INVASION OF RED IMPORTED FIRE ANT NESTS BY SELECTED PREDATORY ANTS: PROSPECTS OF UTILIZING NATIVE ANTS IN FIRE ANT MANAGEMENT

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ABSTRACT

The red imported fire ant, *Solenopsis invicta* Buren, has spread across the United States and is reported to have significantly reduced the diversity of the native ants. This ant has become dominant, particularly in disturbed environments and in newly invaded areas.

Much of this spread is occurring on land that is disturbed repeatedly by continually changing land use practices. *S. invicta* has been described as a weed-like species and exhibits the characteristics of an invasive "tramp ant." As a result, *S. invicta* appears to be able to out compete and even prey on and eliminate other competitive ant species. But is this inference correct? Here in, we review the interaction between the selected predatory/competitive ants and *S. invicta*, and evaluate whether some of these ants are capable of invading and attacking small worker-defended *S. invicta* colonies.

Our results suggest that several of the Texas native ant species studied, such as *Monomorium minimum*, *Pheidole* sp., *Solenopsis molesta*, and exotic tramp ants such as *Tetramorium* sp., and *Monomorium pharonis*, can invade worker-defended colonies *S. invicta* colonies of size varying from 30 to 480 workers. *M. minimum*, *Pheidole* sp., *Solenopsis molesta*, *Tetramorium* sp. and *Monomorium pharonis* were also observed to prey upon *S. invicta* brood. The native species, *Forelius* sp., however, was not observed to invade *S. invicta* colonies, instead, prevented *S. invicta* workers from leaving their nest for foraging which may have contributed to the decline of *S. invicta* colonies of up to 60 workers over time.

INTRODUCTION

The behavior of organisms is influenced by many biotic and abiotic factors. One of the more important biotic factors that affect the behavior of an organism is the risk of predation (Polis et al. 1989; Lima 1998; Werner and Anholt 1996). A perusal of any ecology textbook will confirm the importance of predation of one species by another in molding the complex interactions that form the structure of communities. Predation is important in the evolution of adaptations that range from stealth to a rapid escape response through adaptations such as chemical defenses, cryptic and aposematic coloration, and protective shields (Edmunds 1974; Harvey and Greenwood 1978; Sih 1987). Further, the importance of predation is implicated in the evolution of sociality in populations both in the breeding and non-breeding season (Pulliam and Caraco 1984) and it is considered an important selective force on various reproductive strategies (Burk 1982).

Predator – prey interactions have been documented among most vertebrates and

invertebrates. In some cases, the organism is primarily a predator or prey, but in most cases the roles can reverse depending on the interacting organisms and the situation. Social insects, especially ants, are no exception. Although subjected to predation, they are also well known to be predators of select invertebrates. Although predator – prey relationships are often considered positive for the predator and negative for the prey, these distinctions are rarely clear and may differ at any given location (Callaway and Walker 1997, Holmgren et al. 1997). For example, ants (Hymenoptera: Formicidae) are known to prey on the young chicks of birds as they hatch from the egg and thus the ants are assumed to have a negative impact on the birds. Nevertheless, the same interaction between species can sometimes be positive and sometimes negative. Haemig (1999) reported that the wood ant, *Formica aquilonia* (Espoo), cause some mortality on nesting tits, *Parus major*, and pied flycatchers0, *Ficedula hypoleuca*, both of which avoid the ants. However, when the risk of predation by other organisms such as snakes or rats are high, the birds prefer to nest with the ants that now function as protectors. His work documented that risk of predation can shift species interactions from a predominately predatory to a predominately facilitative process, i. e., a little change in the balance between the predator – prey relationship may alter both the processes and outcome. But can such information be of use in ant management?

It has been suggested that the generalist predator ants probably play an important role in influencing other ant populations (Hölldobler and Wilson, 1990). It is within this group that most of the invasive "tramp ant" species occur. Tramp ants are generally characterized as polygynous, unicolonal, reproduce by budding, and easily dispersed through human commerce (Passera and Keller 1994). Among the tramp ants, it is *Solenopsis invicta* Buren, the red imported fire ant (Hymenoptera: Formicidae), that is considered to be one of the more successful invaders, particularly the polygyne form (Vinson 1994). Further, *S. invicta* has been compared to an invasive weed species (Tschinkel, 1987). Some members of this genus have been described as a keystone species (Risch and Carroll, 1982) that reduce species richness, and pose a threat to invertebrates (Propp and Morgan, 1985; Vinson, 1991) and vertebrates (Grant et al., 1988; Allen, et al., 1994) alike. In fact, *S. invicta* has been considered as an effective biological control agent in certain crop systems (Brinkley, et al.,1991; Reagan,1986; Sterling, 1978) due in part to its dominance or keystone status within the system.

The increasing population density of *S. invicta* in the United States has been attributed to the lack of natural controls, which are associated with the natural enemies native to South America (Jouvenaz et al., 1981; Porter et al., 1992). As *S. invicta* has spread, it has had a major impact that has resulted in a decrease of the native ant complex (Camilo and Phillips, 1990; Jusino-Atresino and Phillips, 1994; Porter and Savignano, 1990; Wojcik, 1994). Whitcomb et al. (1972) reported that *S. invicta* also reduced the native ant complex in agroecosystems. This imported fire ant has largely replaced the native *Solenopsis* species, *S. xyloni* and *S. geminata* (Hung and Vinson, 1978; Porter et al., 1988; Wojcik, 1983). Thus, some of these authors suggest that native ants have little chance against *S. invicta*, but is this true? Wojcik (1994) reported, some native ants persist in *S. invicta* infested areas and Helms and Vinson (2001) observed a number of native ant species co-existing with a small *S. invicta* population in an undisturbed post oak savanna. This coexistence could be due to their ability to defend themselves and maintain dominant positions in certain areas, an aspect that needs to be explored.

Incipient colonies of *S. invicta* are known to suffer high mortality rates before the first workers have a chance to forage (Tschinkel 1987). Most of this mortality is due to predation of founding *S. invicta* queens. Whitcomb et al. (1973) reported that at least nine species of ants are successful predators of founding *S. invicta* queens. None of the *S. invicta* founding queens was observed to have survived to construct a brood chamber in an area occupied by the dolichoderine ant, *Conomyrma insana* (Buckley) that successfully preyed

upon the queen (Nickerson et al. 1975). Nichols and Sites (1991) documented twelve additional ant predators of *S. invicta* queens. The *Solenopsis* subgenus *Diplorhopturm* are also known to be important predators of *S. invicta* queens (Lammers 1987). It is assumed that once workers eclose and begins to forage, queen is protected from many of these predatory ants. Nothing is known of the ability of newly founded *S. invicta* colonies to defend against predatory ants. Thus, we initiated laboratory studies to determine and document the ability of small colonies of *S. invicta* to defend against predatory native ant and other tramp ant species.

MATERIALS AND METHODS

All *S. invicta* colonies used in the experiments were reared from newly mated queens collected from several locations in Brazos County, Texas. Colonies were initiated by placing two *S. invicta* flight queens in a 60 mm castone petri-dish nest with a solid lid with no holes. The nest was placed in a plastic box (17.15 cm x 12.06 cm x 6.02 cm or 31.75 cm x 17.15 cm x 9.5 cm) to serve as a foraging arena. The box was coated with Fluon® on the inside to prevent ant escape. When the workers eclosed, the solid lid was replaced with one entrance hole that allowed *S. invicta* workers to enter and exit. *S. invicta* colonies were maintained with honey water, crickets, and meal worms/pupa ad libitum.

Mature native and other exotic ant colonies used for the experiments were collected from various counties in Texas. The colonies were maintained in castone petri-dishes that served as nests, which were placed in a plastic sweater box (31.75 cm x 17.15 cm x 9.5 cm) with Fluon®-coated sides and the colony was maintained with honey water, crickets and meal worms/pupa ad libitum. The native ant species used in the experiment were *Monomorium minimum* Buckley, *Forelius sp.*, *Solenopsis (Diplorhopturm) molesta* Say, and *Pheidole* sp. In addition we examined the interaction between the *S. invicta* and two exotic species: *Monomorium pharonis* Say and *Tetramorium sp.* The native and other exotic ant species collected were polygyne colonies.

In all the experiments, the size of the experimental native and other exotic ants colonies were kept constant with 500 to1000 workers and 5 to 6 queens depending on the species used. The experimental *S. invicta* colonies consisted of two queens, brood and either a) 30, b) 60, c) 120, d) 240, or e) 480 workers. These *S. invicta* colonies with various worker numbers are referred to as *S. invicta* "colony size" further in this article. Each of the native/other exotic ant colony was provided an access to each one of the *S. invicta* colony size (defined as colony worker numbers) categories separately. As a control to these experiments, interaction of *S. invicta* colonies (with 1000 workers and 5 to 6 queens) with each *S. invicta* colony size category described earlier was observed. Each species combination was replicated five times.

Confrontation between the two species was initiated by placing the *S. invicta* and predatory native/other exotic ant colony trays next to each other and providing worker access to both trays, through a 2.54 cm-wide paper bridge. A rubber cork attached at each end of the paper bridge held the bridge in place. This set up assured equal access by both species tested to each other's nest. The movement of the native/other exotic ant queen and workers was unrestricted. The same was true for *S. invicta* workers and queens. The time required by either species to invade each other's nest was recorded. Invasion in this experiment was defined as the entry by a worker of either species tested into the nest of the opposing species followed by recruitment of its nest mates. After the invasion, the ability of workers to attack the other was also noted. Colony destruction was determined by measuring the time taken from the point of first interactions between the two colonies until the death of the queens of the invaded colony and all their workers. However, this paper only reports the time taken for the worker ants to invade the opposing nest. This time measurement is considered to be

measure of the ability of the ant colony in question to defend itself. The response variable (time taken to invade the *S. invicta* nest) was normalized using log transformation and subjected to Two way ANOVA with predatory ant species and *S. invicta* colony size as two main factors affecting the time to invade. Since the five replications for each species combination was conducted at different times, the effect of replication on response variable was also tested in the model. A multiple comparison analysis was done using Tukey HSD mean separation technique.

RESULTS

In all the experiments conducted, the native/other exotic ant species tested were the first to invade colonies of the *S. invicta*, regardless of the colony size of the latter. Fig. 1 shows the plot of mean hours taken for different predatory species to first invade the *S. invicta* nest of various colony sizes. *M. minimum*, *Pheidole* sp., and *M. pharonis* were successful invaders of *S. invicta* nest of colony size up to 480 workers while *Tetramorium* and *S. molesta* invaded colony size of up to 240 workers. Unlike other species, *Forelius sp.* did not invade *S. invicta* nest except in one replication each with a colony size of 30 and 120 workers.

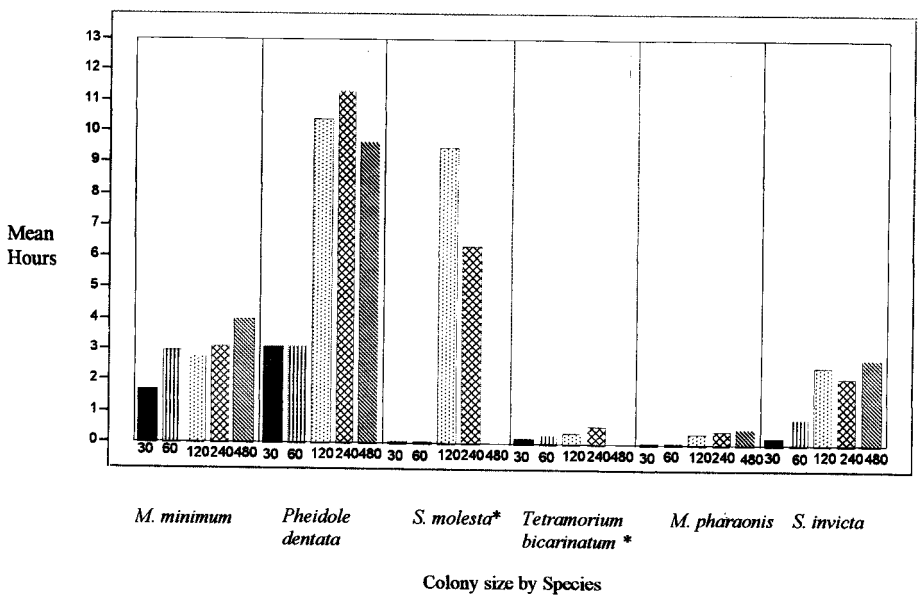

FIG. 1. Mean hours taken by each competitive species to invade *S. invicta* nest of different colony sizes (30,60, 120, 240, and 480). Each colony size within a species was replicated five times and hours presented here are averaged over these five replications.
* Species that did not invade *S. invicta* colony size of 480.

The invasion was not consistent as with other species in the replications and thus *Forelius sp.* was not included in the analysis. In the control colonies, invasion of smaller *S. invicta*

colonies by larger *S. invicta* colonies (with 1000 workers) and vice versa was observed. In comparison to all the species tested, *Pheidole* sp. and *S. molesta* took longer to invade the *S. invicta* nest. *M. minimum* followed a steady increasing trend in time to invade *S. invicta* colony size of 30 to 240, where as *Pheidole denata* and *S. molesta* invaded the colony sizes of 30 and 60 workers faster than any species and drastically slowed down when the colony size increased to 120 and 240. *Tetramorium* sp. and *M. pharonis,* and *S. invicta* and *M. minimum* followed similar trends in time to invade.

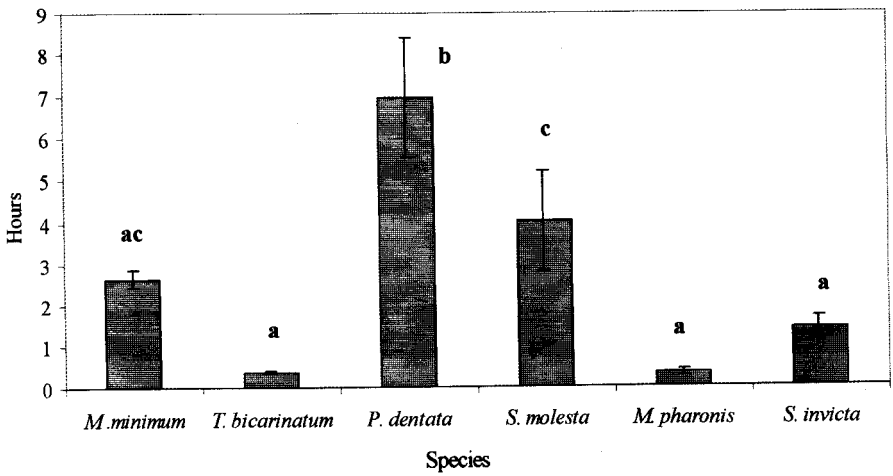

FIG. 2. Comparison of mean hours (averaged across *S. invicta* colony sizes of 30 to 240) taken to invade *S. invicta* colonies by different predatory ant species.
Bars followed by same letters are not significantly different at $p < 0.05$.

Further comparisons between species and between colony sizes were affected by the absence of two species that did not invade the colony size of 480. Thus, to obtain a clearer picture on the actual differences between the species, we omitted the colony size of 480 and further analyzed the data including all species that invaded *S. invicta* colony size of 240 using the two-way ANOVA as described earlier. There was a significant effect of both species and *S. invicta* colony size and their interaction as with the model including the colony size of 480 (Species $F = 17.37$, $df = 5, 96$, $P < 0.001$, Colony size $F = 10.22$, $df = 5, 96$, $P < 0.001$, Species*Colony size $F = 3.78$, $df = 15, 96$, $P < 0.001$). *Pheidole* sp. invaded at significantly different times compared to all other species (Fig. 2). *S. molesta* differed significantly from all other species except *M. minimum.* There was no significant differences observed between *M. pharonis, T. bicarinatum, S. invicta,* and *M. minimum.* The time to invade did not significantly differ when the *S. invicta* colony size increased from 30 workers to 60 workers (Fig. 3). However, the time significantly differed from 60 workers to 120 workers. When the *S. invicta* colony size increased from 120 to 240, there was no significant difference. *Pheidole* sp. and *M. minimum* were good recruiters with *Pheidole* sp. mainly recruiting the major workers after the first encounter with the *S. invicta* colony. These data suggest that most species used in the experiment except *Forelius* were able to invade *S. invicta* colony sizes tested, and the time taken for each of the species to invade differs due to their behavioral differences.

Additionally, after the invasion and attack on *S. invicta* colonies, the native predatory ants such as *M. minimum, S. molesta, Pheidole* sp., and exotic ants, *M. pharonis*

and *Tetramorium* sp. were observed to carry the *S. invicta* brood back to their colony. In contrast, *Forelius* sp., was observed to carry dead bodies of *S. invicta* to their nest. In the control experiments, larger and smaller experimental *S. invicta* colonies were observed to invade each other's nest and merge together in most trials.

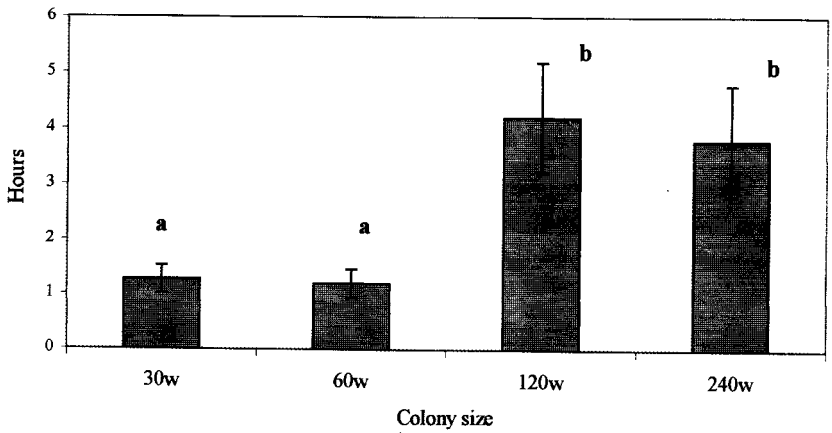

FIG. 3. Comparison of mean hours (averaged across all species that invaded *S. invicta* colony sizes up to 240w or 240 workers) taken by different species to invade *S. invicta* colonies. Bars followed by same letters are not significantly different at $p < 0.05$.

DISCUSSION

Population density of ants is constrained by the type of resources within the space that they occupy, competition for that resource, as well as by predation and diseases (Hölldobler and Wilson 1990), and by their ability to displace other colonies. This displacement can be through resource competition or where one ant species preys upon another. This type of predation is known as intraguild predation (IGP) and differs from classical predation because the act reduces potential exploitative competition resulting in an impact on the population dynamics of the species involved in more complex ways than either exploitative competition or predation (Polis et al., 1989). In fact, predation is known to be an important organizing factor in natural communities. In competitive communities all species except the competitive dominant are eventually excluded from a large segment of suitable habitat. Competitive subordinates can coexist with the dominant only by their ability to persist in refuges that are not suitable for the dominant. However, Paine (1974) has experimentally shown that, despite the presence of a strict dominance hierarchy, high species diversity can be maintained in uniform habitat by "keystone predators" that prevent competitive dominants.

Since social insects are both effective as predators and desirable as prey, it is not surprising to find situations where one species of social insect preys upon another (Wilson 1971, 1976). This circumstance appears to be particularly common among ants. Just as predatory ants may be responsible for the development of colony defense systems, ant predation may also have provided the pressure for much of the caste polymorphism and behavioral specialization seen within many ant species. A closer investigation of each species ecological niche would reveal clues as to what other adaptations may have predisposed them for a particular mode of colony defense. In particular, it is not known to

what degree the food habits of these sympatric species overlap and how resource partition may have influenced the evolution of caste system (Davidson 1978).

The findings from our work provide evidence that small *S. invicta* colonies can be invaded by some species of ants that occur in Texas – *M.minimum*, *Pheidole* sp. and *S. molesta*, and that *S. invicta* cannot defend itself once the workers eclose. These three native Texan ant species had a direct effect on small *S. invicta* colonies as *M.minimum*, and *Pheidole sp.* were able to invade and kill small *S. invicta* worker-defended colonies of sizes up to 480 and *S. molesta* up to the colony size of 240. One exception among the competitor species examined is *Forelius* sp. This species did not invade the *S. invicta* nest but was able to prevent *S. invicta* workers from leaving their nest or foraging, resulting in the decline of *S. invicta* colony over time, including colony sizes up to 60 (personal observation). The two exotic species *M. pharonis* and *Tetramorium* sp. also successfully invaded the *S. invicta* colony size of 480 and 240 respectively. In the control colonies where larger *S. invicta* colonies were confronted with smaller *S. invicta* colonies, the colonies merged together in most replications as one might expect of polygyne *S. invicta* colonies. The data also suggests that *S. invicta*'s ability to defend itself successfully from other invading species increases with the increase in its colony size (worker numbers).

The native species, with an exception of *Forelius* sp., were also observed to carry *S. invicta* brood back to their colonies while the *S. invicta* colony was alive suggesting that these native ants are good predators of *S. invicta*. The *Forelius* sp., however, did not remove brood until the entire *S. invicta* colony was dead. Previous studies on predation have focused only on founding *S. invicta* queens following their nuptial flight until the emergence of minim workers, with an exception of Mackay and Vinson's work in 1989. They reported that the fire ant density in localities with two species of this subgenus. *Solenopsis subterranea* and *S. punticeps* are much lower than other areas (Mackay and Vinson, 1989). They assume the difference to be due to the presence of these general subterranean predatory species.

Although several reports (Porter and Savignano 1990; Gotelli and Arnett 2000) have shown that native ant diversity are adversely affected by the invading *S. invicta*, the four native species discussed above appear to persist (Fowler et al. 1990, Helms and Vinson 2001). This coexistence, along with the demonstration that these native predatory species are capable of successfully invading small *S. invicta* colonies, and, the report that there are periods of time when the different species do not overlap at food resources due to differences in their foraging time (Helms and Vinson 2001), suggests that, if encouraged, these native predatory species could help sustain pressure on and possibly reduce the *S. invicta* population, particularly in concert with phorid fly releases (Porter 1998) and introduction and conservation of other biological control agents.

Predators may not always have a lethal effect on their prey, there are non-lethal effects that are equally important (Lima 1998), for example, reducing or preventing workers from small *S. invicta* colonies from foraging. *Forelius* sp., that was observed to portray this effect, might be exploited in ways that would exert pressure on *S. invicta* colonies.

Considering that several native ant species can reduce the number of newly mated *S. invicta* queens that can initiate a colony and that *S. invicta* queens that escape remain vulnerable even after they have reared some workers, suggests that better use of our native ant species may be possible. Given the predatory behavior of some of the native ant species and the ability of some of these to coexist, can we tilt the balance in favor of native ants and thus change the negative interaction to a positive one by finding factors that facilitates this tilt? We believe the answer is "yes."

Nevertheless, more detailed work on these native ants is necessary to establish their importance in suppressing *S. invicta* densities. We need to determine if there is an ideal density of native ants that can limit the invasion of the *S. invicta* and if we can increase the density of our native ant species through augmentation and conservation of these and other

biological control agents. Can we develop ways to rear these native species in the laboratory? Can we successfully introduce them in areas after removal of the *S. invicta*? If introduced, can they reduce or prevent *S. invicta* reinvasion? We believe that answers to these questions will be positive, but the use of native ants as a biological tactic against the *S. invicta* will only occur if we recognize that all ant species are not pests.

Since the spread of *S. invicta* is known to occur not only by newly mated queens but also by colony budding and ground migration, it becomes inevitable to study the native and other exotic ant species that are still holding their ground in *S. invicta* infested areas. The interactions in the field probably are much more complex than it appears at first and there may be more to these native ants than we may think. The predation of *S. invicta* colonies by some native predatory ant species may already be in progress in the field. If the biology of these predatory/competitor ants are better understood, we may be able to increase their population density by rearing them and releasing them through biological control programs where they can work in concert with other biological control agents to provide sustainable suppression of the *S. invicta* population.

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