# Seasonal Studies of an Isolated Red Imported Fire Ant (Hymenoptera: Formicidae) Population in Eastern Tennessee

ANNE-MARIE A. CALLCOTT, DAVID H. OI,[1] HOMER L. COLLINS, DAVID F. WILLIAMS,[1] AND TIM C. LOCKLEY

USDA, APHIS, PPQ, Gulfport Plant Protection Station, Gulfport, MS

**ABSTRACT**   Seasonal studies on a 1,200-ha isolated infestation of *Solenopsis invicta* Buren located in McMinn County, TN, were initiated in 1993 and continued through 1997. Winter survivability was evaluated and compared with a southern Mississippi site. The impact of *S. invicta* on local myrmecofauna was compared with a Tennessee non-infested site. Data collected over four winters indicate that consecutive days at a low ambient air maximum temperature is more indicative of *S. invicta* winter survivability than minimum temperature. After significant *S. invicta* mortality the first winter (1993–1994), we did not find significant differences in ant species diversity between the *S. invicta* infested Tennessee site and a similar, but non-infested site, 32 km away. Species commonly collected in the *S. invicta* infested site included *Forelius pruinosus* Roger, an unnamed *Forelius* sp., *Paratrechina terricola* (Buckley) and *Pheidole vinelandica* Forel.

**KEY WORDS**   *Solenopsis invicta*, red imported fire ant, winter survivability, interspecific competition

RED IMPORTED FIRE ANTS, *Solenopsis invicta* Buren, currently infest >124,000,000 ha in 13 states and Puerto Rico. A congener species, *S. richteri* (Forel), inhabits a relatively small portion of this infested area in northwestern Georgia, northern Alabama, northeastern Mississippi (Diffie et al. 1988), and southern Tennessee (H.L.C., unpublished data). Interbreeding between *S. invicta* and *S. richteri* occurs and results in the production of a fertile hybrid form. Range expansion continues primarily by *S. invicta* and the hybrid form, by both natural and artificial means. Recent isolated infestations in Phoenix, AZ (H.L.C., unpublished data), several sites in Virginia (Waller 1993), and numerous sites in Tennessee and Delaware (H.L.C., unpublished data) are suggestive that acclimation to harsh environments may result in continued range expansion by this serious pest. Many scientists have speculated that hybrid vigor may enable the hybrid to survive in colder areas than either parental form; however, Diffie et al. (1997) found no evidence that the hybrid could survive winter temperatures better than *S. invicta* in Georgia.

In December 1992 an isolated *S. invicta* infestation ≈1,200 ha in size was detected some 50 km northeast of Chattanooga, TN, near the town of Calhoun, TN (McMinn County). The general *S. invicta* infestation front in 1993 was in the Georgia counties bordering Tennessee, ≈60 km south of this isolated infestation (Code of Federal Regulations 1993). A wood pulp processing plant (Bowater Corporation) appeared to be the source of the infestation. The original infesta-

tion may have been introduced onto the plant site on construction equipment or material; however, this cannot be proven. This population appeared to be well adapted and thriving. A site visit in April 1993 revealed numerous large nests in open areas, presence of alate forms, and generally healthy colonies.

Studies of this isolated population were initiated in 1993 and continued through 1997 in an effort to learn more about this highly adaptable insect. We evaluated winter survivability of *S. invicta* and impact on local myrmecofauna. Results of these studies could lead to better estimates of the ultimate range of imported fire ants although this is not discussed here.

## Materials and Methods

**Winter Kill.** Winter kill (survival) of colonies in the Calhoun, TN, infestation was compared with a control site in Saucier, MS (Harrison County). Initial population estimates in eight 0.1-ha test plots were made in October 1993 at each site using the population indexing system described by Harlan et al. (1981) and modified by Lofgren and Williams (1982). Test plots were reevaluated in April, July, and October 1994 and 1995; May and October 1996; and June 1997. Population indices are classified and weighted by number of workers in a colony and the presence or absence of worker brood. We used this system for standard seasonal evaluations; however, when examining survival of colonies over the winter we evaluated the data by number of workers present only and classified colonies as small (≤999 workers), medium (1,000–9,999 workers), and large (≥10,000 workers). Mean number

of colonies present, as well as population indices, between the Tennessee and Mississippi sites were compared by $t$-test (PROC $t$-test, SAS Institute 1996).

Daily maximum and minimum air temperatures and rainfall were supplied for the Tennessee site by Bowater Corporation personnel for the period of October 1993 through September 1996. Data for the Tennessee site (Cleveland, TN, weather station, 16 km south of Calhoun, TN) for October 1996 through June 1997 and all data for the Mississippi site (Saucier, MS, weather station) were obtained from NOAA, National Climatic Data Center, Asheville, NC. Maximum and minimum temperatures were averaged on a monthly basis usually from the 19th of 1 mo through the 20th of the following month, because most *S. invicta* population assessments occurred around the 20th of the month. From the winter temperature data, daily and average maximum and minimum temperatures; the total number of days with maximum daily temperatures <0°C; the total number of days with maximum daily temperatures ≤1.1°C; the longest consecutive number of days with maximum daily temperatures <0°C; and the longest consecutive number of days with maximum daily temperatures ≤1.1°C were used to characterize winter severity. The association of these characterizations with *S. invicta* winter survivorship was examined with the Pearson correlation (PROC CORR, SAS Institute 1996). Winter survivorship was indicated by either the change in the number of spring colonies or fall colonies from the previous year's fall colony density.

**Impact of S. invicta on Local Myrmecofauna.** Imported fire ants readily compete with different arthropod species including other ants (Porter and Savignano 1990). Ant species diversity in a *S. invicta* infested area of Calhoun, TN (McMinn County), was compared with a non-infested control area (Rhea County) ≈30 km from the *S. invicta* infested area. Four transects, 200 m in length, were placed in the *S. invicta* infested site and three transects were placed in similar habitats in the non-infested site; i.e., open fields, old field successional habitats. Each transect traversed similar habitats and efforts were made to include as much habitat diversity as possible. These transects were used for both bait and pitfall traps. Bait and pitfall stations were alternated along each transect at 10.0-m intervals. Bait transects provided a measure of the abundance and diversity of ants that might compete for food resources with *S. invicta.* Pitfall traps indicated the abundance and diversity of ants that may not be attracted to the diurnally placed baits used in the bait transect.

Each bait transect was comprised of 10 bait stations, five baited with canned sausage, and five baited with maple syrup. Baits were placed in snap-top vials, and were left in place for 1 h before collecting. Collections were immediately frozen and returned to the Gulfport Plant Protection Station (Gulfport, MS) to be counted and identified.

In total, 10 pitfall traps located along the 200 m transect were used at each site. Pitfall traps at each site consisted of test tubes (20 by 150 mm) containing 70%
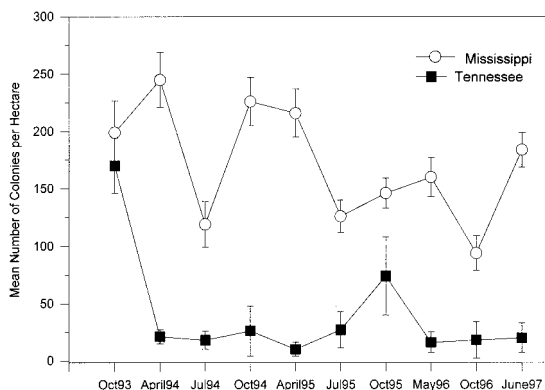


**Fig. 1.** Number of *S. invicta* colonies present over time at two climatically different sites: Tennessee and Mississippi.

ethanol placed in preset PVC sleeves spaced 20 m apart along the transect. Traps were collected 24 h after placement. All samples from the site were composited, placed in 50 ml polyethylene bottles, and mailed to the Gulfport Plant Protection Station for counting and identification. Species identification was made by T. C. Lockley and voucher specimens were kept at the Gulfport Plant Protection Station.

Collections were made at monthly intervals and then grouped by season. Spring samples were comprised of collections from March to May; summer from June to August; fall from September to November; and winter from December to February. The number of ant species collected from the *S. invicta* infested and uninfested Tennessee sites was compared by analysis of variance (ANOVA) (PROC GLM, SAS Institute 1996). Brillouin diversity index (Zar 1984) was calculated for each site among the seasons and sampling year, and compared by ANOVA (PROC GLM, SAS Institute 1996).

### Results and Discussion

**Winter Kill.** During the 3-yr study, two Tennessee plots were dropped because of construction; one before 13 October 1994 and the other before 29 October 1996. One Mississippi plot was dropped because of pasture improvements before 29 October 1996. Because the number of *S. invicta* colonies present and population indices trends were similar over the course of the study, we will discuss both trends but only show colony number data.

In the initial sampling of October 1993, both the Tennessee and control (Mississippi) sites had similar population indices and numbers of colonies present ($t = 0.778$, df = 14, $P = 0.450$) (Fig. 1). The number of colonies per hectare over all sampling dates after the winter of 1993–1994 was significantly higher ($t = 14.3$, df = 119.1, $P < 0.001$) in the Mississippi site than in the Tennessee site, with 169.0 ± 28.0 (mean ± SEM) and 25.0 ± 24.0 colonies per hectare, respectively. Among the characterizations of winter severity, the longest consecutive number of days with maxi-

**Table 1. Overwinter survivability of Tennessee *S. invicta* population and corresponding temperature data**

| Winter | % change in no. spring colonies from fall assessment | % change in no. fall colonies from previous fall assessment | Lowest mean monthly max temp (°C) overwinter | Lowest mean monthly min temp (°C) overwinter | Consecutive winter days with max temp below 0°C | Consecutive winter days with max temp ≤1.1°C |
|---|---|---|---|---|---|---|
| 1993–1994 | −87.5 | −90.5 | 4.3 | −4.6 | 3 | 7 |
| 1994–1995 | −61.2 | +234.4 | 7.3 | −0.4 | 1 | 2 |
| 1995–1996 | −78.9 | −77.4 | 6.3 | −1.8 | 4 | 5 |
| 1996–1997 | +9.1 | +9.1 | 10.1 | −6.5 | 2 | 3 |
| $r^a$ for % change from fall to spring | | | 0.70 | 0.13 | −0.41 | −0.73 |
| $r$ for % change from fall to fall | | | 0.65 | 0.32 | −0.64 | −0.86 |

[a] Pearson correlation coefficient.

mum daily temperatures ≤1.1°C was the most highly correlated ($r = -0.855$, df = 26, $P < 0.001$) with the winter survivorship of *S. invicta* colonies (Table 1). Temperatures at the Tennessee site between 20 December 1993 and 19 January 1994 averaged a maximum temperature of 4.3°C (range, −8.9–14.4°C) and a minimum temperature of −4.6°C (range, −17.8–5.5°C). There were 5 d that winter where maximum temperatures did not exceed 0°C, three of which were consecutive (Table 1). During mid-January there were seven consecutive days where the maximum temperature did not exceed 1.1°C. On 8 February 1994, Greg Adyelotte (USDA, APHIS, PPQ Officer, Knoxville, TN) observed considerable mound mortality, and stated that it was difficult to find active mounds (temperature range, 14.4–19.4°C). This dramatic decline, indicating winter kill, was quantitatively noted in our April 1994 population assessment which showed 87% colony mortality between October 1993 and April 1994 (Table 1). Of those colonies that survived the winter of 1993–1994, 58% were classified as large colonies.

The Tennessee population did not rebound over the summer months of 1994, but remained at very low levels, with minimal increases in population indices and colony numbers between April and October (Fig. 1). In April 1995, there was a drop in both population indices and colony numbers in the Tennessee plots compared with the previous fall count (October 1994), again indicating some over winter kill that season (Table 1; Fig. 1). Lowest temperatures were recorded between 20 January 1995 and 20 February 1995 when the mean maximum temperature was 7.3°C (range, −3.3–19.4°C) and the mean minimum temperature was −0.4°C (range, −12.2 to 11.1°C). With only one exception (−3.3°C on 8 February 1995), daily maximum temperatures were at least 0°C that winter season. Of those colonies that survived the winter of 1994–1995, 58% were classified as small and medium colonies.

*Solenopsis invicta* populations began to rebound over the summer of 1995. By October 1995, populations had risen substantially compared with the previous year. Between April 1995 and October 1995, the number of colonies present had increased over sixfold, as had population indices (Fig. 1).

There was, again, a substantial decrease in mean colony numbers over the winter of 1995–1996 in the Tennessee plots (Table 1; Fig. 1). The coldest temperatures that winter were between 20 December 1995 and 19 January 1996, and between 20 January 1996 and 19 February 1996, with a mean maximum temperature of 6.3°C (range, −5.0–19.4°C) and 6.6°C (range, −5.6–17.2°C), respectively, and a mean minimum temperature of −1.9°C (range, −11.1–8.9°C) and −1.8°C (range, −17.8–7.2°C), respectively. Records show 8 d that winter when the maximum temperature did not exceed 0°C; four of these were consecutive days in early February. This cold weather affected the *S. invicta* populations as indicated by the substantial winter kill (Table 1). Of those colonies that survived the winter of 1995–1996, 55% were classified as large colonies.

By October 1996, mean number of colonies present at the Tennessee site had not increased significantly (Fig. 1); however, those colonies that had survived the previous winter increased in size between May 1996 and October 1996.

The final evaluation was made in early June 1997. At that time, little or no winter kill was noted in the Tennessee plots (Table 1; Fig. 1). The late count (June versus April/May) may have allowed surviving colonies to grow before our count and new colonies to develop into visible colonies. Although the site had some very low temperatures during the 1996–1997 winter, mean maximum temperatures were warmer than in previous winters. The lowest mean monthly maximum temperature for the winter was 10.1°C (range, −3.3–20.5°C) and occurred between 20 December 1996 and 19 January 1997. Although there were numerous nights when the minimum temperature was below 0°C, as evidenced by a mean minimum temperature of −6.5°F (range, −17.8–11.7°C) between 20 January 1997 and 19 February 1997, there were only 2 d when the maximum temperature did not exceed 0°C. Therefore, no extended period of constant freezing temperatures occurred during that particular winter. Of those colonies that survived the winter of 1996–1997, 58% were classified as small and medium colonies.

The Mississippi site showed a large reduction in population indices and number of colonies at the July 1994 assessment (Fig. 1). This midsummer drop in *S. invicta* populations may be a natural phenomenon in the hot, dry summer climate of southern Mississippi (A.-M.A.C. and H.L.C., unpublished data). Popula-

tions had rebounded well by the October 1994 counts. Another dramatic decrease occurred in populations in the July 1995 assessment, which reinforced the observation of a summer decline phenomenon. However, populations did not rebound in October 1995 as they had the previous year. In 1995, the summer was exceptionally long and hot in southern Mississippi, which probably attributed to the slow recovery. Three months during the summer in 1995 (July, August, September) had mean maximum temperatures that exceeded 32.2°C (33.7, 33.5, 33.3°C, respectively). Again, the Mississippi *S. invicta* populations showed an increase between October 1995 and May 1996, and between October 1996 and June 1997, and a decrease over the hot summer months into fall. The final count in June 1997 showed both the mean number of colonies and the mean population index almost identical to those when the trial was initiated 3.5 yr previously.

In general, little numerical differences existed in mean monthly summer temperatures, both maximums and minimums, between the Mississippi and Tennessee sites, although the Mississippi site sustained the high summer temperatures over a longer period of time. However, large and significant differences in both the mean maximum temperatures and the mean minimum temperatures between the two sites existed during the winter months. For example, in January 1995, the Mississippi mean maximum temperature was 16.9°C and the Tennessee mean maximum temperature was 10.6°C (difference = 6.3°C, $t = -8.60$, df = 30, $P < 0.0001$). During the same period, the Mississippi mean minimum temperature was 6.4°C and the Tennessee mean minimum temperature was 1.1°C (difference = 5.3°C, $t = -6.96$, df = 30, $P < 0.0001$). The lowest mean minimum temperature at the Tennessee site was over the 1996–1997 winter ($-6.5$°C). However, the mean maximum temperature during this period was 10.1°C, and there were only three consecutive days when the maximum temperature was at or below 1.1°C. During that winter, the mean number of *S. invicta* colonies at the Tennessee site actually increased by 9% (population index decreased by 8%). The 1993–1994 winter had the lowest mean maximum temperature (4.3°C), 7 d where the maximum temperature was at or below 1.1°C, and the greatest decrease in mean number of *S. invicta* colonies (87%) and in mean population index (92%).

If we define a hard winter as one with at least five consecutive days of maximum temperatures at or below 1.1°C, and mean winter maximum temperature of <9.4°C, then the winters of 1993–1994 and 1995–1996 would be considered hard winters. During these winters, there was >78% reduction in colony numbers, and during the subsequent active "growing season" (spring to fall), the number of colonies increased by only 0–5%. After the mild winter of 1994–1995, colony numbers between spring and fall increased sixfold.

We found that in hard winters, those colonies that best survived the cold temperatures were large colonies; those with >10,000 workers. Although some small and medium colonies were active in the spring after a hard winter, they represented <45% of the surviving colonies. After a more mild winter, small and medium colonies survived fairly well and represented >55% of the colonies observed in the spring. Limited increases in colony numbers and population indices in the summer and fall following a hard winter indicated that those colonies that did survive the winter may not have produced many mating flights and thus few small, incipient colonies were detected in the fall. However, in the summer and fall following a mild winter, increases in colony numbers and population indices were dramatic (sixfold), indicating growth of surviving colonies, successful spring mating flights, and the development and subsequent detection of numerous small, incipient colonies in the late summer and fall.

Winter survival of *S. invicta* may be more dependent on the overwinter mean maximum temperatures in an area rather than the mean minimum temperatures. Our study indicated that five consecutive days with maximum temperatures at or below 1.1°C, with winter mean maximum temperature <9.4°C, severely reduced *S. invicta* winter survivorship. In other words, successful overwintering of *S. invicta* was most influenced by the degree of sustained, near freezing weather. This theory is somewhat different from other investigations that have stated that high winter mortality occurs in years when temperatures are below "normal" for the area evaluated (Morrill 1977, Morrill et al. 1978, Diffie et al. 1997) or when lowest air temperatures were as low as $-15.0$°C (Thorvilson et al. 1992). At the other extreme, prolonged summer high temperatures adversely affected *S. invicta* populations in southern Mississippi and has been observed in other studies in southern Mississippi (Collins et al. 1992). Through years of unpublished data, this summer decline probably was probably the result of a combination of our sampling technique, where colonies that have retreated deep within the ground for moderate temperatures and moisture are missed and subsequently reappear in the fall months, and natural mortality caused by the extreme heat and drought.

**Impact of *S. invicta* on Local Myrmecofauna.** Over the winter months, very few ants were collected in any of the traps; therefore, this data has been omitted from the discussion. Many specimens could not be identified past genus (either by T. C. Lockley or other experts to whom they were sent) because of a lack of suitable keys or present controversy surrounding taxonomy of certain genera and species. In particular, *Forelius* spp. were identified as either *Forelius pruinosus* (Roger), or as various unnamed species, denoted as sp. A., sp. B., and so forth.

Generally, there were greater ant densities in the bait traps because of the aggressive recruitment behavior of *S. invicta* and other ant species, and greater ant diversity in the pitfall traps. However, diversity indices within a trap type between infested and noninfested sites were similar. This study was not intended to detect differences between trap types, but rather to detect all ant species present in an area, therefore, the data presented here represent all ant species collected and their densities in all traps.
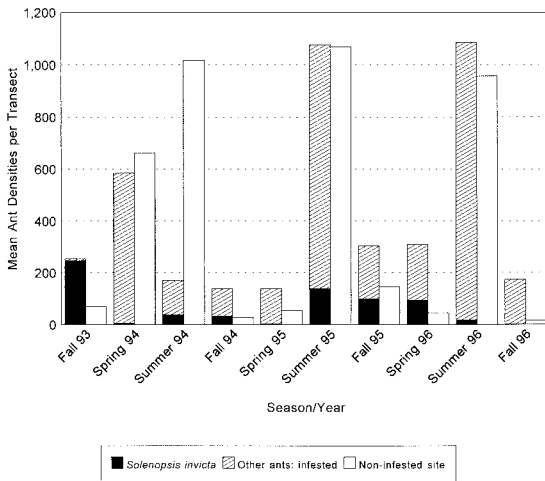
**Fig. 2.** Seasonal ant densities in *S. invicta* infested and non-infested sites in Tennessee. Left bar in each season/year represents ant densities in *S. invicta* infested site, separated into mean density of *S. invicta* and mean density of other ants.

Over the course of the study, ant density averaged 4,230 ants (including *S. invicta*) in the *S. invicta* infested area per transect and 2,368 in the non-*S. invicta* infested area. Excluding *S. invicta* in the infested site, ant density averaged 3,557 other ants per transect. Numerically, *S. invicta* comprised 97% of the ants collected in the fall of 1993 at the infested site (Fig. 2). In the spring of 1994, *S. invicta* comprised only 7.7% of the total number of ants collected (a 98% decrease from fall 1993 numbers), and by the fall of 1995, they comprised 32.8% of the sample. After the significant winter kill over the winter of 1993–1994, *S. invicta* densities remained very low until the summer and fall of 1995 when densities were ≈55 and 40%, respectively, of the initial fall 1993 density. This moderate level of *S. invicta* activity corresponded with the time frame (October 1995) in which we found the greatest number of active *S. invicta* colonies at the site since the original fall 1993 count. Non-*S. invicta* species densities in the *S. invicta* infested site were higher in all subsequent seasons and years than the initial density in the fall of 1993.

Total number of species collected from October 1993 through October 1996, excluding *S. invicta*, was 27 in the infested plots, and 32 in the non-infested plots, of which 25 species were represented in both sites (Table 2). There were significant differences in the number of non-*S. invicta* species present between the infested and uninfested sites ($F = 5.62$; df $= 1, 64$; $P = 0.0208$) and among seasons ($F = 17.95$; df $= 2, 64$; $P < 0.0001$). Over the course of the study, mean number of non-*S. invicta* ant species collected was 7.3 in the non-infested site and 5.5 in the *S. invicta* infested site. The mean number of non-*S. invicta* species present was significantly higher in the summer, with 9.8 species, than in the spring and fall, which had 4.0 and 5.3 species, respectively ($P \leq 0.05$, Tukey honestly significant difference).

**Table 2.** Species list of ants collected in *S. invicta* infested and non-infested sites in Tennessee listed by subfamily

| Infested site | Non-infested site |
| --- | --- |
| Myrmicinae | |
| *Aphaenogaster* sp. A | *Aphaenogaster lamellidens* Mayr |
| *Crematogaster ashmeadi* Mayr | *A. treatae* Forel |
| *C. clara* Mayr | *Aphaenogaster* sp. A. |
| *C. lineolata* (Say) | *Crematogaster ashmeadi* Mayr |
| *C. missouriensis* Emery | *C. clara* Mayr |
| *Leptothorax pergandei* Emery | *C. lineolata* (Say) |
| *Leptothorax* sp. A. | *C. missouriensis* Emery |
| *Monomorium minimum* (Buckley) | *Crematogaster* sp. A. |
| *Monomorium* sp. A. | *Leptothorax pergandei* Emery |
| *Pheidole dentata* Mayr | *Leptothorax* sp. A. |
| *Ph. tysoni* Forel | *Monomorium minimum* (Buckley) |
| *Ph. vinelandica* Forel | *Monomorium* sp. A. |
| *Pheidole* sp. A. | *Pheidole dentata* Mayr |
| *Solenopsis molesta* (Say) | *Ph. tysoni* Forel |
| *S. invicta* Buren | *Ph. vinelandica* Forel |
| | *Pheidole* sp. A. |
| | *Solenopsis molesta* (Say) |
| | *Trachymyrmex septentrionalis* (McCook) |
| Dolichoderinae | |
| *Forelius pruinosus* Roger | *Forelius pruinosus* Roger |
| *Forelius* sp. A. | *Forelius* sp. A. |
| *Forelius* sp. B. | *Forelius* sp. B. |
| *Forelius* sp. C. | *Forelius* sp. C. |
| *Tapinoma sessile* (Say) | *Tapinoma sessile* (Say) |
| Formicinae | |
| *Formica dolosa* Wheeler | *Formica dolosa* Wheeler |
| *Lasius neoniger* Emery | *Formica* sp. A. |
| *Paratrechina arenivaga* (Wheeler) | *Formica* sp. B. |
| *P. parvula* (Mayr) | *Lasius neoniger* Emery |
| *P. terricola* (Buckley) | *Lasius* sp. A. |
| *Paratrechina* sp. A. | *Paratrechina arenivaga* (Wheeler) |
| | *P. terricola* (Buckley) |
| | *Paratrechina* sp. A. |
| Ecitoninae | |
| *Labidus* sp. A. | |
| Ponerinae | |
| *Proceratium silaceum* Roger | |

Over seasons and years, species diversity (Brillouin index) was significantly greater in the non-infested site than in the *S. invicta* infested site ($F = 6.65$; df $= 1, 50$; $P = 0.0129$). Mean diversity index was 0.41 in the non-*S. invicta* infested plots and 0.32 in the infested plots. Diversity among seasons was significantly different ($F = 14.49$; df $= 2, 50$; $P = 0.0001$) where mean species diversity was highest in the summer, followed by fall and spring. There was also a significant season × year interaction ($F = 4.95$; df $= 4, 50$; $P = 0.0019$). Thus, data were analyzed separately for each season, and no significant differences in diversity were found between the infested and non-infested sites, among years, and their interaction for the spring and summer seasons (Figs. 3 a and b). For the fall data, there was a significant difference in diversity among the sample years ($F = 8.11$; df $= 3, 27$; $P = 0.001$) (Fig. 3c). Species diversity in the *S. invicta* infested site was higher in all subsequent seasons and years than the initial diversity in the fall of 1993. This suggested that low numbers of
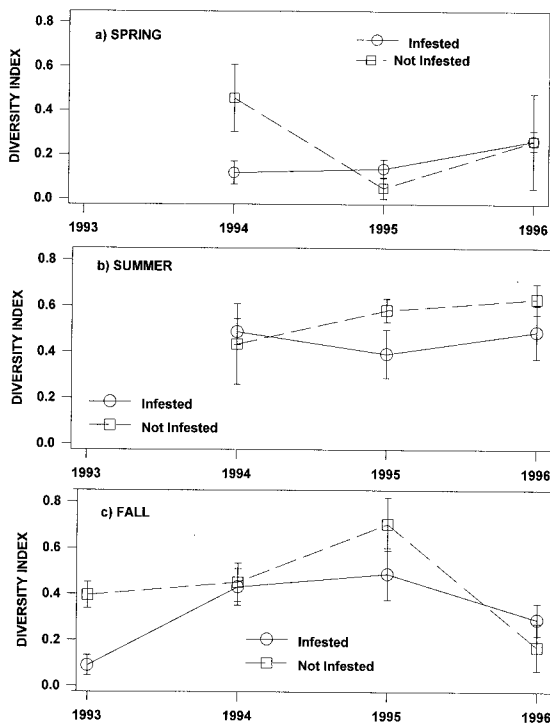
**Fig. 3.** Seasonal ant diversity indices in *S. invicta* infested and non-infested sites in Tennessee. (a) Spring. (b) Summer. (c) Fall.

*S. invicta,* caused by the high mortality that occurred over the winter of 1993–1994, resulted in an increase in other ant species (Fig. 2). Other researchers have noted that increasing *S. invicta* densities adversely affect species diversity (Whitcomb et al. 1972, Camilo and Phillips 1990). Low diversity in the *S. invicta* infested plots in the spring of 1994 was a result of extremely high densities of *Forelius* sp.A that were present in the plots (Fig. 3). The large drop in the fall 1996 diversity in the non-infested plots was caused by small numbers of ants collected during this time. Numerous ants were collected in the *S. invicta* infested plots during the same time frame, so the reason for this drop in diversity is unknown.

The most numerous ants collected in the *S. invicta* infested area were *Forelius pruinosus, Forelius* sp. A, and *S. invicta. S. invicta* was collected during all 10 seasonal collections, as were *Paratrechina terricola* (Buckley) and *Pheidole vinelandica* Forel. *Forelius* sp. A was collected in nine of the 10 seasonal collections and six other ant species were collected in at least seven of the 10 seasonal collection periods: *Cremato-gaster clara* Mayr, *C. missouriensis* Emery, *Monomo-rium minimum* (Buckley), *Paratrechina arenivaga* (Wheeler), *Pheidole dentata* Mayr, and *Pheidole tysoni* Forel.

In the site not infested with *S. invicta,* the most numerous ants were *Forelius* sp. A, *Monomorium min-imum,* and *Crematogaster clara. Leptothorax pergandei* Emery was collected during all 10 seasonal collections,

and *Monomorium minimum* was collected during nine seasons. Six other species were collected in at least seven of the 10 collections: *Aphaenogaster treatae* Forel, *Crematogaster clara, Forelius* sp. A, *Formica do-losa* Wheeler, *Pheidole dentata*, and *Pheidole vine-landica.*

*Forelius* sp. A was most prevalent in the infested sites in the springs of 1994 and 1995, representing >85% of the total number of ants collected during those periods; times when the *S. invicta* populations were low. By spring 1996, when *S. invicta* had in-creased to 30% of the collection, *Forelius* sp. A de-creased to 53% of the collection. Over the course of the study there was no correlation between the two spe-cies (Spearman's correlation; $r = 0.334$, $n = 26$, $P = 0.095$). In the non-infested site, *Forelius* sp. A was most prevalent in the spring and summer of 1994, repre-senting 44 and 47% of the collections, respectively. Over the course of the study, mean densities of *Fore-lius* sp. A were much greater in the *S. invicta* infested site than in the non-infested site.

*Forelius pruinosus* was collected only once at either site before summer 1995. It was most numerous in the *S. invicta* infested site in the summers of 1995 and 1996, comprising 65 and 69% of the collections, respectively. At these times, *S. invicta* represented only 13 and 1.6% of the collections, respectively. Initially, it appeared that there may be a positive correlation between *S. invicta* and *F. pruinosus;* however, data from the third year of sampling negated that possibility (Spearman correlation; $r = 0.379$, $n = 26$, $P = 0.056$). In the non-infested site, *F. pruinosus* was one of the dominant species collected in the summers of 1995 and 1996, with 16 and 30% of the collections, respectively. Over the course of the study, mean densities of *F. pruinosus* were much greater in the *S. invicta* infested site than in the non-infested site.

*Crematogaster clara* was collected routinely at both sites, but represented a much larger portion of the collections in the non-infested site, both during sea-sonal collections, and over the course of the study. Mean density was also greater in the non-infested site over the course of the study. *M. minimum* also was collected regularly at both sites, and like *C. clara*, it represented a much larger portion of the non-infested site collections and mean density was greater in the non-infested site over the course of the study. Thus, it appears that *C. clara* and *M. minimum* can survive in *S. invicta* infested areas in eastern Tennessee, but at lower levels when *S. invicta* were present.

*Pheidole vinelandica* was collected consistently in both sites in similar patterns and densities, although in low numbers. Thus, this particular species may be able to retain its niche in the habitat even when *S. invicta* is present.

One ant that may benefit by the presence of *S. invicta* is *Paratrechina terricola.* This ant was collected in all collection periods in the *S. invicta* infested site, although generally in low numbers. In the non-in-fested site, only four ants were collected during two seasonal collections.

Ant species that do not appear to compete well with *S. invicta* were *Aphaenogaster treatae, Formica dolosa,* and *Leptothorax pergandei.* These ants were collected regularly, although in small numbers, from the non-infested site, but were collected rarely, if at all, from the *S. invicta* infested site.

Stein and Thorvilson (1989) found that although *S. invicta* made up 98.5% of their bait trap collections, several other species were collected regularly during a 12-mo study in Texas: *Paratrechina terricola, Pheidole* spp., *Monomorium minimum,* and *Tapinoma sessile* (Say). Phillips et al. (1987), also in Texas, found many of these same ants, and others, in pitfall traps with predominately *S. invicta: S. geminata* (F.), *Pheidole* spp., *M. minimum, F. pruinosus,* and *P. terricola.* Our study regularly collected all of these species, except *T. sessile* (one ant collected once) and *S. geminata* (not known to be present in Tennessee, Trager 1991). This indicates that those ant species found persistently in all of these studies may be able to compete with *S. invicta* when *S. invicta* numbers are low, but because *S. invicta* populations increase and surpass some, as yet unknown, threshold, these species may become limited in their ability to effectively compete.

In conclusion, we found the lower winter temperatures at the Tennessee site, coupled with *S. invicta* mortality during the winter months, strongly indicate that Tennessee winter temperatures have a severe adverse impact on *S. invicta* colonies. Specifically, we found that winter mortality of imported fire ants in eastern Tennessee was highly correlated with consecutive days of near freezing winter maximum temperatures rather than low winter minimum temperatures. Conversely, southern Mississippi colonies were adversely affected by weather in the summer when high temperatures were sustained for 2–3 mo, whereas the brief high summer temperatures in Tennessee (1 mo) did not appear to inhibit *S. invicta* growth.

A comparison of other ant species present in *S. invicta* infested and non-infested sites in Tennessee found that *S. invicta* in our study site had less impact on ant species density and diversity than has been noted in the literature. This is probably because of the low population of *S. invicta* on our site after the severe overwinter kill the first winter of our study. There were several species that this study and the literature indicate may be able to compete with or coexist with *S. invicta: Forelius* spp., *Paratrechina terricola, Pheidole* spp., and *Monomorium minimum.*

## Acknowledgments

## References Cited

**Camilo, G. R., and S. A. Phillips, Jr. 1990.** Evolution of ant communities in response to invasion by the fire ant *Solenopsis invicta*, pp. 190–198. *In* R. K. Vander Meer, K. Jaffe, and A. Cedeno [eds.], Applied myrmecology, a world perspective. Westview, Boulder, CO.

**Code of Federal Regulations. 1993.** Title 7. Section 301.81. Subpart-imported fire ant.

**Collins, H. L., A.-M.A. Callcott, T. C. Lockley, and A. L. Ladner. 1992.** Seasonal trends in effectiveness of hydramethylnon (AMDRO) and fenoxycarb (LOGIC) for control of red imported fire ants (Formicidae: Hymenoptera). J. Econ. Entomol. 85: 2131–2137.

**Diffie, S., R. K. Vander Meer, and M. H. Bass. 1988.** Discovery of hybrid fire ant populations in Georgia and Alabama. J. Entomol. Sci. 23: 187–191.

**Diffie, S., M. H. Bass, and K. Bondari. 1997.** Winter survival of *Solenopsis invicta* and the *Solenopsis* hybrid (Hymenoptera: Formicidae) in Georgia. J. Agric. Entomol. 14: 93–101.

**Harlan, D. P., W. A. Banks, H. L. Collins, and C. E. Stringer. 1981.** Large area test of AC-217,300 bait for control of imported fire ant in Alabama, Louisiana, and Texas. Southwest. Entomol. 8: 42–45.

**Lofgren, C. S., and D. F. Williams. 1982.** Avermectin B1a, a highly potent inhibitor of reproduction by queens of the red imported fire ant. J. Econ. Entomol. 75: 798–803.

**Morrill, W. L. 1977.** Overwinter survival of the red imported fire ant in central Georgia. Environ. Entomol. 6: 50–52.

**Morrill, W. L., P. B. Martin, and D. C. Sheppard. 1978.** Overwinter survival of the red imported fire ant: effects of various habitats and food supply. Environ. Entomol. 7: 262–264.

**Phillips, Jr., S. A., W. M. Rogers, D. B. Wester, and L. Chandler. 1987.** Ordination analysis of ant faunae along the range expansion front of the red imported fire ant in south-central Texas. Tex. J. Agric. Nat. Res. 1: 11–15.

**Porter, S. D., and D. A. Savignano. 1990.** Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71: 2095–2106.

**SAS Institute. 1996.** User's manual, release 6.12. SAS Institute, Cary, NC.

**Stein, M. B., and H. G. Thorvilson. 1989.** Ant species sympatric with the red imported fire ant in southeastern Texas. Southwest. Entomol. 14: 225–231.

**Thorvilson, H. G., J. C. Cokendolpher, and S. A. Phillips, Jr. 1992.** Survival of the red imported fire ant (Hymenoptera: Formicidae) on the Texas high plains. Environ. Entomol. 21: 964–968.

**Trager, J. C. 1991.** A revision of the fire ants, *Solenopsis geminata* group (Hymenoptera: Formicidae: Myrmicinae). J. N.Y. Entomol. Soc. 99: 141–198.

**Waller, D. 1993.** Current status of fire ant infestations in Virginia, pp. 2–5. *In* Proceedings, 1993 Imported Fire Ant Conference, Charleston, SC, 15–18 June.

**Whitcomb, W. H., H. A. Denmark, A. P. Bhatkar, and G. L. Greene. 1972.** Preliminary studies on the ants of Florida soybean fields. Fla. Entomol. 55: 129–142.

**Zar, J. H. 1984.** Biostatistical analysis. Prentice-Hall, Englewood Cliffs, NJ.