

# Invasion of Red Imported Fire Ants (Hymenoptera: Formicidae): Microgeography of Competitive Replacement

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**ABSTRACT** The invasion of Brackenridge Field Laboratory, Austin, Texas, by the multiple-queen form of the red imported fire ant, *Solenopsis invicta* Buren, was monitored for 3 yr. This invasion provides a rare glimpse of competitive replacement in progress. It has been remarkable for two reasons. First, imported fire ant colonies replaced colonies of the native fire ant, *Solenopsis geminata* (F.), at a ratio of 6:1, indicating a radical restructuring of the arthropod community rather than a simple one-for-one substitution of an equivalent species. Secondly, the invasion proceeded at a very slow rate (about 35 m/yr) along a continuous front in a pattern best explained by colony budding and considerable biotic resistance from the native ant community. These data indicate that the invasion process may continue at the local level for years or even decades after the passage of the main invasion front.

**KEY WORDS** *Insecta*, *Solenopsis invicta*, polygyne colonies, competition

THE CONCEPT OF COMPETITION between individual organisms with similar resource requirements has been of fundamental importance in the development of models for evolutionary and ecological changes. Competition is frequently difficult to document under natural conditions, but it is occasionally conspicuous when organisms invade new continents or islands (Elton 1958, Mooney & Drake 1986). Opportunities to study the invasion process have usually been missed because such community revolutions are generally very swift and most research is applied toward control. Invasion processes are not only of basic scientific interest but also have considerable practical potential because detailed knowledge of why native species lose ground to introduced species may provide unsuspected or novel methods for control.

A number of ants are well known invaders, including *Iridomyrmex humilis* (Mayr) (Erickson 1971, Lieberburg et al. 1975), *Ochetomyrmex* (= *Wasmannia*) *auropunctata* (Roger) (Clark et al. 1982), *Pheidole megacephala* (F.) (Fluker & Beardsley 1970, Lieberburg et al. 1975), and *Solenopsis invicta* Buren (Vinson & Greenberg 1986). When these species invade new areas, they often displace native ants as well as each other. For instance, after *S. invicta* was introduced into the southeastern United States from South America, it is known to have displaced two previously introduced species, *I. humilis* and *Solenopsis richteri* Forel, plus a number of native species including *Solenopsis geminata* (F.), *Solenopsis xyloni* McCook, and *Pogonomyrmex badius* (Latreille) (Wilson 1951, Wilson & Brown 1958).

It is important to note that our study involves the polygyne form of *S. invicta*. Colonies of this form contain dozens or even hundreds of fertile queens (Glancey et al. 1975, Fletcher et al. 1980) compared with only one in the monogyne form. Monogyne populations predominate in the United States, but polygyne populations have become more than just curious anomalies; they are expanding in some areas (Glancey et al. 1987) and currently occupy thousands of square kilometers in at least six states. Genetic, biochemical, and taxonomic evidence support the conclusion that the polygyne and monogyne forms are the same species (Ross et al. 1987).

Here we document the course of events as the imported fire ant, *S. invicta*, replaces its native counterpart, *S. geminata*, at a biological research station in central Texas. Information provided by this study is important in characterizing the dynamics of polygyne fire ant invasions, particularly at the local level. Our data also constitute a rare glimpse of competitive replacement in progress and set the stage for further studies of the mechanisms behind this phenomenon.

## Materials and Methods

This study was conducted at the Brackenridge Field Laboratory (BFL) of the University of Texas, Austin. BFL includes a mixture of wooded areas and grassy fields situated on calcareous and loamy soils. Vegetation is characteristic of the Edwards Plateau and the Blackland Prairie of central Texas.

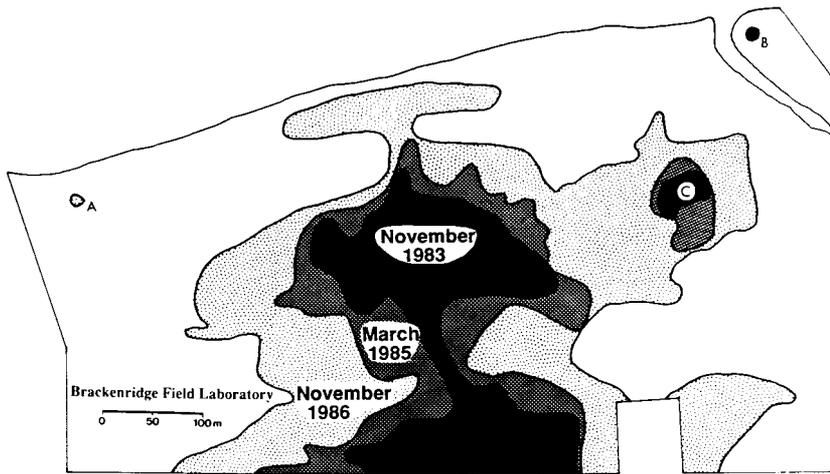


Fig. 1. Expansion of the imported fire ant, *Solenopsis invicta*, at the Brackenridge Field Laboratory, Austin, Texas, 1983–1986. Letters A–C indicate colonies located outside the main front.

The entire 32-ha BFL site was censused four times between October 1983 and November 1986. Active *S. invicta* and *S. geminata* colonies were plotted on a map using a compass and landmarks. Nests were included if they were at least 10 cm in diameter and 50 cm from the nearest neighbor. Smaller nests were excluded because they are difficult to distinguish from temporary excavations, whereas nests much closer than 50 cm probably do not function as discrete units. Most nests, however, were much larger and farther apart than this. Census dates were: October–November 1983, February–April 1984, February–March 1985, and November 1986. Partial censuses were conducted in October–November 1984 and January 1986.

Voucher specimens of both *S. invicta* and *S. geminata* have been placed in the BFL and Harvard University (MCZ) collections. *S. geminata* at BFL is apparently the *rufa* form of the species (Creighton 1950); *S. geminata* colonies at BFL contained up to 10 apparently fertile queens (Adams et al. 1976).

## Results

The fire ant, *S. invicta*, has advanced through BFL property along an irregular but sharply defined front since sampling began in October 1983 (Fig. 1). The rate of advance along open sunny roads, where it is naturally most abundant, was about  $35 \pm 15$  m/yr compared with  $18 \pm 10$  m/yr in cooler wooded areas. Based on this rate, we expect two or three more years will elapse before this ant completes its expansion through BFL. Similarly, a reverse extrapolation (based on this expansion rate and the extent of the infestation in 1983) (Fig. 1) indicates that it began at two points in 1980—at the center of the station and near the laboratory building. This date is supported by the absence of imported fire ants in detailed censuses before 1978 (Feener 1978) and the observation that

imported fire ants first appeared on the state capitol grounds, 3.5 km from our study site, in 1978 or 1979 (M. Trostle, personal communication).

Although the advancing front was essentially continuous, imported fire ants were discovered at three locations outside the main front (Fig. 1). Two of these sites (Fig. 1, A and B) involved only one colony. Of more than 100 colonies inspected so far, only colony B has been monogyne. This colony was very isolated and located in a heavily wooded site; it is unknown whether this colony was secondarily monogyne or a remnant of the initial invasion. The third site (Fig. 1C), became a major focus of growth until it fused with the main front sometime in 1986. Site C is a highly disturbed area which is plowed yearly and occasionally treated with insecticides; these activities probably weakened the native arthropod community and facilitated the establishment of imported fire ants.

Over the past 3 yr, the advancing front of *S. invicta* colonies has progressively eliminated all colonies of the native fire ant in its path (Fig. 2). Occasionally, a native colony temporarily survived behind the advancing front, but this was infrequent and usually lasted only a few months. The number of *S. invicta* mounds on BFL rose from about 500 in 1983 to almost 2,300 in 1986 (Fig. 3). During the same period, the number of *S. geminata* mounds dropped from approximately 400 to 200 (Fig. 3). Between 1983 and 1986, about 180 *S. geminata* colonies were overrun by the advancing front and replaced by more than 1,100 *S. invicta* mounds (Fig. 2), a 6:1 ratio. Approximately 200 additional *S. invicta* mounds also were added to wooded areas not previously occupied by *S. geminata*. The density of *S. invicta* mounds in prime BFL habitat is about 400 mounds/ha. Densities of over 600 mounds/ha have been reported for the polygyne form elsewhere (Greenberg et al. 1985, Vinson & Sorensen 1986); by comparison, mature populations of the monogyne form generally range be-

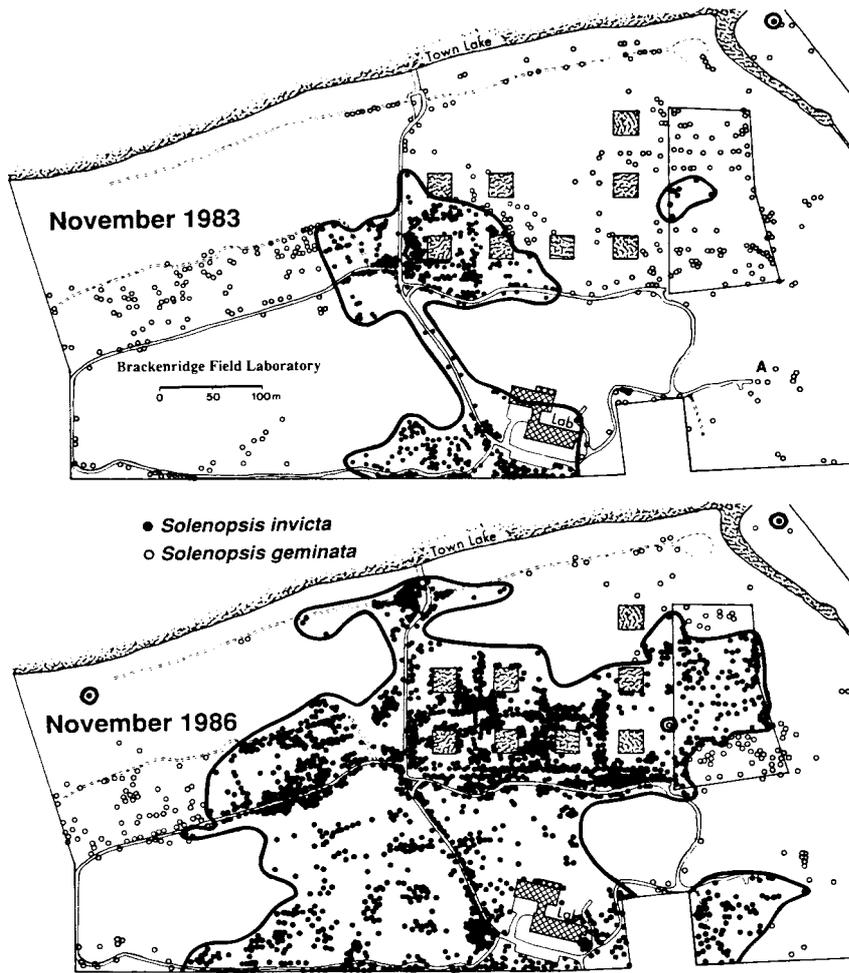


Fig. 2. Distribution of native and imported fire ant mounds at Brackenridge Field Laboratory in November 1983 and November 1986. A heavy solid line separates the two populations. Note heavy line around two outlying and one inlying colonies. The eight shaded squares are experimental ponds.

tween 50 and 120 mounds/ha (Vinson & Greenberg 1986, Vinson & Sorensen 1986). Colonies of the native species reached densities of 90 mounds/ha at BFL.

To determine if the 6:1 replacement ratio was simply an artifact of *S. invicta* having smaller and more abundant colonies, we conducted two surveys. First, we measured the mound areas of 24 colonies from each species. The average surface area of *S. invicta* mounds was  $1,160 \pm 490$  cm<sup>2</sup> compared with  $1,000 \pm 550$  cm<sup>2</sup> for *S. geminata* mounds ( $P > 0.05$ ). Second, we placed unbaited pitfall traps 1 m from eleven randomly chosen colonies of each species. *S. invicta* foragers were three times more likely to be collected in these traps than *S. geminata* (17.9 versus 6.2 workers per trap per day; Mann-Whitney test,  $U = 15.0$ ,  $P < 0.01$ ,  $n = 10,11$ ).

To determine if hybridization was occurring between *S. invicta* and *S. geminata*, we sent 25 samples of ants from the interface area to R. K. Vander Meer for gas chromatographic analysis of hydrocarbons and venom alkaloids (Vander Meer 1986).

He reported that all samples were clearly one species or the other.

Polygyny strongly diminishes a colony's reproductive potential. Multiple queens pheromonally inhibit the production of reproductives (Vargo & Fletcher 1986); consequently, polygyne colonies produce about 30% fewer winged queens than monogyne colonies (Vargo & Fletcher 1987). Fire ant queens normally establish or found new colonies claustrally; that is, one or a few newly mated queens rear the first generation of workers entirely from energy previously stored in body tissues. Work by D. J. C. Fletcher in Georgia (unpublished data) shows that founding queens of *S. invicta* produced by polygyne colonies are not as successful as those produced by the monogyne form. He found that queens from polygyne colonies each weighed about 30% less and produced about 40% fewer workers than did queens from monogyne colonies. Our results are similar. The average weight of 51 founding *S. invicta* queens collected at BFL (May-June 1987) was  $11.8 \pm 2.2$  mg; this compares with  $15.5 \pm 0.8$  mg for queens produced in Florida mono-

gyne colonies (Porter & Tschinkel 1986). About 30% of the founding queens collected at BFL produced a first generation of workers, but only 20% produced sufficient workers (>20) to have been reasonably successful. This compares with about a 75% potential of success for founding queens produced by the monogyne form (Porter & Tschinkel 1986). Part of the reason for the poor founding ability of newly mated queens at BFL can be attributed to their low weights, but a second major reason was that only 60% were inseminated compared with nearly 100% in the monogyne form (Glancey & Lofgren 1985). The low insemination rate may have been caused by the unusually high proportions of sterile diploid males in polygyne populations (Hung et al. 1974, Ross & Fletcher 1985a).

### Discussion

Our results, combined with data from those of previous workers (Wilson & Brown 1958, Hung & Vinson 1978, Vinson & Greenberg 1986), suggest that the invasion of imported fire ants in central Texas is a complex, multiphasic phenomenon. The fact that the local invasion front at BFL moved three orders of magnitude slower than the main front (10–40 m/yr versus 10–50 km/yr; Wilson & Brown 1958, Vinson & Greenberg 1986) indicates that fire ant invasions occur in two phases. The first or pioneer phase results from long-distance dispersal of either winged queens during mating flights or small colonies transported in items of commerce such as nursery stock (Wilson & Brown 1958, Vinson & Greenberg 1986). These pioneers are aided by any disturbance that clears a site of heavy vegetation and disrupts the native ant community. Newly invaded areas thus become a patchwork of many invasion foci. The second phase of the invasion is the occupation phase. During this phase, invasion foci gradually expand and increase in number, eventually fusing to form broadly continuous distributions. In the case of large and relatively undisturbed sites like BFL, the occupation phase evidently requires many years or even decades to complete.

One interesting aspect of the occupation phase at BFL is that the invasion progressed along a continuous front. Part of the reason for this is that polygyne colonies proliferate by budding (unpublished data); in other words, a portion of the queens and workers simply split off to form a new sister colony. Reproduction by budding naturally results in an ameoboid pattern of expansion similar to that which we observed (Fig. 1).

In addition to its slow spread and continuous front, the invasion at BFL revealed a striking lack of overlap between native and imported fire ants (Fig. 2). This situation is unusual considering that fire ant queens mate 100 m or more in the air, and wind currents normally disperse them over a wide area and in many directions (Markin et al. 1971).

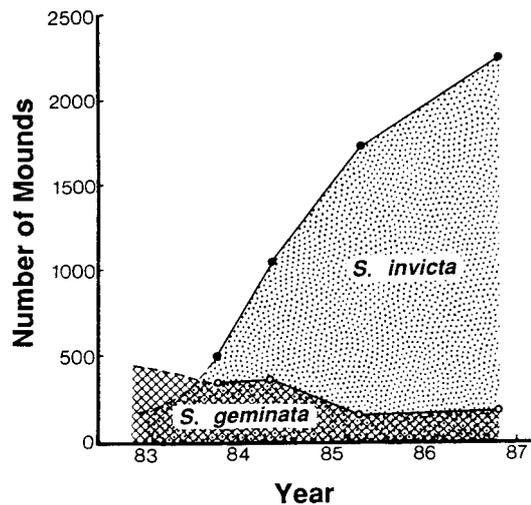


Fig. 3. Change over time in the number of native (hatched) and imported (stippled) fire ant mounds at Brackenridge Field Laboratory.

In spite of this, neither species was consistently able to establish pioneering or founding colonies within the other's distribution. Admittedly, the production of founding queens by polygyne colonies is reduced compared with monogyne colonies; nevertheless, we estimate that hundreds of thousands of suitable founding queens (of both species) were produced in the area during this study. Biotic resistance is a probable reason for the poor success of these founding queens. Several ants are known to attack and kill founding fire ant queens (Whitcomb et al. 1973). Presumably, *S. geminata* and other species in BFL's abundant and diverse ant community (Feener 1978) have been important in eliminating founding *S. invicta* queens and incipient colonies from non-infested areas and vice versa.

Founding queens of both the native and imported species may compete in scramble fashion for disturbed sites during the pioneer phase, but during the occupation phase, competition shifts primarily to interactions among mature colonies. The exact mechanism of competition between mature colonies has not been established, but the sharply defined invasion front suggests aggressive interactions are likely (Jones & Phillips 1987). Differences in foraging success, thermoregulatory capabilities, and interference from natural enemies (Feener 1981) also are possibilities.

Whatever the mechanism, the continuing lack of overlap between *S. invicta* and *S. geminata* (Fig. 2) is a clear result of competitive replacement. The ability of *S. invicta* colonies to eliminate mature *S. geminata* colonies is no mean accomplishment because *S. geminata* can be very dominant in its own right (Risch & Carroll 1982). In fact, *S. geminata* is an important introduced pest in parts of Africa, India, Australia, and Polynesia (Fluker & Beardsley 1970, Wilson 1978). Although several authors have reported that *S. invicta* displaces or replaces native *S. geminata* populations in the

United States (Wilson & Brown 1958, Hung & Vinson 1978, Wojcik 1983), these authors did not map the spatial and temporal aspects associated with the displacement of individual colonies. In some regions, *S. invicta* restricts native fire ants to less desirable wooded locations (Wilson & Brown 1958, Tschinkel 1988), but this is not the case at BFL—*S. geminata* is being eliminated from the station entirely.

It remains a mystery how and when polygyne *S. invicta* populations arose, but frequency of this form seems to be increasing (Glancey et al. 1987). We hypothesize that because polygyne populations have apparently arisen independently on a number of occasions (Ross & Fletcher 1985b), this social mode may be initiated by a simple developmental or mutational event (probably a failure in the nest-mate-queen recognition system). As the occupation phase nears completion, monogyne colonies would have less opportunity to expand through the pioneering efforts of founding queens. Variants giving rise to polygyne colonies would be favored because these expand locally by budding in a manner similar to vegetative reproduction in plants.

The microgeography of invading monogyne populations has not been carefully examined, but they do not appear to advance along continuous fronts as seen at BFL; rather, new colonies are broadly scattered across suitable sites. Clearly, we need a better understanding of the occurrence of multiple- and single-queen systems in time and space. For instance, is the polygyne condition genetic or developmental? Was it absent in early surveys (1948–1973) because conditions did not favor polygyny, or was it simply overlooked? Have mass attempts at chemical control provided conditions that favor polygyny?

The invasion process observed at BFL is similar to invasions of other polygyne pest ants (Fluker & Beardsley 1970, Lieberburg et al. 1975). For instance, *O. auropunctata* and *I. humilis* also invade along solid fronts (Erickson 1971, Clark et al. 1982). Not surprisingly, both species reproduce by colony budding and exhibit rather slow rates of expansion. Polygyne ants often form interconnecting supercolonies and are commonly found in extremely high densities (Hölldobler & Wilson 1977). Furthermore, the high densities and aggressive behavior associated with polygyne pests has led to the elimination or severe reduction of other sympatric ants. In fact, monopolization rather than dominance may be a more appropriate description of how these ants affect their host communities.

The high replacement ratio between *S. invicta* and *S. geminata* (6:1) indicates that *S. invicta* is not simply replacing its native congener (Fig. 2 and 3). Additionally, preliminary bait transects at BFL indicate that the diversity of other ants is much lower in areas occupied by the imported species than it is in similar areas outside the advancing front. A negative effect of *S. invicta* on other species of ants has been reported by other

authors (Wilson 1951, Glancey et al. 1976). Fire ants may also cause a substantial drop in the numbers and species richness of other taxa which compete with them for food (Hooper 1976, Risch & Carroll 1982). Finally, *S. invicta* may cause major changes in the abundance of certain prey species, including organisms as diverse as ticks and boll weevils (Harris & Burns 1972, Jones & Sterling 1979). This information indicates that *S. invicta* colonies may have revolutionary impacts on community structure. A thorough understanding of these consequences is important from both the basic and applied points of view. If the polygyne form of *S. invicta* continues to spread, it may be a serious threat to biological diversity throughout much of southern United States.

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