenolepis	60 minutes
		Prenolepis	60 minutes
		Prenolepis	45 minutes
Pasture Habitat			
	Forelius	*Solenopsis*	60 minutes
	Monomorium	*Solenopsis*	15 minutes
	Solenopsis (*Diplorhoptrum*)	*Solenopsis*	60 minutes
	Solenopsis	*Forelius*	105 minutes
		Forelius	90 minutes
		Forelius	60 minutes
		Monomorium	120 minutes
Post-poison			
Field Habitat			
	Forelius	*Prenolepis*	120 minutes
	Lasius	*Prenolepis*	135 minutes
		Prenolepis	75 minutes
		Prenolepis	75 minutes
		Prenolepis	75 minutes
		Prenolepis	45 minutes
		Prenolepis	30 minutes
		Prenolepis	15 minutes
		Solenopsis	60 minutes
		Solenopsis	30 minutes

Table 12. (continued)
Baits that changed control (i.e., numerical dominance) during observation periods for field and pasture habitats, pre-poison and post-poison.

	genus with initial control	genus that took over	time into observation period when change occurred
Post-poison			
Field Habitat			
	Monomorium	*Prenolepis*	105 minutes
		Solenopsis	60 minutes
	Prenolepis	*Lasius*	60 minutes
		Lasius	60 minutes
		Solenopsis	120 minutes
		Solenopsis	90 minutes
		Solenopsis	45 minutes
		Solenopsis	30 minutes
	Solenopsis	*Monomorium*	60 minutes
		Prenolepis	15 minutes
Pasture Habitat			
	Lasius	*Prenolepis*	15 minutes
	Monomorium	*Solenopsis*	75 minutes
	Solenopsis (*Diplorhoptrum*)	*Solenopsis*	60 minutes

the field habitat, fire ants were able to take over baits that were initially numerically dominated by *Monomorium* and *Prenolepis*. *Prenolepis* was able to take over baits initially dominated by *Lasius* and *Solenopsis*. In total, 12 baits initially had a different ant genus controlling them than at the end of the observation period. In the pasture habitat, fire ants took over baits from *Forelius*, *Monomorium*, and *Solenopsis* (*Diplorhoptrum*) while *Forelius* and *Monomorium* wrested baits from fire ants (Table 11). Numerical control of 7 baits changed in the pasture habitat. When control of a bait did change, no aggressive interactions were involved. There appeared to be gradual declines and increases of the number of individuals of the genera involved.

Effect of population density on competitive outcome (post-poison)

A count of the number of mounds in the study area in each size class before poisoning and after poisoning confirmed that ants from poisoned mounds did not relocate inside the study area (Table 5).

Post-poison, native ants discovered more baits first and recruited to more baits first than did fire ants. In the field habitat, native ants discovered more baits first and recruited to more baits first than did fire ants (Table 13). However, native ants and fire ants controlled equal numbers of baits post- poison (Table 13). I obtained similar results for the pasture habitat. Native ants discovered more baits first and recruited to marginally significantly more baits first than did fire ants (Table 13).Again, however, native ants and fire ants controlled equal numbers of baits at the end of the observation period (Table 13).

Table 13. Post-poison competitive performance of fire ants and native ants in field and pasture habitats. Binomial tests were performed on all variables.

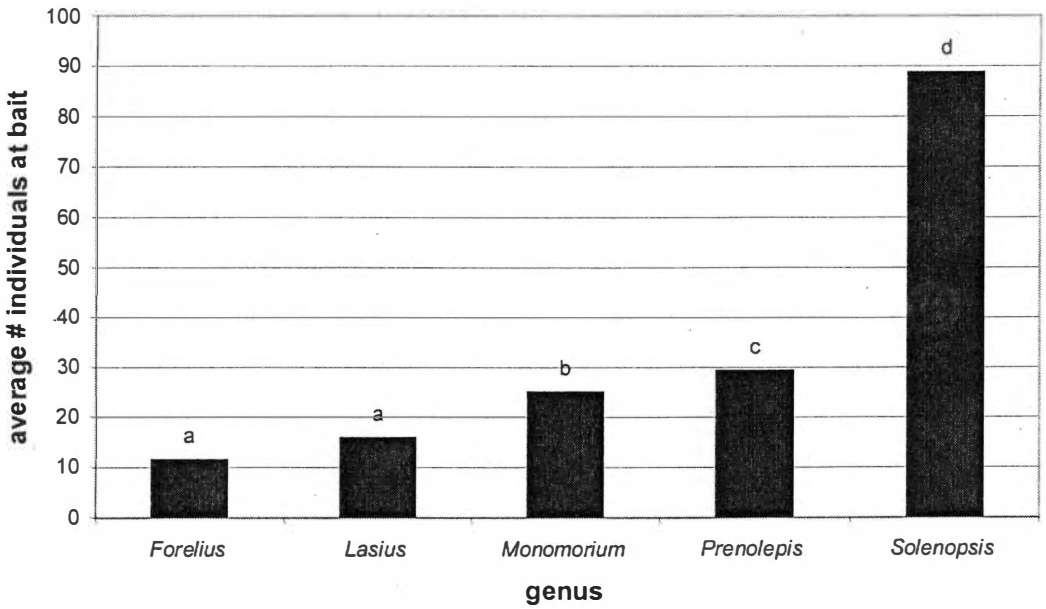
	fire ants	native ants	Z-value	p-value
Field Habitat				
# baits discovered first	18	42	3.0984	=0.001
# baits recruited to first	19	41	2.8402	<0.01
# baits controlled	26	28	0.2722	=0.39
Pasture Habitat				
# baits discovered first	22	35	1.7219	<0.05
# baits recruited to first	21	32	1.5110	=0.07
# baits controlled	23	29	0.8321	=0.20

Post-poison, fire ants still discovered and recruited to baits more quickly than native ants, but they recruited to a lower portion of baits discovered than all native ant genera besides *Lasius* (Tables 7 and 8). However, the time it took *Solenopsis* to recruit to a bait after discovery was still less than for all native genera, except for *Monomorium* in the field habitat (Table 9). Post-poison, fire ants were present at baits in higher densities, on average, than were native ants (Figures 6a and 6b) (Table 10).

For 120 baits and 72 hours of observation time, I again observed very few aggressive interactions. Post-poison, in the field habitat, I observed three instances of aggressive interactions. Once, a *Solenopsis* individual fought with and killed a *Prenolepis* individual. In this instance, *Solenopsis* occupied the bait before the arrival of *Prenolepis*. Twice, a *Monomorium* individual gaster-flagged a *Solenopsis* individual, and *Solenopsis* retreated. In the pasture habitat, a *Monomorium* individual gaster-flagged a *Solenopsis* individual, and *Solenopsis* retreated. I also observed one instance in which a *Prenolepis* individual attacked a *Solenopsis* individual, and *Solenopsis* fled. In this instance, *Prenolepis* occupied the bait before the arrival of *Solenopsis*.

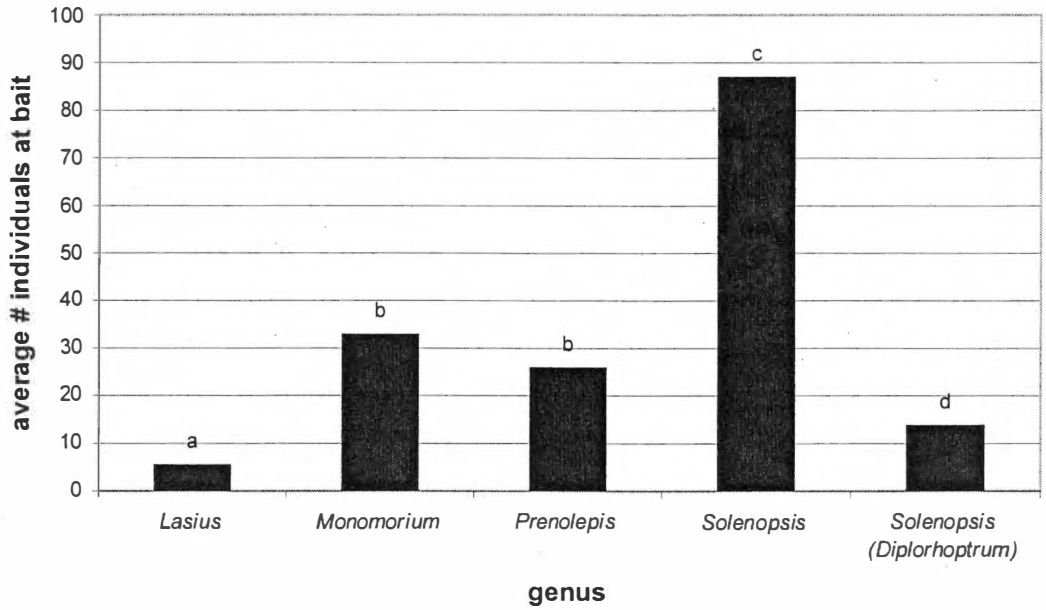
A comparison of the post-poison results to the pre-poison results shows that native ants discovered first, recruited to first, and controlled more than twice as many baits post-poison as pre-poison (Table 14). Fire ants discovered first and recruited first to almost half as many baits post-poison than pre-poison. However, fire ants controlled equal numbers of baits pre-poison and post-poison (Table 14). Additionally, fire ants were present at baits in higher densities, on average, than were native ants both pre- and post-poison (Figs. 5 and 6). On average, native ant genera recruited to a higher portion of

Field Habitat



a. Average number of individuals at a bait, post-poison, in a field habitat.

Figure 6. Average number of individuals at a bait, post-poison. Number of individuals was averaged across all time steps. All differences are significant below the 0.05 level using the Wilcoxon Rank Sum test (continued on next page).



b. Average number of individuals at a bait, post-poison, in a pasture habitat.

Figure 6. (continued)
Average number of individuals at a bait, post-poison. Number of individuals was averaged across all time steps. All differences are significant below the 0.05 level using the Wilcoxon Rank Sum test.

Table 14. Competitive performance of fire ants and native ants, pre-poison vs. post-poison, in field and pasture habitats. Binomial tests were performed on all variables.

	pre-poison	post-poison	Z-value	p-value
Fire Ants				
Field Habitat				
# baits discovered first	36.5	18	2.5060	<0.01
# baits recruited to first	36	19	2.2923	=0.01
# baits controlled	31	26	0.6623	=0.25
Pasture Habitat				
# baits discovered first	39	22	2.1766	=0.01
# baits recruited to first	31	21	1.3868	=0.08
# baits controlled	30	23	0.9615	=0.17
Native Ants				
Field Habitat				
# baits discovered first	17.5	42	3.1762	<0.001
# baits recruited to first	15	41	3.4744	<0.001
# baits controlled	11	28	2.7222	<0.01
Pasture Habitat				
# baits discovered first	15	35	2.8284	<0.01
# baits recruited to first	15	32	2.4797	<0.01
# baits controlled	15	29	2.1106	<0.05

baits discovered post- than pre-poison (Tables 7 and 8), and their times between discovery of a bait and recruitment to a bait decreased post-poison (Table 9). In the field habitat, fire ants recruited to a lower portion of baits discovered post-poison (Table 7). In the pasture habitat, it took fire ants longer to recruit to baits post-poison, but they recruited to a higher portion of baits discovered post-poison (Table 8). The time between discovery and recruitment for fire ants was longer post-poison in the pasture habitat (Table 11).

Some interesting trends can be seen among individual ant genera. In the field habitat, all native ant genera perform better on all variables post-poison than they do pre-poison, and fire ants perform worse in all variables post-poison than pre-poison (Table 15). In the pasture habitat, all native ant genera but *Forelius* perform better on all variables post-poison than pre-poison. *Forelius* and *Solenopsis* perform better in all variables pre-poison than they do post-poison (Table 15). Also, *S.* (*Diplorhoptrum*) discovered first, recruited to first, and controlled baits in the pasture habitat but did not do so at any baits in the field habitat. Again, I did not test the statistical significance of differences in parameters for individual ant genera because statistical integrity would be lost with such small sample sizes.

Post-poison, the spatial partitioning of the bait between ant genera resembled that for the interspecific (pre-poison) observations. Ant genera rarely recruited to a bait at the same time (Table 11), but if they did so, they tended to avoid each other by spatially partitioning the bait. Fire ants usually covered the hotdog first then spread along the bait from there while native genera usually remained on the cosmetic pad, away from the hotdog. In the field habitat, 32 of 60 total baits were recruited to by more than one genus

Table 15. Competitive performance of individual ant genera. Binomial tests were not performed on these variables since statistical integrity would be lost. "Pre" refers to pre-poison data; "post" refers to post-poison data.

	Solenopsis (Diplorhoptrum)		*Forelius*		*Monomorium*		*Lasius*		*Prenolepis*		*Solenopsis*	
Field Habitat												
	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post
# baits discovered first	0	0	0	1	4	7	2	13	11.5	21	36.5	18
# baits recruited to first	0	0	0	1	4	7	2	12	9	21	36	19
# baits controlled	0	0	0	0	2	5	0	4	9	19	31	26
Pasture Habitat												
	pre	post	pre	post	pre	post	pre	post	pre	post	pre	post
# baits discovered first	2	4	3	0	7	17	3	5	0	9	39	22
# baits recruited to first	1	3	2	0	12	16	0	3	0	10	31	21
# baits controlled	0	2	4	0	11	15	0	1	0	11	30	23

simultaneously, many more than in the pre-poison condition (5 baits). In the pasture habitat, only 4 of 60 total baits were recruited to by more than one genus at the same time, less than the number (7 baits) for the pre-poison condition.

Control of a bait switched more often in the field habitat post-poison than pre-poison (Table 12). Fire ants took over baits from *Lasius*, *Monomorium*, and *Prenolepis*. *Lasius* took over one bait from *Prenolepis*. *Lasius* took over baits from *Prenolepis*. *Monomorium* took over one bait from *Solenopsis*. *Prenolepis* wrested baits from *Forelius*, *Lasius*, *Monomorium*, and *Solenopsis*. In total, control of baits changed 11 times in the field habitat. In the pasture habitat, control of baits changed 3 times, with fire ants taking over baits from *Monomorium* and *Solenopsis* (*Diplorhoptrum*), and *Prenolepis* taking over a bait from *Lasius* (Table 12).

Discussion

Interspecific competition (pre-poison)

The results of this study show that the hybrid imported fire ant, *Solenopsis invicta* x *S. richteri*, is a superior competitor to native ants and competitively excludes native ants from baits in field and pasture habitats in southeast Tennessee. Fire ants were better than native ants at finding baits and recruiting to baits, and they did so faster, in higher densities, and for longer periods of time. Fire ants also controlled more baits (maintained numerical dominance) than did native ants. These results are similar to the findings of others on the red imported fire ant, *S. invicta*, and indicate that the hybrid imported fire ant, like *S. invicta*, is superior to native ants at exploitative competition. Baroni Urbani and Kannowski (1974) found that *S. invicta* discovered first up to 96% of randomly distributed baits in a pasture habitat in Louisiana. Fraelich (1991) also found that *S. invicta* was a superior competitor in terms of first arrival, surrounding, and domination at baits in a pasture; fire ants found 48.3% of baits first and surrounded (or controlled) 46% of all baits. Porter and Savignano (1990) reported that *S. invicta* found and recruited to food items more quickly than native ants in the field. The invasive Argentine ant, *Linepithema humile*, also demonstrates superior competitive ability to native ants in terms of discovery and recruitment to food items and control of food items. Argentine ants recruit to baits more quickly than native ants and control a greater portion of baits than native ants (Cammell et al. 1996, Human and Gordon 1996, Holway 1999). Argentine ants also find and recruit to baits more consistently and in higher numbers and forage for longer periods of time than native ants (Human and Gordon 1996).

Contrary to what others have found and predicted concerning competition in ant communities (Hölldobler and Wilson 1990, Holway and Suarez 1999), particularly communities containing invasive ants (Bhatkar et al. 1972, Jones 1985, DeKock 1990, Human and Gordon 1996, 1999, Holway 1999, Morrison 2000a) exploitation competition appears to be the dominant form of competition in this study; aggressive interference competition, at least at baits, plays a negligible role. Usually, only one genus fed at a bait at any given time. When more then one genus was present at a bait, individuals appeared to actively avoid each other interspecifically, staying amongst their congeners and positioning themselves on baits as far as possible away from other ant genera. Possibly this avoidance mechanism is chemically mediated. Unlike native ant genera, fire ants, if not the first to recruit to a bait, positioned themselves closer to the genus already present. Many studies suggest that fire ants consistently win aggressive encounters (Bhatkar et al. 1972, Bhatkar 1988, Fraelich 1990, Morrison 2000a), so it is reasonable to assume that fire ants would risk provoking aggressive encounters to obtain resources. I rarely observed aggressive encounters at baits, but when I did, they were short-lived (<2 seconds) and involved only 2 individuals, never more, with the loser retreating very quickly.

Territoriality could play an important role in the lack of aggressive interactions at baits. Most of the ants observed in this study maintain territories (Hölldobler and Wilson 1990). If ants forage mainly within their own territory, one would not expect to see different ant genera co-occur at baits very often. In the instances when ants did co-occur, baits were probably near a territorial boundary or between territories. Even so, aggressive interactions would have been expected to occur at baits that did clearly belong in one

territory (Wilson et al. 1971). The gain potentially incurred from aggressive disputes over food at baits may not have been worth the risk for these ant genera. Nonacs and Dill (1991) found that *Lasius pallitarsis* and *Monomorium incompleta* decreased their use of high quality food patches when the mortality risk associated with these patches increased. In my study, if food in the habitats, or even at the baits themselves, was not limiting, there may have been no reason for ant individuals to risk death to gain the resource. Additionally, competitive outcomes between ants are often determined by relative numbers of individuals involved (Hölldobler and Wilson 1990). If a bait was already numerically dominated by a genus when one or more individuals of a different genera arrived, it would be riskier and costlier for them to try to usurp the bait than to continue foraging elsewhere for unclaimed resources. It is possible that chemical mediation occurred at baits. Perhaps the ants in this study can detect pheromones that indicate the presence and density of other genera in a given area. Interspecific and intraspecific chemical cues could have played a role in an individual's decision to feed at only one part of a bait, to recruit to or retreat from a bait, or to instigate or avoid aggressive interactions.

As reported by others (Baroni Urbani and Kannowski 1974, Jones 1985, Fellers 1987, Jones and Phillips 1987), I found that *Monomorium* individuals performed well in encounters with other ants. *Monomorium* individuals spray repulsive chemical compounds onto other ants in interference interactions and are thus able to win many individual encounters (Baroni Urbani and Kannowski 1974, Jones 1985, Jones and Phillips 1987), as was the case here. *Monomorium* individuals were able to drive off all individuals of other genera encountered, even *Solenopsis*, by gaster-flagging and spraying

them with this chemical. This finding suggests that for *Monomorium* individuals, aggressive interference can play an important role in competitive interactions.

When control of a bait (i.e., numerical dominance at a bait) switched, there were no aggressive interactions involved. The number of individuals of each genus at the bait simply changed over time, one decreasing and one increasing, eventually leaving one genus to dominate and control the bait. Fire ants took over more baits than did any native ant genus, and they were able to do so at later times after the bait had been provided. This may relate to the natural process of recruitment in ants. Recruitment involves a buildup of individuals at a food source followed by a reversal of this process after food is retrieved (Gordon 1983). If as one ant genus began to retreat from a bait another was beginning to build up its numbers at the same bait, one would not necessarily expect aggressive interactions to occur. What is surprising, however, is that ants would stop recruiting to a food source even though the food supply was still available in relative abundance. Perhaps colonies reach a satiation level after which they no longer forage, or they forage only for a maximum amount of time. This phenomenon could also be related to the costs of a potential aggressive encounter versus the relative benefits of the disputed resource, as discussed previously.

Baroni Urbani and Kannowski (1974) also found that control of baits can switch without aggressive interactions. As *S. invicta* arrived at baits in greater numbers, *M. minimum* left without conflict. *S. invicta* dominated baits during the first 40 minutes of the experiment while *M. minimum* was virtually absent from baits. However, over the course of the experiment (3 hours) *M. minimum* succeeded in completely eliminating all remaining ant species from baits (Baroni Urbani and Kannowski 1974). In this study, fire

ants forfeited control of only 10 of 61 baits initially controlled. Unlike Baroni Urbani and Kannowski's (1974) results, *Monomorium* gained control of only one bait initially controlled by fire ants. *Prenolepis* and *Forelius* performed better in this respect. In a study of competition among ant species in a Maryland woodlot, *Prenolepis imparis* recruited large numbers of workers and fell into a dominant group of ant species (Fellers 1987). If the *Prenolepis* species in my study possess similar characteristics to *P. imparis* in Fellers' (1987) study and recruit large numbers to baits, they may have taken the opportunity to recruit to baits once *Solensopsis* numbers began to decrease.

Temperature also probably influenced which genera were at a bait and when. The genera observed in this study forage at different but overlapping temperature intervals (Hölldobler and Wilson 1990). *Solenopsis invicta* has a wide foraging temperature range (15-43°C), and even its peak foraging temperature range is quite wide (22-36°C) (Porter and Tschinkel 1987). During the time of this study, fire ants may have been able to forage throughout the entire day, since temperatures in southeastern Tennessee during July and August can range from 15°C to 37°C. Only *Forelius* can take advantage of higher temperatures, and it might have recruited to more baits later in the day, at higher temperatures. *Prenolepis* was probably past its peak foraging temperature at the times of day and temperatures when this study was conducted, which could have contributed to the small number of baits it recruited to. *Lasius* and *Monomorium* were at their peak foraging temperatures during the observation periods of this study, and this fact undoubtedly contributed to their recruitment to baits (Hölldobler and Wilson 1990).

Fire ants typically recruited to the hot dog piece first, overflowing onto the sugar-sodium hydroxide saturated cosmetic pad. This may reflect a dietary need for protein in

ants in general (Davidson 1998), coupled with competitive superiority in fire ants. During the time of this study, many fire ant colonies were producing brood (*personal* observation). Fire ants feed protein directly to their brood (Sorensen et al. 1983) and seem to collect it mainly when larvae are present in their colonies (Porter and Tschinkel 1987). Interestingly, the only native ant genus to recruit to the hot dog piece if it was the first genus to discover the bait was *Monomorium*, which also feeds its brood proteins and lipids (Haack et al. 1995). Perhaps many *Monomorium* colonies were also producing brood at the time of this study. All other native ant genera recruited to the sugar mixture if they were the first to discover a bait.

Effect of population density on competitive outcome (post-poison)

When fire ant population density within the study area was reduced to half the original density, fire ants performed worse than native ants as a group on most variables measuring competitive ability. Native ants' performance on all variables increased by more than twice as much post-poison, and fire ants' performance in discovery and recruitment ability decreased by almost half. This observation suggests that fire ants are consuming resources that native ants would otherwise consume, if fire ants were not present, and that fire ant population density is an important factor contributing to their competitive ability. Importantly, however, reducing the population density of fire ants affected only their short-term competitive ability. After poisoning, fire ants discovered and recruited first to fewer baits than did native ants, and native ants in general recruited to a higher portion of baits discovered, but fire ants still controlled equal numbers of baits as all native ants combined at the end of the three hour observation period. Again, this

long-term recruitment ability probably relies upon relatively large population sizes. Further evidence to support this hypothesis comes from the finding that fire ants still discovered and recruited to baits more quickly than native ants, even after poisoning, suggesting either superior foraging efficiency or an increased probability of discovering and recruiting quickly to baits because of a large number of individuals searching the area. Also, fire ants still recruited to baits in much higher densities than did native ants. It is clear from this study's findings on ant abundance and diversity in these habitats (Chapter II) that fire ants would still be overwhelmingly numerous in these ant communities even if their abundance were reduced by half. With more foraging individuals, fire ants would be able to maintain a dominant presence at baits for longer periods of time.

Many studies have found that when population sizes of fire ants and other ant species of interest are equal, fire ants do not exhibit dramatic competitive superiority. This fact suggests their overwhelming competitive ability as invaders is strongly influenced by relatively higher population sizes. Phillips et al. (1986), for example, pitted equal numbers of *S. invicta* and *Pheidole dentata* against each other, and *S. invicta* did not exhibit competitive superiority. Morrison (2000) found similar results when he equalized colony density of *S. invicta, S. geminata,* and *S. geminata* x *S. xyloni*. It seems to be the general consensus among researchers that larger population sizes of invasive ants are largely responsible for competitive superiority (Bhatkar et al. 1972, Jones 1985, Phillips et al. 1986, Fraelich 1991, Porter and Savignano 1990, Perfecto 1994, Human and Gordon 1996, 1999, Davidson 1998, Holway 1999, Morrison 2000). Even among non-invasive ants, population size is an important determinant of competitive outcomes

(Hölldobler and Wilson 1990). The extremely high population densities of fire ants in this study (see also Chapter II) are clearly important in their competitive superiority.

How do fire ant population densities become so high? One hypothesis concerns an escape from natural enemies in fire ants' introduced range. There is ample evidence that larger population densities result when fire ants leave their native range and their native parasites along with it (Briano et al. 1995, Porter et al. 1997, Calcaterra et al. 1999, Feener 2000). Native ants, subject to population pressure from parasites, may have reduced population sizes or reduced foraging rates relative to parasite-free invasive ants. Important parasitoids of ants are phorid flies, in the family Phoridae, each specific for a particular ant species. Under attack by this fly, ants reduce their foraging and either assume an immobile defensive posture or flee into hiding (Orr et al. 1995, Morrison 1999, Feener 2000). Phorid flies exact an indirect cost on an ant colony by causing a colony to abandon resources or by reducing its foraging rate, foraging intensity, or its ability to defend resources against other ant species (Feener 2000). Even one phorid fly is sufficient to disrupt recruitment (Orr et al. 1995). Thus, phorid flies alter the way ant species interact and can alter competitive outcomes, which have direct effects upon the fitness of a colony. Although fire ant-specific phorid flies induce this behavior in laboratory studies, no natural enemies of fire ants have existed in North America until recently, when efforts at establishing biocontrol agents began succeeding (*Karen Vail, personal communication*).

Ants normally show a trade-off between exploitative abilities and interference abilities (Fellers 1987, Davidson 1998), but invasive ants, and invasive species in general, may be able to break this trade-off and excel at both forms of competition (Davidson

1998, Holway 1999, Morrison 2000a). Holway (1999) reports that the invasive Argentine ant excels at both interference and exploitative competition, thus breaking the trade-off. Although I observed very few instances of interference competition in this study, it is apparent that *S. invicta* x *S. richteri* is superior to native ants at exploitative competition, and many other studies show that fire ants perform very well at interference competition (Bhatkar et al. 1972, Phillips et al. 1986, Jones and Phillips 1987, Fraelich 1991, Morrison 2000a). It would be interesting and informative to create a trade-off curve for communities of ants in an area recently invaded by fire ants, or perhaps one further along in the invasion process, to see if fire ants, like invasive Argentine ants, are able to break an exploitative-interference ability trade-off.

As in the pre-poison observations, very few aggressive interactions were observed post-poison. *Monomorium* individuals were again the victors in all their interference interactions, probably owing to their noxious chemical repellant. Which genus occupied the bait first also seemed to be an important factor determining which individual fled an aggressive encounter. These observations lend more support to my finding that exploitation competition is an important mode of competition in these communities. Territoriality or unseen chemical interference at baits could account for the few instances of aggressive encounters observed.

Differences between the field and pasture habitats and individual trends

The pasture habitat has been invaded longer than the field habitat (approximately 5 years and 1 year, respectively), and as one might expect, different dynamics occurred in each. The same general outcome occurred in both habitats—fire ants performed better on

all measures of competitive ability than native ants, and native ants performed better when fire ant density was reduced. Although the difference was not large, native ants tended to do better post-poisoning in the field habitat than in the pasture habitat, perhaps because their populations had not yet been affected to the same degree as in the pasture habitat. Interestingly, even though *S. (Diplorhoptrum)* was present in the field habitat (see Chapter II), it recruited to only one bait , and that occurred after poisoning. In the pasture habitat, however, *S. (Diplorhoptrum)* discovered, recruited to, and controlled several baits. *Monomorium* performed much better on all measures of competitive ability in the pasture habitat than in the field habitat while *Lasius* and *Prenolepis* performed worse. Importantly, the average number of *Monomorium* individuals at baits was much higher in the pasture habitat than in the field habitat. In the pasture habitat pre-poisoning, there were distinctly more *Monomorium* individuals at baits, on average, than there were of any other native genus. Also in the pasture habitat, *Forelius* occurred at baits pre-poison but disappeared from baits post-poison. Perhaps fire ants have an indirect positive effect on *Forelius*'s competitive abilities by decreasing the degree of competition from other ant genera. Interactions between all other native genera and fire ants appear to have a net negative effect on native genera's competitive abilities. The time it took fire ants to recruit to a bait once it had discovered it was much shorter in the pasture habitat, both pre- and post-poison, than in the field habitat. This could be due to higher densities of fire ants present in the pasture habitat (see Chapter II). Also in the pasture habitat, fewer takeovers occurred, in general, than in the field habitat; importantly, fewer takeovers from *Solenopsis* occurred. These findings suggest that fire ants face less competition

from native ants in the pasture habitat, probably ultimately because of higher densities of fire ants in this habitat.

Chapter IV

Final Conclusions

It is clear that imported fire ants pose a biological threat to native communities and an economic threat to society (see Chapters I and II). What is unclear, however, is how to control these pests effectively. Important in controlling any pest species is understanding the reasons for its success. For the imported fire ant in North America, one hypothesis with considerable support is that fire ants are competitively superior to most native ant species and can thus negatively impact native ant communities, establishing a strong presence. Much evidence indicating that fire ants are competitively superior to naitve ants is indirect and focuses on how native ant species abundance and diversity decrease after invasion by fire ants (Porter et al. 1988, Porter and Savignano 1990, Jusino-Atresino and Phillips 1994, Vinson 1994, Wojcik 1994, Gotelli and Arnett 2000, Kaspari 2000, Wojcik et al. 2001). Laboratory experiments have shown that fire ants are competitively superior to native ants in interference competition (Bhatkar et al. 1972, Jones 1985, Phillips et al. 1986, Jones and Phillips 1987, Morrison 2000a) and exploitative competition (Jones 1985, Phillips et al. 1986), although most studies focus on the interference component of competition. The handful of studies that have been conducted in the field have also shown that fire ants are superior competitors (Bhatkar et al. 1972, Baroni Urbani and Kannowski 1974, Porter and Savignano 1990, Fraelich 1991). Some studies indicate that the extremely high population densities of fire ants are an important factor in their success (Bhatkar et al. 1982, Jones 1985, Phillips et al. 1986, Bhatkar 1988, Morrison 2000a).

Competition, especially exploitative competition, is very difficult to document. Invasive species often offer the best opportunity to study and document competition (Simberloff, in press). In North America, the Argentine ant, *Linepithema humile*, is an important invasive species. It, too, reduces native ant species abundance and diversity (Cammell et al. 1996, Human and Gordon 1999), probably through competition. The Argentine ant is superior to most natives at both interference and exploitative competition (Human and Gordon 1996, 1999; Holway 1999). Like the fire ant, the Argentine ant's numerical dominance contributes importantly to its competitive superiority and invasion success (DeKock 1990, Cammell et al. 1996, Holway 1999, Human and Gordon 1999). The invasive gecko, *Hemidactylus frenatus*, is competitively superior to the native gecko, *Lepidodactylus lugubris*, and this superiority seems to be the factor causing the numerical decline of *L. lugubris* (Petren and Case 1996). In Britain, the invasive grey squirrel, *Sciurius carolinensis*, is a more efficient forager than the native red squirrel, *Sciurius vulgaris*. This competitive superiority lead to a decline in the red squirrel population (Williamson 1996).

The role of population density, at least for invasive ants, appears to be pivotal to competitive superiority and invasion success. One of the best supported hypotheses explaining why fire ants have such high population densities in their introduced ranges concerns their escape from native parasites. According to this hypothesis, when fire ants left their native range, they also left behind their native parasites. Free from parasites and the indirect and direct costs of them, fire ants have been able to escape a trade-off that exists between interference ability and exploitative ability, excelling at both forms of competition (Fellers 1987, Davidson 1998, Feener 2000). Argentine ants appear also to

have broken this trade-off, thus outcompeting native ants for valuable resources (Holway 1999). From my study it is clear that fire ants are competitively superior to native ants and keep native ants from obtaining resources that they otherwise would if fire ant densities were reduced. Although very few instance of aggressive interference competition were observed in this study, other studies have shown that fire ants are very proficient at interference competition and engage in it often (see Chapter III), so it is reasonable to presume that fire ants excel at both forms of competition.

It has been shown that the presence of parasites, particularly phorid flies, results in decreased foraging rates and decreased competitive dominance of fire ants (Feener 1981, 2000; Orr et al. 1995; Morrison 1999). Since the success of ant colonies depends ultimately on their ability to retrieve food (Bernstein 1979), decreased foraging probably leads to a decreased level of fitness and reduced abundances (Jones 1985, Morrison 1999). Indeed, in areas where fire ants are parasitized by phorid flies, their population densities are lower than in similar areas where they are not parasitized (Porter et al. 1997). In my study, when fire ant population densities were reduced by poison, their competitive ability was also reduced; importantly, native ants' competitive ability increased after fire ant population density was reduced. These results support the hypothesis that the high population densities of fire ants, which are probably a result of an escape from native parasites, are important to their competitive superiority and invasion success.

Perhaps through the use of biological control mechanisms in addition to direct poison applications to fire ant mounds, fire ant population densities can be reduced enough to allow native ants to obtain more resources, resulting in subsequent increases in

native ant abundance. However, it might be too late for control efforts to have any significant effect on the amount of resources fire ants obtain and prevent native ants from using. For example, Morrison (2000b), found, in laboratory studies, that when *S. invicta* foragers are exposed to phorid flies, *Pseudacteon tricuspis*, they alter their foraging strategy, removing foragers from the area with phorid flies and sending more foragers to areas without phorid flies. By altering their foraging strategy in the presence of phorid flies, *S. invicta* colonies are able to obtain the same amount of resources in the presence and absence of phorid flies (Morrison 2000b). Although higher phorid densities are associated with lower resource retrieval rates of fire ants in the field (Morrison 1999), fire ants may be able to alter their foraging strategies in the same way in the field. Fire ants may send more foragers to areas without phorids, send out foragers smaller than the minimum size required by phorid flies to parasitize them, or conduct the majority of their foraging at night, when phorid flies are not active.

It would be both interesting and informative to rank imported fire ants and native ants on a dominance-discovery trade-off curve, as Holway (1999) has done for Argentine ants. This type of research can help elucidate the mechanisms contributing to the invasion success of organisms. Along those lines, the same type of study conducted here would be very informative if used in areas in fire ant-infested areas of North America where phorid flies have been established and similar areas where they have not been established. If the escape from parasites hypothesis is correct, the competitive ability of fire ants in areas with phorid flies should be lower than in areas without phorid flies. If the trade-off hypothesis is correct, there should be a marked difference in the shape of trade-off curves for the two areas. Additionally, there should be differences in native species abundance

and diversity patterns, with higher native ant abundance and diversity in the parasitized area. Long-term and large-scale fire ant poisoning experiments might yield similar results and information, but these types of experiments would be difficult to establish and maintain.

In conclusion, this study found indirect and direct quantitative support of the hypothesis that fire ants are competitively superior to native ants and that fire ants' ability to reach extremely high population densitites is a primary contributing factor to their success. This study is the first, to my knowledge, to report the competitive ability of hybrid imported fire ants (*Solenopsis invicta* x *S. richteri*) and their effects on native ant species.

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Vita

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