Ant Predators of Founder Queens of *Solenopsis invicta* (Hymenoptera: Formicidae) in Central Texas

BECKY J. NICHOLS AND ROBERT W. SITES[1]

Department of Agronomy, Horticulture, and Entomology,
Texas Tech University, Lubbock, Texas 79409

ABSTRACT   Vials containing founder queens of the red imported fire ant, *Solenopsis invicta* Buren, were placed under the soil surface at four locations in central Texas; two within the current range of *S. invicta* and two outside, to compare founder queen predation mortality and also to document ant predators of the queen. The screen mesh covering vial openings was sufficiently small to prevent queens from escaping but allowed predacious ants as well as other organisms to enter. Queen mortality was compared between treatments and controls and at four locations. Of the four locations studied during 1988, predation by ants had the most pronounced effect on queen survival within the range of *S. invicta*. Twelve species of ants that previously have not been recorded as predators of *S. invicta* founder queens were observed killing queens during this study. Also, diversity of the ant community was found to be less within the range of *S. invicta* than outside the range.

KEY WORDS   Insecta, *Solenopsis invicta*, biological control, predation

THE USUAL METHOD of colony founding among ants consists of a nuptial flight, after which the queen descends, removes her wings, excavates and enters a small cavity in soil or wood, and plugs the tunnel entrance. Using the food reserves in her body, she lays her first cluster of eggs and raises the resulting brood to miniature adult workers (Markin et al. 1973, O'Neal & Markin 1975). During the establishment of new colonies, reproductive ants are subject to heavy aerial and terrestrial predation. Dispersing queens of *Solenopsis invicta* Buren, the red imported fire ant, are attacked by various species of birds (e.g., chimney swift, purple martin, tree swallow), dragonflies, and robber flies while airborne (Whitcomb et al. 1973, Glancey 1981). After landing, these queens are subject to predation by terrestrial insects and arachnids (Edwards et al. 1974, Lucas & Brockman 1981). In areas of low *S. invicta* population density in Florida, predators of queens include other species of ants (e.g., *Conomyrma* spp., *Lasius neoniger* Emery, and *Pogonomyrmex badius* Latreille), *Cicindela punctulata* Oliver (Coleoptera: Cicindelidae), *Labidura riparia* Pallas (Dermaptera: Labiduridae), and *Lycosa timuga* Wallace (Araneae: Lycosidae) (Whitcomb et al. 1973). In northern Florida, *Conomyrma insana* (Buckley) was considered by Nickerson et al. (1975) to be an important factor in limiting local populations of *S. invicta*. In areas where *S. invicta* already is established, conspecific workers are the most active predators on the soil surface, where they dismember foreign queens and take body parts back to their mounds (Whitcomb

et al. 1973). At Caseres, Mato Grosso, Brazil, species of *Conomyrma*, *Ephebomyrmex*, and *Pheidole* (Hymenoptera: Formicidae) attack *S. invicta* and other fire ant queens on the ground; and at Piracicaba, Brazil, the ants *Ectatomma edentatum* Roger and *Pheidole oxyops* Forel also attack *S. invicta* queens on the ground (Williams 1980).

After the nuptial flight, the *S. invicta* queen begins a nest which consists of a vertical tunnel 3–12 cm deep ($\bar{x}$, 7 cm) with a small chamber at either end (Markin et al. 1972). During this colony initiation, workers from established *S. invicta* mounds tunnel underground to destroy conspecific founder queens and brood (Whitcomb et al. 1973). Species of *Solenopsis* (*Diplorhoptrum*) are important subterranean predators of founder queens (Lammers 1987). The eastern bobwhite, *Colinus v. virginianus* (L.), *Lasius neoniger*, and *Labidura riparia* also prey on queens in their chambers (Whitcomb et al. 1973).

Natural environmental regulation of *S. invicta* populations occurs in Argentina and Uruguay because outbreaks seldom occur. This natural population control is achieved through the predacious and parasitic habits of various arthropods, birds, lizards, etc. (Silveira-Guido et al. 1973), and through long periods of low soil moisture (Lofgren et al. 1975). However, most natural enemies of *S. invicta* do not occur in the United States (Jouvenaz 1983).

Buren (1983) suggested competitive displacement by predator and competitor ant species as a possible method for permanently suppressing *S. invicta* populations in the United States. Possibly >1,000 species of ants from various areas of the world are available for consideration in an artificial, or scientifically selected, ant fauna. In partic-

[1] Department of Entomology, University of Missouri, Columbia, Mo. 65211.

ular, *S.* (*Diplorhoptrum*) spp. (subterranean predators) may have more influence on *S. invicta* populations than any other group of ants because they attack the nest-founding queens (Buren 1983).

Overall, >99% of female reproductive ants are killed by predators (Whitcomb et al. 1973), suggesting that predation on founding queens represents an important limiting factor on expanding ant populations (Carroll & Janzen 1973). The objectives of the current research are to compare survival among founder queens placed in four ant communities in central Texas and to document ant predators of *S. invicta* founder queens.

Materials and Methods

Vials containing *S. invicta* founder queens were placed in four central Texas locations to compare differences in survival rates when placed in different ant communities. Treatment vials allowed entrance of potential arthropod predators, whereas control vials prevented entrance.

Treatment vials were constructed from 20-ml plastic vials with snap-on plastic lids. Each lid was modified by cutting a hole (2 cm diameter) through the center. Wire screen (1.6 mm^2 mesh) was placed over each vial opening and was held in place by the modified lid. This screen allowed workers of most ant species and other small arthropods to enter but prevented the escape of queens. Control vials were similar to treatment vials except nylon screen (0.8 mm^2 mesh) was placed over each opening to prevent the entrance of potential arthropod predators. The bottom of each vial contained 3 ml of Castone dental plaster which, when dry, was remoistened by adding water with a squeeze bottle, thereby preventing desiccation of the queen. When moistening the plaster, vials were manipulated as little as possible to minimize disturbance to the queen and surrounding soil. Each vial was placed in a small depression in the soil and covered with a rock to simulate the colony founding situation.

Four sites in central Texas were chosen for the experiment during the summer of 1988, two outside and two within the currently known range of *S. invicta*. Outside the range, queens were placed at a site 8.4 km southeast of Junction, Kimble County, and at 3.7 km southeast of Midway, Kimble County. Within the range of *S. invicta*, sites for queen placement were 1.6 km northeast of Mountain Home, Kerr County, and 6.4 km northwest of Kerrville, Kerr County. These sites were chosen to allow sampling on a transect from an area heavily infested with *S. invicta* (Kerrville) to an area that is not infested (Junction).

Small depressions were dug in the soil with a trowel 2–3 d before queen placement to minimize effects of soil disturbance on arthropod activity. At each site, two spatially separated trap grids (5 by 10) were established, each containing 50 vials (25 treatment, 25 control) spaced 3 m apart. Treatment and control vials were randomized within each grid.

Solenopsis invicta queens collected from late May and late June mating flights were placed in vials within 2–3 d after collection. The first trial was conducted from 1 to 22 June and the second from 6 July to 2 August 1988. Queens were examined at 2-h intervals for the first day beginning at 1530 hours (CDT), at 24-h intervals for the next 2 d, and at 3-d intervals for the remainder of each study. Data collection continued until all treatment queens were dead. During each examination period, the condition of queens was recorded and observations on their behavior, on the behavior of associated arthropods, and on environmental conditions were noted. Organisms were recorded as predators only if they were directly observed killing the queen, or if it could reasonably be inferred that they were responsible for queen death. When a dead queen was present with other ants, all were collected and preserved in 75% ethyl alcohol. Eight pitfall traps containing ethylene glycol were placed at each of the four locations to monitor and characterize the local ant fauna. Samples were taken from 7 to 10 June and 21 to 24 July, corresponding with the time periods of each queen cohort study. Voucher specimens of all ants collected during 1988 (numbers 7772–7847) were deposited in the Texas Tech University Entomological Collection.

Analysis of variance with a split plot arrangement of a randomized complete block design was used to test queen survival differences between treatment and control vials, over time and at each location. The main plots (treatment) were assigned randomly within each block. The subplot factors were the time intervals at which queens were observed. Treatment effects, time effects, and treatment × time interactions were evaluated. At each location, species diversity was characterized by calculating Shannon-Weiner's index, and dominance relations were characterized using Simpson's index (Krebs 1972).

Results and Discussion

Ant Fauna Diversity. Ants collected from monitor pitfall traps and from queen containers were used to characterize the local ant faunas. For all habitats, 22 ant species were collected, representing five subfamilies (i.e., Dolichoderinae, Ecitoninae, Formicinae, Myrmicinae, and Ponerinae). Seventy-three percent of these species were contained in the subfamily Myrmicinae. Seventeen of the 22 species collected were observed as predators of the queen, and 83% of these were myrmicines. Twelve ant species that previously have not been recorded as predators of *S. invicta* founder queens were observed killing queens (Table 1).

The ant fauna at Junction, the study site farthest from the range of *S. invicta*, showed the highest species diversity and, thus, the lowest dominance values of the four areas (Table 1). Fifteen species

Table 1. Number of vials occupied[a], and mean number per vial (in parentheses), of ant taxa observed preying on *S. invicta* founder queens, followed by diversity[b] and dominance[c] indices, at four locations both outside and inside the current range of *S. invicta* during June and July 1988

Taxon	New predation record[d]	Outside range				Inside range			
		Junction		Midway		Mountain Home		Kerrville	
		June	July	June	July	June	July	June	July
Dolichoderinae									
Conomyrma flava	X	0	2 (3)	0	0	0	0	0	0
Conomyrma insana	—	6 (2)	5 (3)	0	0	0	0	0	0
Ecitoninae									
Labidus coecus	X	0	0	1 (14)	0	0	0	0	0
Formicinae									
Paratrechina vividula/terricola	—	0	0	0	0	1 (1)	0	0	0
Myrmicinae									
Crematogaster clara	X	4 (2)	1 (2)	3 (1)	9 (7)	0	0	0	0
Crematogaster laeviuscula	X	0	0	0	0	1 (8)	0	0	0
Diplorhoptrum sp.	—	3 (9)	3 (20)	1 (9)	0	0	0	0	0
Monomorium minimum	X	5 (13)	3 (12)	3 (2)	5 (66)	12 (9)	4 (30)	0	0
Pheidole dentata	—	0	0	3 (4)	1 (4)	2 (2)	1 (25)	0	0
Pheidole hyatti	X	4 (7)	2 (6)	0	0	0	0	0	0
Pheidole lamia	X	1 (10)	2 (4)	0	0	0	0	0	0
Pheidole metallescens	X	0	0	1 (39)	1 (46)	0	0	0	0
Pheidole porcula	X	0	0	19 (15)	15 (16)	4 (6)	5 (18)	0	0
Pheidole sitarches	X	1 (8)	0	0	0	0	0	0	0
Pogonomyrmex imberbiculus	X	2 (2)	0	0	0	0	0	0	0
Solenopsis invicta	—	0	0	0	0	0	0	50 (25)	50 (15)
Solenopsis xyloni	X	5 (2)	8 (14)	0	0	0	0	0	0
Diversity index	—	1.80	1.51	0.85	1.16	0.79	0.95	0.00	0.00
Dominance index	—	0.22	0.29	0.63	0.37	0.60	0.42	1.00	1.00

[a] $n = 50$ treatment vials.

[b] Shannon-Weiner diversity index (Krebs 1972).

[c] Dominance index (Krebs 1972).

[d] X, not previously recorded as preying on *S. invicta* founder queens.

were collected from this location (including species from treatment vials and monitor traps), and of these, 10 were observed inside treatment vials, either in the process of killing queens or having already done so.

At Midway, 10 species comprised the local ant fauna and 7 were observed killing queens. Species diversity here, near the edge of the *S. invicta* range, was less than at Junction. The fauna was concentrated mainly in two species, *Pheidole porcula* Wheeler and *Monomorium minimum* (Buckley), which together comprised 80% of the total number of individuals (Table 1).

The ant community at Mountain Home, within the range of *S. invicta*, was composed of eight species, five of which were predacious on queens. Species diversity was slightly less than at Midway during both months (Table 1). This site was very similar to Midway, with *M. minimum* and *P. porcula* being the two most abundantly collected species, comprising 90% of the total number of individuals. Also, the number of specimens collected in vials at this site was nearly three times less than at the other three sites. *S. invicta* was present in low numbers but was not observed as a predator of founder queens.

The Kerrville site had higher numbers of *S. invicta* than any of the other three sites, and only *S. invicta* workers were found in treatment vials and monitor traps. These results concur with many studies (e.g., Buren et al. 1974, Wojcik 1983) reporting that *S. invicta* dominates local ant communities and reduces species diversity within its range.

Predation Behavior. Queen predation was directly observed during this study, and the number of ants per vial collected throughout the summer was recorded (Table 1). Observations were made on the behavior of predators. Majors and minors of the polymorphic predacious ant species *Pheidole dentata* Mayr, *P. hyatti* Emery, *P. porcula,* and *Solenopsis xyloni* McCook participated in stinging the queen, dismembering her, and carrying away body parts. *P. porcula* workers were commonly observed attempting to take the head or gaster of an *S. invicta* queen out through the screen. When attacking a queen, *Crematogaster clara* Mayr workers were present in groups of up to 20 individuals and usually encircled the queen, removed legs first, then the head and gaster. Also, *P. dentata* and *S. xyloni* tried to remove live queens from the vial by pulling on legs or antennae through the screen. Small, monomorphic ants (i.e., *S. (Diplohoptrum)* spp., *M. minimum*) apparently rely on recruitment of many individuals (up to 50) to kill a queen. When only a few individuals of *M. minimum* were present in the vial (<10), they approached the queen but would not attack until
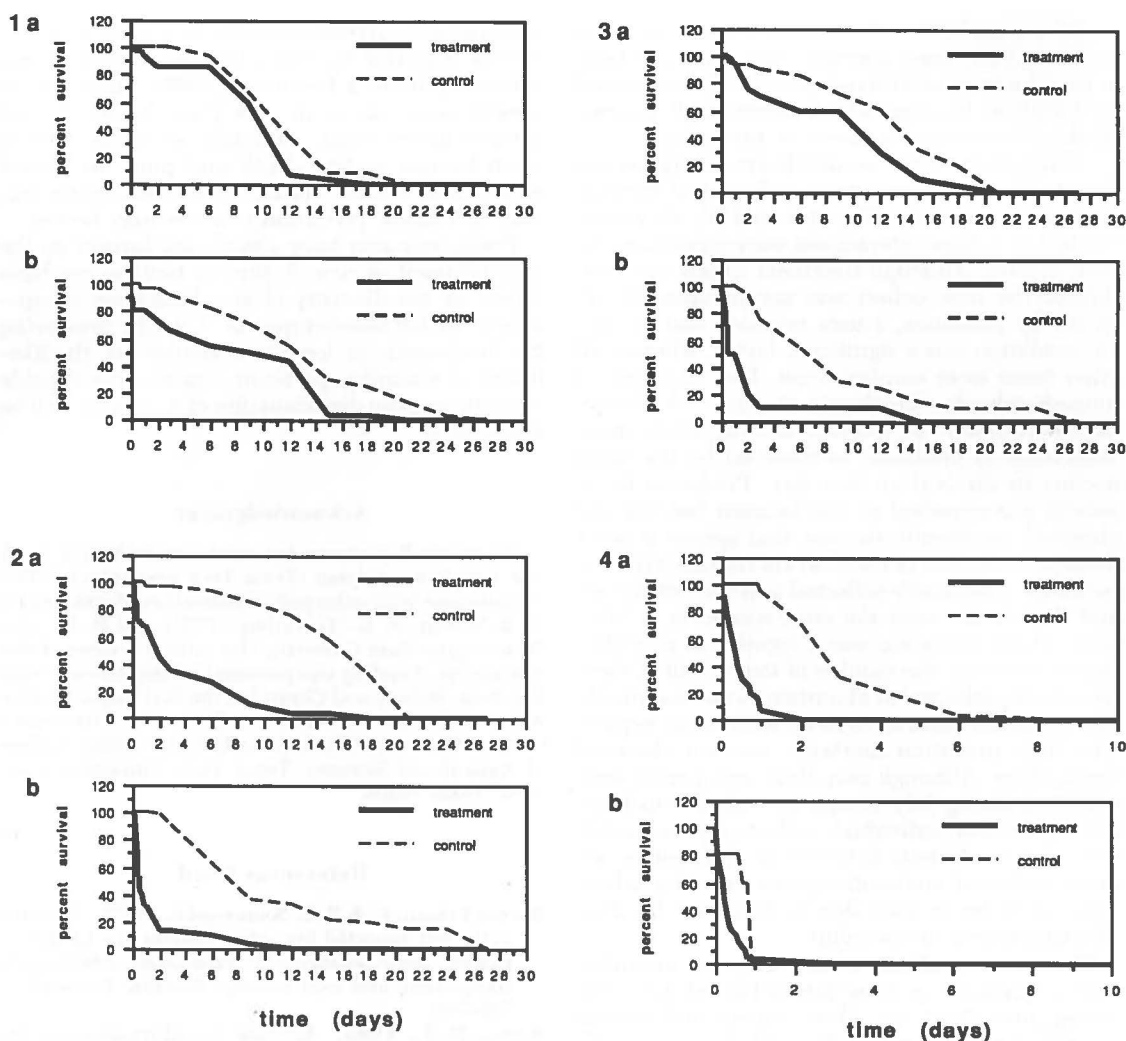
Fig. 1–4. Percentage survival of *S. invicta* queens over time at (1) Junction, (2) Midway, (3) Mountain Home, and (4) Kerrville, for (a) June and (b) July.

more conspecifics arrived. Individuals of *M. minimum* were frequently observed in the vial near the queen with their gasters oriented vertically (gaster flagging), probably emitting a characteristic repellent that is effective against *S. invicta* (Baroni Urbani & Kannowski 1974), whereas other individuals appeared to be stinging the queen.

Soon after placement in vials, many queens laid eggs and actively tended them; however, no eggs hatched, probably due to desiccation or predation. Ants such as *M. minimum* were observed entering the vial, either singly or in groups, and carrying eggs out in their mandibles. If another cluster of eggs was laid, it also disappeared quickly. Some queens appeared to protect eggs by standing over them, but they usually were unsuccessful.

Queen Survival. The analyses of variance on queen survival data suggested that neither the treatment effect nor the treatment × time inter-

action was significant at Junction for either June or July (Fig. 1 a and b). Allowing predators to enter a vial with a queen did not result in increased queen mortality compared with vials in which the queen was protected from predators (controls). Time was a significant factor affecting queen survival during both trials.

Treatment queens placed at Midway had significant mortality during June, indicating that predation was taking place, but not during July (Fig. 2 a and b). A treatment × time interaction occurred during June, and through a series of *t* tests comparing treatment versus control queen survival at each observation period, it was determined that from hour 8 of the first day until day 18, treatment queens exhibited significantly higher mortality. Therefore, predation was significant throughout most of June. However, during July, a treatment × time interaction occurred, but *t* tests revealed

no differences between treatment and control queen survival at any time interval. This may have been in part due to an additional mortality factor caused by localized flooding which affected all queens, thereby obscuring the effects of predation.

At Mountain Home, no significant difference was detected between treatment and control survival during June or July (Fig. 3 a and b). However, treatment × time interactions were significant for both months. Although treatment queen survivorship of the June cohort was not significantly affected by predation, t tests revealed that on day 12, predation was a significant factor, whereas all other times were nonsignificant. Day 12 occurred immediately after flooding in the area, which may have weakened the queens, making them more vulnerable to predation as observed by the rapid decline in survival on that day. Predation by $S.$ $invicta$ was expected at this location but was not observed, apparently because that species is not a dominant member of the local ant community. The two most abundantly collected ants ($M.$ $minimum$ and $P.$ $porcula$) were the same species as at Midway, where predation was a significant mortality factor. However, the number of individuals of these two species collected at Mountain Home was nearly three times less than at Midway, which may explain why high predation mortality was not observed during June. Although only three ant species were collected during July compared with five in June, the numbers of individuals collected were double that of June. T tests detected no differences between treatment and control queen mortality, which may again be in part due to localized flooding affecting queen survivorship.

There was significant treatment queen mortality and a treatment × time interaction at Kerrville during June (Fig. 4a). All treatment and control queens were dead within 2 and 9 d, respectively. Significant times of predation were from hour 4 of the first day until day 3. Mortality of the control queens may have been due to stress caused by the constant threat of $S.$ $invicta$ workers trying to enter the vial. During data collection periods, workers were present on all vials and occasionally pulled at the antennae or legs of the queen through the screen of control vials. No treatment or interaction significance was observed during July (Fig. 4b). During this month, all queens were dead after 3 d.

Of the four locations studied during 1988, predation by ants had the most pronounced effect on queen survival within the range of $S.$ $invicta.$ In the moderately infested $S.$ $invicta$ area, predation did not have such a dramatic effect on survival, probably because of the relatively low numbers of $S.$ $invicta.$ This observed lack of dominance may be because $S.$ $invicta$ has been in the area for only a short period of time and has not increased in numbers sufficiently to displace the dominant members of the local ant community. Also, when native ants are relatively abundant, they may re-

duce the ant-carrying capacity to a point where $S.$ $invicta$ is unable to obtain food to develop strong colonies (Vinson & Greenberg 1986). Although the queens were placed in vials 7 cm below the soil surface under rocks, naturally occurring queens often burrow to this depth and plug the tunnel entrance (O'Neal & Markin 1975); thus, under natural conditions, predation pressure may be less.

Predacious ants have a profound impact on the establishment of new $S.$ $invicta$ nests as we have shown by the diversity of ants (including conspecifics) that kill founder queens. Thus, by preserving the biodiversity of local ant populations, the likelihood of retaining species or communities capable of inhibiting the dissemination of $S.$ $invicta$ will be maximized.

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