

## The Fire Ant (*Solenopsis invicta*): Still Unvanquished\*

---

Walter R. Tschinkel<sup>1</sup>

The fire ant (*Solenopsis invicta*) Buren has caused considerable commotion in the United States since its first appearance about 50 years ago (Lofgren 1986a). A native of the seasonally flooded Pantanal region of southern Brazil (Fig. 1), this ant was first noticed in the vicinity of the harbor at Mobile, Alabama around 1940. Although it probably made its way from Brazil by way of some form of shipping, its arrival has not been linked to any particular commodity. In any case, *S. invicta* joined the slower spreading *S. richteri* Forel from northern Argentina, which had appeared in Mobile in 1918. From this initial point of introduction, *S. invicta* began a rapid range expansion, partly by means of its own dispersive mating flights but mostly through the aid of man. By the mid-1950s, its range consisted of a contiguous zone around Mobile and numerous incipient populations centered on nurseries throughout the southeastern U.S. (Fig. 2). Mated queens or young colonies had apparently hitched rides on nursery stock transported throughout the Southeast. While USDA quarantine procedures reduced the rate of spread by nursery stock, this and other human modes continue to be important means of range extension for *S. invicta*. Almost all of the range expansion in the U.S. since the mid-1950s has consisted of filling in the spaces between incipient populations established during the first 10 to 15 years. In 1982 the ant appeared in Puerto Rico, and outlying populations are presently found in San Antonio and Oklahoma City (Fig. 2). *Solenopsis richteri* is now confined to northern Mississippi, having been displaced from its earlier range by *S. invicta* (Lofgren 1986a).

The prediction of *S. invicta*'s ultimate range limits is somewhat contentious and depends on certain biological assumptions. Because the ant has no true hibernation, its northward spread must ultimately be limited by winter-cold or brevity of a season warm enough for colony development and reproduction. There is evidence that the northern range limit is being approached in northern Mississippi, Alabama, Georgia, and the Carolinas. The southern latitudinal limits in South America are roughly similar to the northern ones in the U.S.—about 32°S and 34°N, respectively.

Most of the recent spread has been westward in Texas. While this brings the ant into increasingly arid zones, there is little knowledge of how or whether aridity will limit the ant's spread. The timing of rainfall may be as important as the total amount, because the mating flights and successful colony founding take place only on warm days after heavy rains. Mediterranean climates such as those of the western coastal states, with their cold winter rains and hot rainless summers, may prevent successful reproduction of fire ant colonies. Little is known about the southward spread into Mexico, though it has been speculated that the native ant fauna may become increasingly resistant to invasion as the tropics are approached.

The final range is likely to result from the combined effects of climate, physi-

---

\*For a synopsis of a general ant life cycle, see Appendix, p. 135.

1. Department of Biological Science, Florida State University, Tallahassee, FL 32306-3050

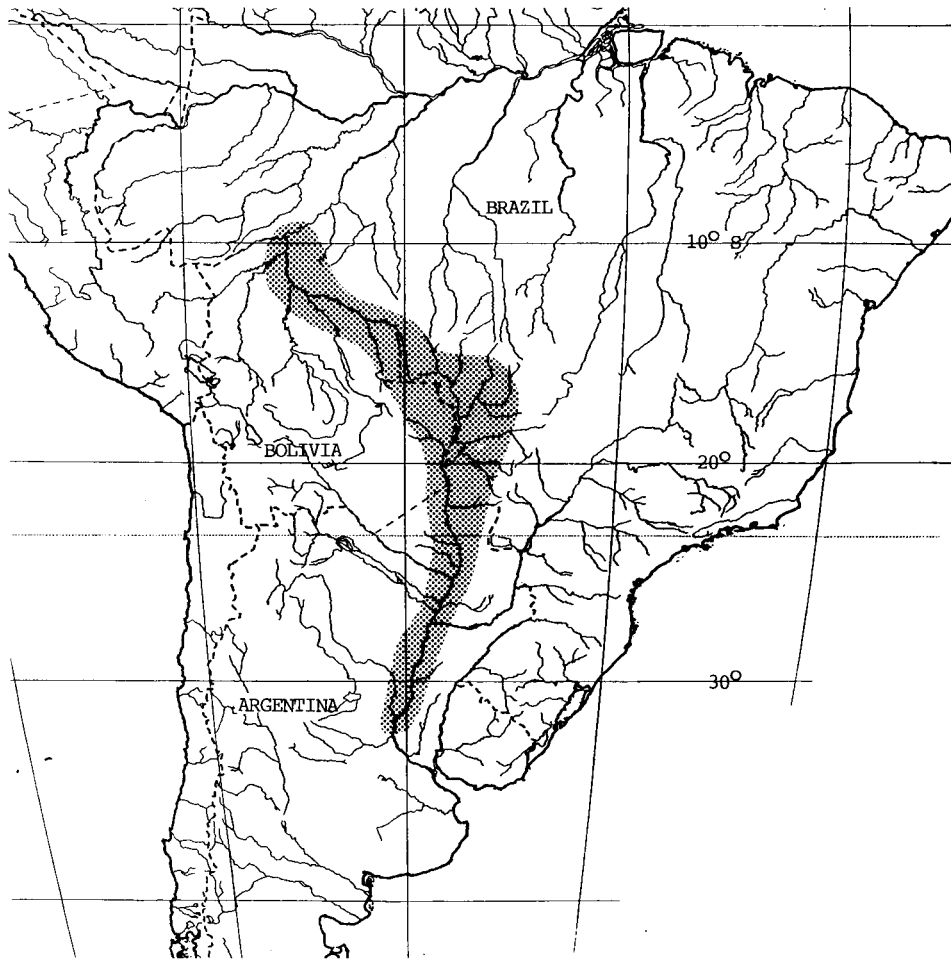


FIGURE 1.—Range of *Solenopsis invicta* in its South American homeland. The range includes the flood plains of two major river systems. Data from Buren et al. 1974 and Ross and Trager 1990.

cal, and biotic factors. In less favorable areas and at the margins of its eventual range, we can expect the fire ant to be a less dominant element of the fauna.

### IMPACT OF THE FIRE ANT IN THE U.S.

Much controversy has surrounded the claims of economic, social, and biological impacts of *S. invicta* (Lofgren 1986b; Davidson and Stone 1989). The early “parade of horrors” that formed the mythic underpinnings of such pork-barrel programs as the USDA’s Mirex program has more recently given way to more careful attempts to quantify the ant’s impacts (Lofgren 1986b). The human response to fire ants is often deeply emotional, as even brief conversations with many southerners will establish. This emotionality is based on the fact that fire ants readily and effectively sting people who blunder into their nests. The unaware can easily sustain dozens of stings in a single encounter. Compared to other ants, individual fire ant stings only rate a “moderate” on the “Richter pain scale,” but they often make up for this through their numbers. The venom in-

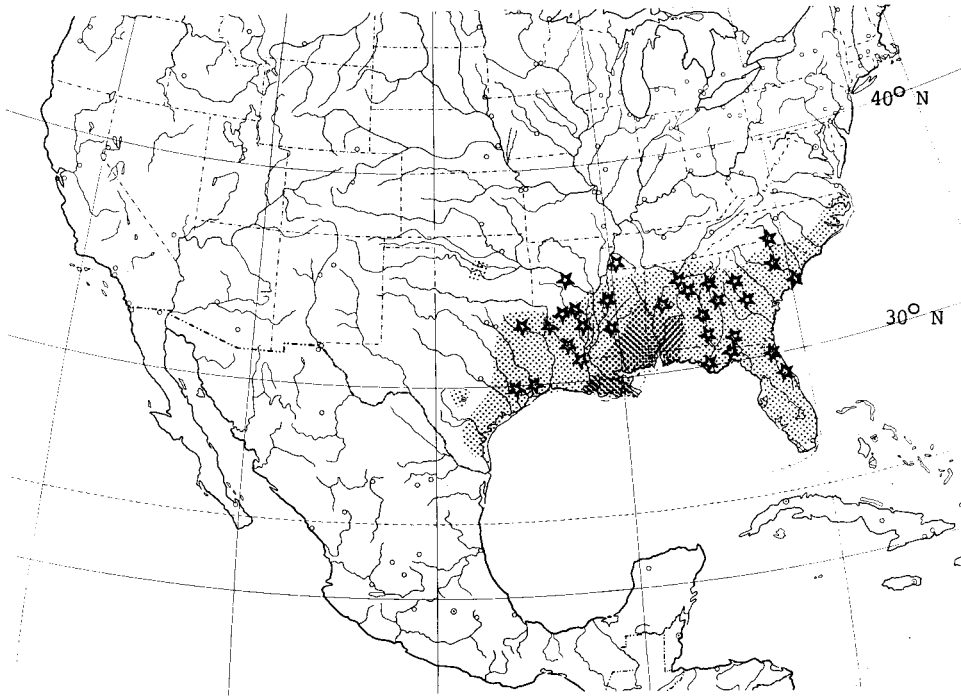


FIGURE 2.—Range of *S. invicta* in 1953 (dark shading and stars) and in 1986 (light shading). Much of the early spread was by transport of nursery stock. Most of the incipient populations in 1953 (stars) were centered on nurseries (redrawn from Lofgren 1986).

jected by the stinging worker soon causes the formation of a sterile pustule because white blood cells move in to clean up the venom-killed cells. The great majority of humans suffer only discomfort from the stings, but a small fraction are hyper-allergic to varying degrees. The response of such people may range from regional swelling to anaphylactic shock and death. Although many southerners are stung, only a small fraction need to seek medical treatment (Lofgren 1986b). In general, the stinging of people makes the fire ant a predominantly urban and suburban problem, in spite of its early attention from the agricultural sector.

While the impact of *S. invicta* directly on people is decidedly negative, its impact on agriculture is mixed (Lofgren 1986b; Davidson and Stone 1989). Claims of interference with harvesting and farm machinery have been made, though most remain sketchily documented. The ants are known to damage some crops such as eggplants, okra, and orange tree seedlings, but the quantification of proportional economic impact is difficult. On the other hand *S. invicta* has been shown to reduce hornflies and lone star ticks (pests of cattle) as well as several crop pests, including those of cotton and sugar cane. Being the general predator that it is, it is no surprise that fire ants can be beneficial in certain situations.

In the last 15 years a new phenomenon has come to light, one that may have a major biological impact. While fire ant colonies are generally monogyne (have a single egg-laying queen), there exist population enclaves throughout the Southeast in which colonies are polygyne (multiple egg-laying queens) (Glancey et al. 1987). In east Texas, fire ants exist as a mosaic of populations, about half of which are polygyne. The change in queen number brings about a major shift in colony biology—colonies are no longer territorial, so that ant density is no longer

limited by territoriality; mating flights are small and most resources are invested in worker production, resulting in very high growth rates; colonies (nests) reproduce by budding or fission and disperse on foot, causing the population to spread as a contiguous front (Fig. 3) (Porter et al. 1988). Fire ant densities in polygyne populations are up to six times that in monogyne, causing a massive shift in the fauna. As the polygyne population moves in, the diversity and abundance of native arthropods and even vertebrates plummets. What food material sustains these high ant densities is not clear, but the prospect of the displacement of many native species is a serious concern (Porter et al. 1988).

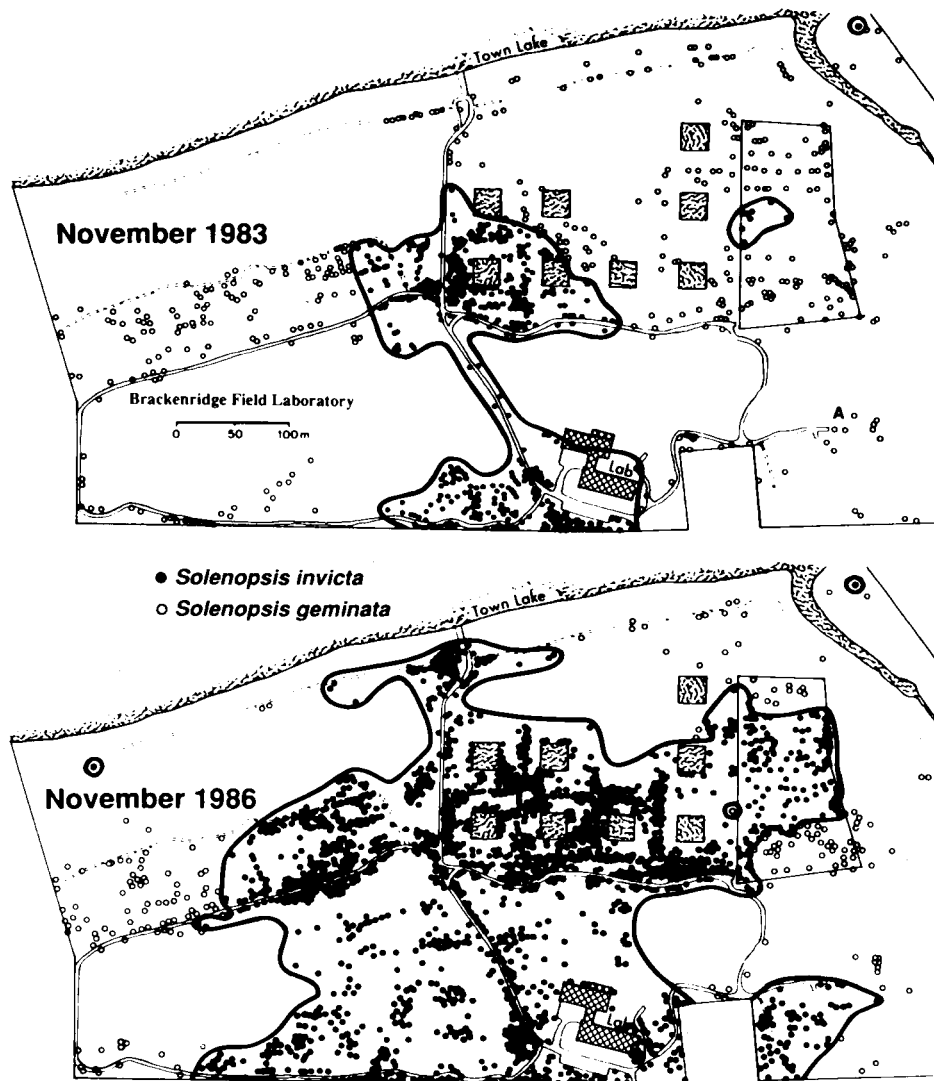


FIGURE 3.—Spread of the polygyne form of *S. invicta* at Brackenridge Field Laboratory near Austin, Texas. The polygyne form reproduces colonies by fission rather than independently through nuptial flights of queens. The population of colonies thus spreads as a contiguous front. Open circles, *S. geminata*; closed circles, *S. invicta* polygyne form (from Porter et al. 1988).

WHY IS *S. INVICTA* INVASIVE?

The answer to this question is suggested by the types of habitats in which fire ants are abundant, both in the U.S. and in Brazil. In both cases, fire ants are found mostly in habitats that have been disturbed by man or by natural processes such as flooding, landslide, or disastrous storms. For example, in the natural coastal plain forests in northern Florida, *S. invicta* is limited to disturbed roadsides, heavily disturbed clearing sites, pond margins or areas with a high water table (Fig. 4) (Tschinkel 1988a). This distribution pattern suggests that *S. invicta* is a "weedy" species, an animal counterpart to the familiar plant weeds that invade cleared land and other disturbed sites.

Like plant weeds, some animals are adapted for opportunistic exploitation of ecologically disturbed habitat (Ito 1978). Under natural circumstances, occurrence of these habitats is unpredictable in time and space. The habitats are ephemeral, reverting to the climax vegetation through succession. In order to exploit these habitats, weeds and weed-like animals often share a number of characteristics. Habitat unpredictability selects both to invest heavily in large numbers of propagules. Spatial unpredictability is overcome by good dispersal ability. Seeds are lofted by the wind or carried by animals, while sexual ants fly long distances. Having landed in disturbed habitat, both must colonize it effectively, and because the habitat reverts to an unfavorable state, they must grow rapidly, reproduce early and continuously. Weeds and weed-like animals lead a sort of fugitive existence, from disturbed patch to patch. Success depends on their ability to arrive, as the Confederate General DeForrest said, "the firstest

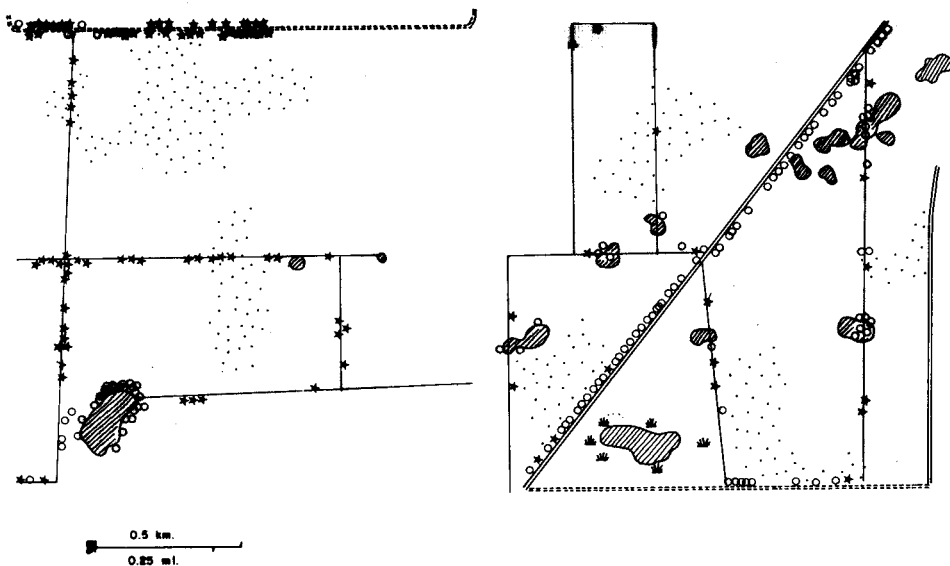


FIGURE 4.—Distribution of *Solenopsis invicta* (open circles) and *S. geminata* (stars) nests along transects in the high pinelands near Tallahassee, Florida. *S. geminata* is closely related to *S. invicta* but is probably a native species. Each symbol designates one nest within sight (2–3 m) of the transect line. *S. invicta* dominates disturbed areas and pond-margins, while *S. geminata* dominates the less disturbed upland areas. Management condition of forest is indicated by shading: shaded, mature longleaf pine forest; stippled, seed trees only; unshaded, recently clearcut, site prepared, and replanted with longleaf pine. Ponds indicated by cross-hatching. Paved roads, solid double lines; graded dirt roads, dashed double lines (from Tschinkel 1988a).

with the mostest,” and to prevail in the scramble for space and resources before the habitat becomes unsuitable.

Comparing *S. invicta* with weeds gives us an immediate insight into its rapid spread in the United States. The primeval condition of the southeastern United States was unbroken broadleaf and pine forest, with small patches of early succession scattered haphazardly as windfalls, sandbars or clearings for Indian agriculture. By the early 20th century most of the forest had been cleared for living space and agriculture, creating vast new opportunities for early succession species. Availability of so much early succession habitat and an ant fauna not fully capable of exploiting it set the stage for the rapid spread of *S. invicta* (Buren 1983). The synergism between fire ants and man will continue as long as humans depend on early succession communities for their existence—man is truly the fire ant’s best friend.

How well does *S. invicta* fit the stereotype of a weed? Let us survey the major biological attributes of fire ants in this light.

### DEPENDENCE UPON DISTURBANCE

As noted above, fire ants occur mostly in areas of disturbance such as lawns, pastures, roadsides, and agricultural land (Fig. 5). Less obviously, in addition to gross disturbance, *S. invicta* is favored by a high water table and seasonal flooding (Tschinkel 1988a). The Brazilian homeland, the Pantanal, is a seasonally flooded headwater of two major rivers. As a partial adaptation to this hydroregime, fire ant



FIGURE 5.—Typical aspect of fire ant colonies in a pasture. Colonies of such monogyne populations are well-spaced and defend territories against neighboring colonies. Inset is of a single nest, ca. 50 cm in diameter and 25 cm high. (photo by author)



FIGURE 6.—A floating colony of fire ants at a flooded pond-side site. The ability to float as a mat is probably an adaptation to the seasonal flooding to which *S. invicta* is sometimes subjected in South America. (photo by author)

colonies have the capacity, when the waters rise, to float as a mat of ants, surviving for weeks until the waters recede or they drift ashore (Fig. 6) (Morrill 1974). At least in the U.S., seasonal flooding eliminates most other ants. Thus in north Florida, fire ants have invaded wet-savanna even in the absence of human disturbance.

Specific disturbance of the ant community may be sufficient to favor *S. invicta*. Plots in which *S. invicta* was a minor component of the ant community were treated with poison bait, killing all ants. Upon recolonization, the community was heavily dominated by *S. invicta* (Fig. 7) (Buren et al. 1978; Summerlin et al. 1977). Apparently the colonizing ability and speed of fire ants exceeded that of our native ants. These findings make it likely that, by eliminating native ants, large-scale control programs such as the Mirex program ultimately helped the fire ant spread more rapidly and achieve higher dominance.

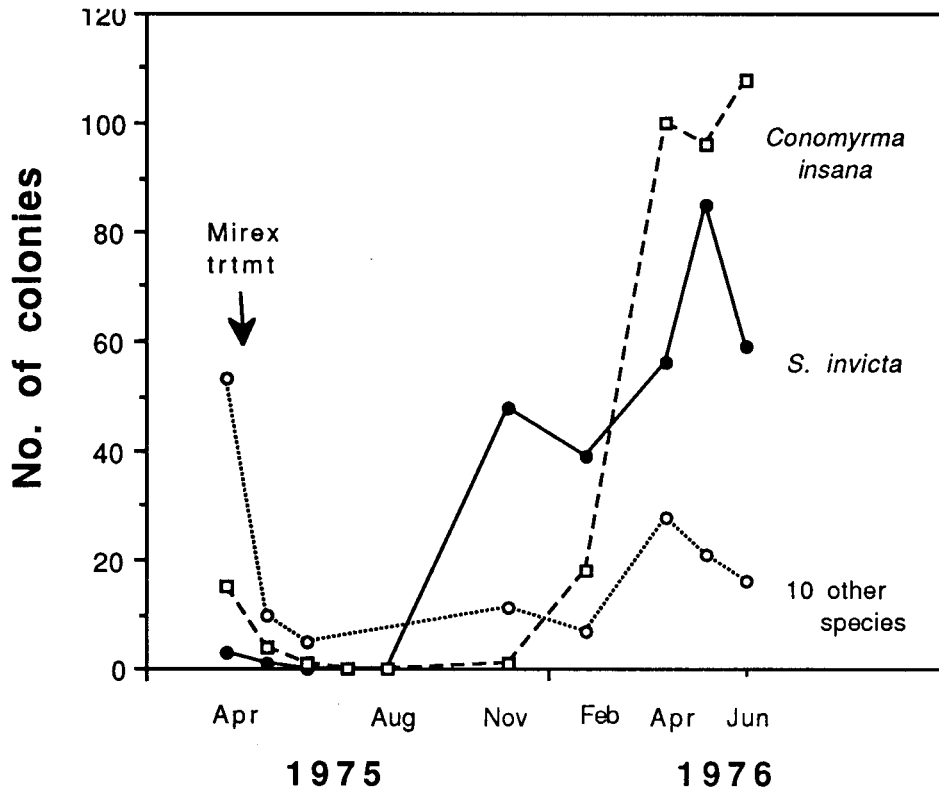


FIGURE 7.—Disturbance of the ant community and its effect on subsequent recolonization by several species. Most ants were killed with a single treatment of poison bait (Mirex). The fire ant *S. invicta* changed from a minor member of the ant community before treatment to a dominant member after. *Conomyrma insana* colonies, while more numerous than *S. invicta* colonies, are only about one-twentieth the mature size. Data from Summerlin et al. (1977).

## INVESTMENT IN REPRODUCTION

The fire ant invests heavily in propagules in the form of sexual males and females. Having entered the reproductive phase, fire ant colonies invest about one-third of their annual production in sexuals. This translates into about 4,000 to 6,000 sexuals per year, very high in comparison to the small number of other ant species for which data are available, and in the range of plant weeds (Tschinkel 1992b).

## DISPERSAL

Like the winged seeds of many plant weeds, fire ants disperse by means of winged sexual females. Mating flights take place on warm days after heavy rains. As late spring weather fronts sweep across the southeastern United States, they are followed by enormous synchronized mating flights of fire ants. Millions of winged males and females leave their natal nests, fly up into the sky, and mate 300 to 800 feet above the ground (Lofgren et al. 1975). The female stores a lifetime supply of sperm, about 7 million, in her spermatheca (Tschinkel 1987), and after a dispersal flight varying from a few dozen meters to a kilometer or more (Lofgren et al. 1975), she descends to the ground.



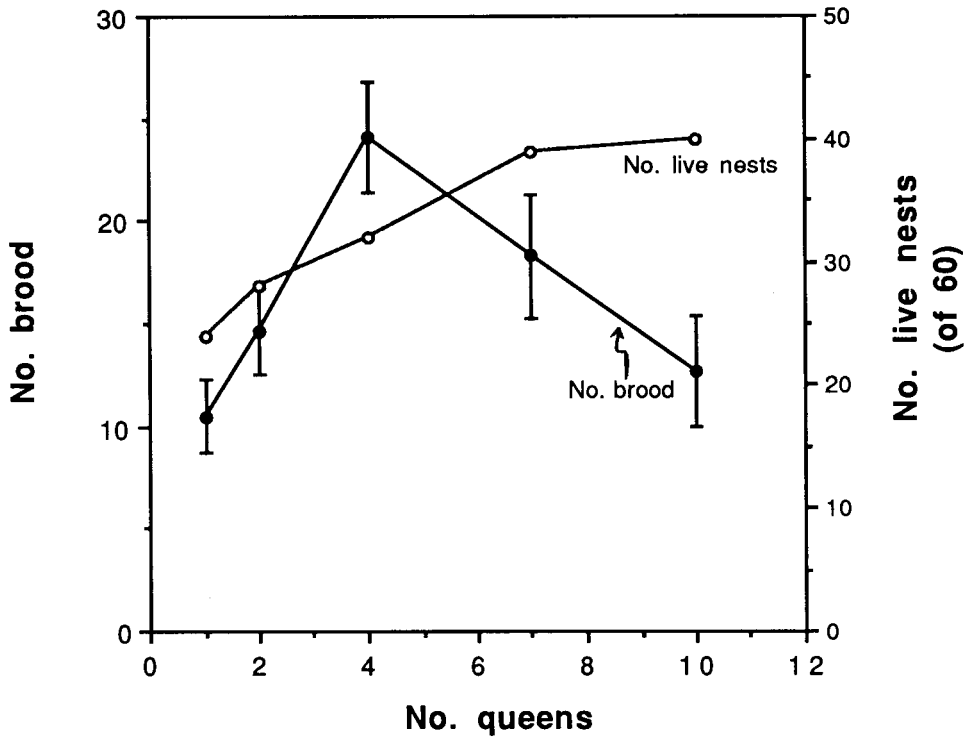


FIGURE 8.—The effect of cooperative colony founding and queen number on brood production and colony survival. Progeny production and the likelihood of founding success are maximum at intermediate group sizes (Tschinkel, unpubl. data).

### EFFECTIVE COLONIZATION

Unlike plant weeds, fire ant females choose their landing site while still airborne. Sites that are *partially* vegetated as a result of recent disturbance are especially attractive to them, and they often colonize these in large numbers. On one 1200 m<sup>2</sup> study plot in Tallahassee, I estimated that between 10,000 and 20,000 mated queens attempted colonization in the course of one summer (Tschinkel 1992a).

Having landed, the newly mated queen breaks off her wings, and usually within a radius of 4 to 5 m of her landing spot, she digs a 5 to 15 cm deep tunnel at the end of which she forms a chamber. She seals herself into this nest for the duration of the founding period and rears the first brood of 5 to 35 minim workers from reserves stored in her body, losing 70 percent of her energy content in the process (Tschinkel, unpubl.).

Fire ants have evolved two ways of improving the success of this population founding phase. Queens often join one another to rear the first worker brood, bringing about improved survival and higher worker production (Fig. 8) (Tschinkel and Howard 1983). Those nests that succeed in producing minim workers engage in brood-raiding as soon as the nests are opened to the surface (Tschinkel 1992a). In brood-raiding, workers from incipient nests seek out neighboring incipient nests in order to steal their brood, and because the host workers often steal them back, a reciprocal raid develops. These can sometimes involve many nests (Fig. 9), although most raids are small. The winners are

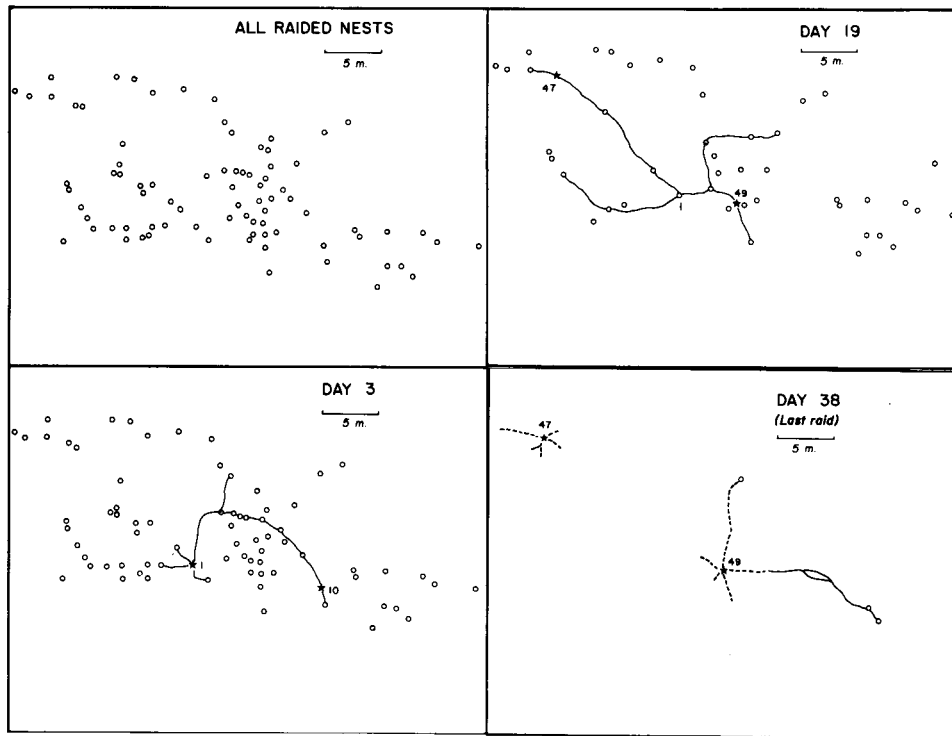


FIGURE 9.—The course of a very large brood raid. This raid lasted for 38 days and included hundreds of meters of raiding trails. By the end, over 80 incipient colonies had coalesced into two colonies (stars, 47 and 49) (from Tschinkel 1992a).

usually the nests that had the most workers initially, i.e., those founded by groups of queens, underscoring the importance of cooperative founding. The losing workers generally join the winners, and the losing queens can often be seen wandering on the surface, sometimes trying to enter incipient nests. The outcome of raiding is the coalescence of many small nests into a small number of much larger ones. Workers soon kill all but one queen. The lone survivor and new queen mother is not necessarily one that founded that nest. The nest now stands on the threshold to growth.

### RAPID COLONY GROWTH

The importance of cooperative founding and brood-raiding becomes clear in the next weedy property—rapid growth. The ephemeral habitat requires that growth be rapid and reproduction early. Early growth in fire ant colonies is exponential, i.e., multiplicative (Tschinkel and Howard 1983; Tschinkel 1988b). A colony beginning growth with 50 minims will be 10 times as large as one beginning with 5 minims as long as exponential growth continues. This brings the importance of initial brood number into sharp focus because the winner of the scramble for space will be the colony which achieves the largest size at the earliest date.

Like other weeds, fire ant colonies are capable of rapid growth. Lab and field studies suggest that colony growth rates are strongly food-limited (Tschinkel 1988b). In a few cases, lab-reared newly mated queens produced 500,000 work-

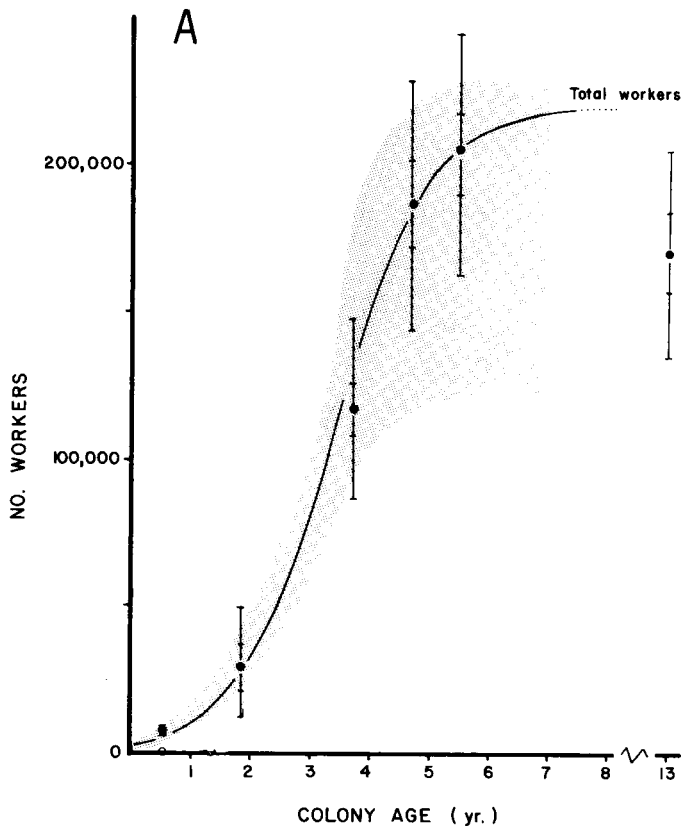


FIGURE 10.—Mean growth curve of fire ant colonies in moderately productive habitat. Growth is logistic, and colonies reach full size in 5 to 7 years. Shading shows the limits of seasonal variation in colony size (modified from Tschinkel 1988b).

ers in their first year of life (Tschinkel and Porter 1988). In average habitat, fire ant colonies grow to sizes of about 200,000 workers in 5 to 6 years (Fig. 10) (Tschinkel 1988b). Growth is forced by a feedback loop in which the older larvae produce a substance which stimulates the egg-laying rate of the queen (Tschinkel 1988c). In mature colonies, queens may lay up to their own body weight in eggs daily, about 3,000 to 5,000 eggs per day. Such queens are 75 percent ovary, by weight, and are egg-laying machines (Fig. 11).

### EARLY AND CONTINUING REPRODUCTION

The ephemeral nature of the habitat also selects for early and continuing reproduction in weeds. When fire ant colonies are only 10 percent of their final size, they begin to invest 30 percent of their annual production into sexuals (Tschinkel 1992b). Sexual production therefore increases in direct relation to colony size.

Moreover, sexual production and release is less seasonal than in many other ants. *Solenopsis invicta* produces sexuals during any part of the winter, spring, and early summer warm enough to allow it. They release these on mating flights over several months, beginning with the first warm spring rains and ending with exhaustion of the supply of sexuals (Fig. 12) (Lofgren et al. 1975). In the Tallahassee area, flights begin in early May and taper off through July.



FIGURE 11.—A fire ant queen and her retinue. Workers in the retinue groom the queen, feed her a special liquid diet, and take away the eggs she lays. This queen was laying about 70 eggs per hour. Ovaries make up most of the abdominal volume. (photo by author)

## CAPACITY FOR VEGETATIVE REPRODUCTION

Many weeds, having established in a suitable patch of habitat, increase their dominance in it by vegetative reproduction—runners, asexual seed production, root shoots, and so on. In an analogous sense, fire ants have undergone a similar change of biology. Throughout the range of the fire ant, both in Brazil and the U.S., are found population enclaves of polygyne colonies. As noted above, these colonies invest little in sexual production. Rather, most resources are invested in colony growth (worker production), which results in asexual-like colony reproduction by budding or fission. Like many asexually reproducing plant weeds, these polygyne populations achieve very high dominance of their habitat.

## NON-WEEDY TRAITS

Of course, no category is perfect. Several aspects of fire ant biology do not fit the weedy syndrome. Large size is not often typical of weeds, and fire ant colonies rank among the largest ant colonies, often containing up to 250,000 workers.

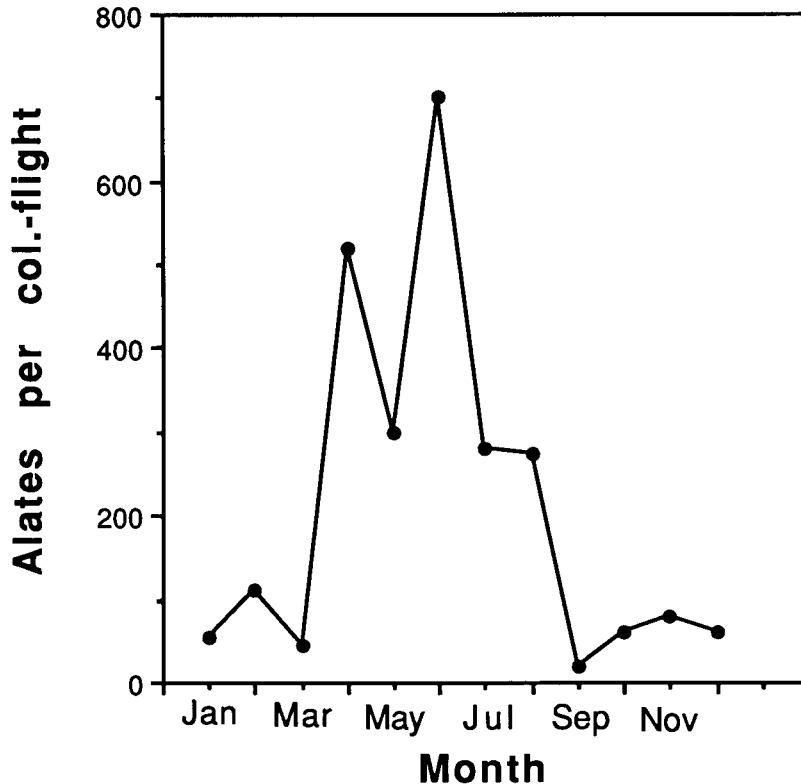


FIGURE 12.—The release of winged sexuals (alates) on nuptial flights throughout one year in north Florida. Large mating flights can occur during most of the late spring and early summer (data from Morrill 1974).

Across species, ant colonies probably average a few hundred workers. Competitiveness of weeds is thought to rely heavily on speed of growth and less on direct interactions among individuals. However, soon after the brood-raiding phase, monogyne fire ant colonies become territorial, excluding members of neighboring colonies from their foraging territory by means of aggression and warfare (Fig. 13) (Wilson et al. 1971). Long life is another non-weedy property. While an individual queen runs out of sperm (and therefore worker-producing capacity) after 5 to 7 years (Tschinkel 1987), she is often replaced with a new one (Tschinkel and Howard 1978), making colonies potentially immortal, at least until the habitat becomes unfavorable. Thus fire ants act like weeds early in the population cycle, and competitors later.

## THE FUTURE

The chimera of fire ant eradication (Lofgren and Weidhaas 1972) that floated over the decades of the 1960s and 1970s seems to have faded. The fire ant is here to stay. With respect to the monogyne form, public demand for relief has softened. Most households accomplish their own fire ant control with the many baits and mound drenches available for this purpose. In agriculture, the marketplace has determined, on the one hand, just how much of a problem the fire ant really is and, on the other, ants may also have value. These issues will continue to draw refining discussion and new data.

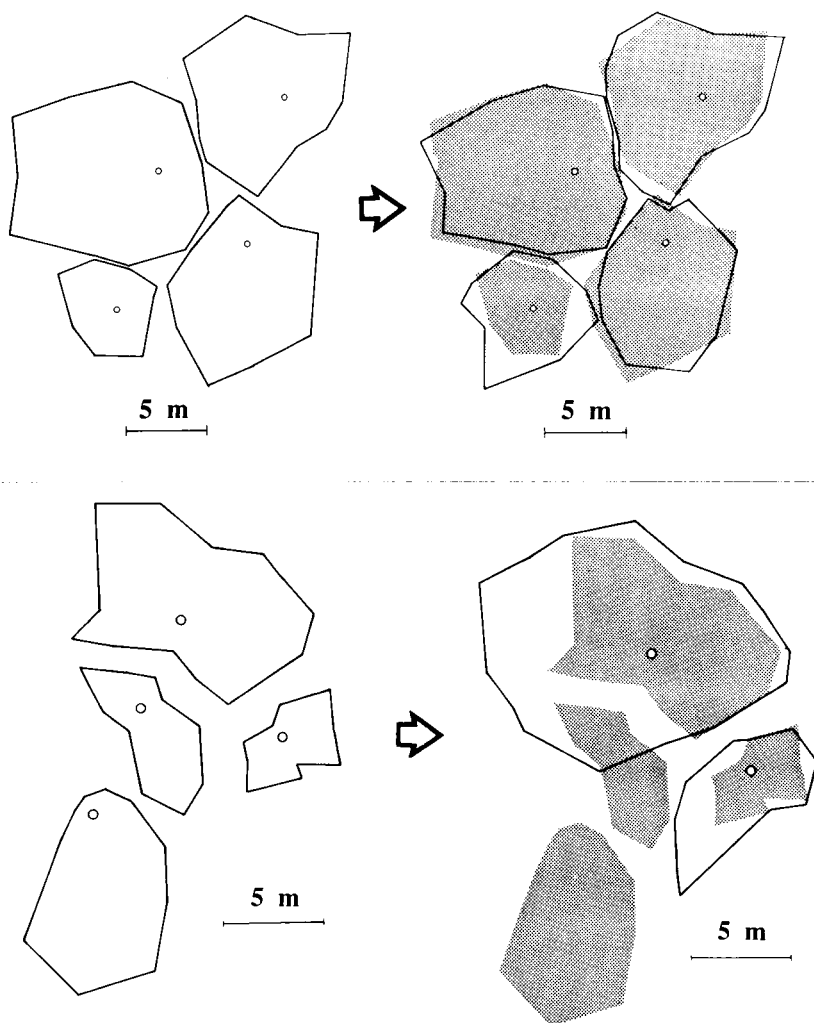


FIGURE 13.—Map of two groups of adjacent territories of fire ant colonies near Tallahassee, Florida. The mound position is shown by the circles. In the lower group, two colonies were removed, causing the remaining two to expand their territories (lower right) and demonstrating that territory size results from active defense. Shaded areas show original territory size. The controls showed little net change in territory area over the same period (upper right) (Adams, Macom and Tschinkel, unpubl.).

The polygyne form may yet be seen as causing unacceptable dislocations in our native ecosystems, but the full-scale and nature of its impact is not yet known. Presently the only known biological deterrent to its spread is the monogyne, territorial form of *S. invicta*, leading to the ironic situation in which the Texas Department of Agriculture recommends landowners to husband their monogyne colonies.

Because chemical control is unspecific and *S. invicta* is such an effective re-colonizer, the only long-term hope of reducing fire ant dominance is through bio-control. While a number of potential biocontrol agents are in hand, no releases have been attempted (Jouvenez 1990). As is so often the case, it will probably require release of multiple agents to achieve substantial reduction of fire ant populations. The goal should be to reduce the fire ant's competitive advantage to

a level comparable with native species. If this can be achieved, the fire ant will probably appear more like a normal component of our ant fauna rather than an overdominant alien (Buren et al. 1978; Buren 1983). It should be added that no biocontrol against a social insect has ever been attempted.

Finally, there is one area in which the fire ant has repaid us richly. Its abundance, ease of experimental manipulation, and high profile have enabled researchers to make it the best understood ant. Fire ant research will continue to contribute important insights into the biology of social insects, evolution, population genetics, and perhaps as yet undiscovered realms. As far as biologists are concerned, fire ants have more than compensated for the aggravation they have caused.

## APPENDIX: A PRIMER OF ANT LIFE CYCLES

All ants are social and live in colonies in which some individuals called queens (or a single one) are fertile and lay most of the eggs, while others (the workers) are sterile, raise the brood, and do all other colony work, including foraging (Hölldobler and Wilson 1990). All socially functional individuals are female. The differences between queens and workers are the result of developmental not genetic differences. Males develop from unfertilized eggs and are produced only for colony reproduction. The most typical form of colony reproduction in ants occurs when winged sexual males and females produced at the proper season (usually spring or summer) leave the nest on a nuptial flight. Mating takes place on the ground, on vegetation, or in the air, and the male dies within a short time. The female alights on the ground after a dispersive flight of variable length, breaks off her wings, and digs or seeks a chamber in which she seals herself during the founding period (claustral period). From material derived from stored nutrients and degenerating wing muscles, she lays eggs and feeds the resulting larvae until they become a brood of a few to a few dozen tiny workers (minim workers). These minims then open the nest, begin foraging, and take over all the work duties such as brood-rearing and nest construction. The queen becomes an egg-laying machine. Colony growth ensues through worker production until the colony contains enough workers to produce winged sexual females and males, closing the cycle.

Alternately, in some species, colonies may be polygyne, containing more than one egg-laying queen. Typically these queens are adopted as newly mated queens after mating flights. Colonies then reproduce by budding or fission of a portion of the workers and queens in each fragment.

## REFERENCES

- BUREN, W. F. 1983. Artificial faunal replacement for imported fire ant control. *Florida Entomol.* 66:93–100.
- BUREN, W. F., G. E. ALLEN and R. N. WILLIAMS. 1978. Approaches toward possible pest management of the imported fire ants. *ESA Bulletin*, 24:418–21.
- DAVIDSON, N. A. and N. D. STONE. 1989. Imported fire ants. Pages 196–217 in *Eradication of exotic pests: analysis with case histories*. D. L. Dahlsten and R. Garcia (eds.). Yale Univ. Press, New Haven, Conn.
- GLANCEY, B. M., J. C. E. NICKERSON, D. WOJCIK, et al. 1987. The increasing incidence of the polygyne form of the red imported fire ant, *Solenopsis invicta*, in Florida. *Florida Entomol.* 70:400–02.
- HÖLLDOBLER, B. and E. O. WILSON. 1990. *The ants*. Belknap/Harvard Press, Cambridge, Mass.
- ITO, Y. 1978. *Comparative ecology*. Cambridge Univ. Press, N.Y.
- JOUVENEZ, D. P. 1990. Approaches to biological control of fire ants in the United States. Pages 620–17 in *Applied Myrmecology: a world perspective*. R. K. Vander Meer, K. Jaffe and A. Cedeno (eds.). Westview Press, Boulder, Colo.
- LOFGREN, C. S. 1986a. History of imported fire ants in the United States. Pages 36–47 in *Fire ants*

- and leafcutting ants, biology and management. C. S. Lofgren and R. K. Vander Meer (eds.). Westview Press, Boulder, Colo.
- . The economic importance and control of imported fire ants in the United States. Pages 227–55 in Economic impact and control of social insects. S. B. Vinson, ed.
- LOFGREN, C. S., W. A. BANKS and B. M. GLANCEY. 1975. Biology and control of imported fire ants. *Ann. Rev. Entomol.* 29:1–30.
- LOFGREN, C. S. and D. E. WEIDHAAS. 1972. On the eradication of imported fire ants: a theoretical appraisal. *Bull. Entomol. Soc. Amer.*, 18:17–20.
- MORRILL, W. L. 1974. Dispersal of red imported fire ants by water. *Florida Entomol.* 57:39–42.
- PORTER, S. D., B. VAN EIMEREN and L. E. GILBERT. 1988. Invasion of red imported fire ants (Hymenoptera: Formicidae): microgeography of competitive replacement. *Ann. Entomol. Soc. Amer.* 81:913–18.
- ROSS, K. G. and J. C. TRAGER. 1990. Systematics and population genetics of fire ants (*Solenopsis saevissima* complex) from Argentina. *Evolution* 44:2113–34.
- SUMMERLIN, J. W., A. C. F. HUNG and S. B. VINSON. 1977. Residues in nontarget ants, species simplification and recovery of populations following aerial applications of Mirex. *Environ. Entomol.* 6:193–97.
- TSCHINKEL, W. R. 1987. Fire ant queen longevity and age: estimation by sperm depletion. *Ann. Entomol. Soc. Amer.* 80:263–66.
- . 1988a. Distribution of the fire ants *Solenopsis invicta* and *S. geminata* in north Florida in relation to habitat and disturbance. *Ann. Entomol. Soc. Amer.* 81:76–81.
- . 1988b. Colony growth and the ontogeny of worker polymorphism in the fire ant, *Solenopsis invicta* Buren. *Behav. Ecol. Sociobiol.* 22:103–15.
- . 1988c. Social regulation of egg laying rate in queens of the fire ant, *Solenopsis invicta*. *Physiol. Entomol.* 13:327–50.
- . 1992a. Brood-raiding and the population dynamics of founding in the fire ant, *Solenopsis invicta*. *Ecol. Entomol.* In press.
- . 1992b. Sociometry and sociogenesis in colonies of the fire ant, *Solenopsis invicta*. *Ecol. Monogr.* In review.
- TSCHINKEL, W. R. and D. F. HOWARD. 1978. Queen replacement in orphaned colonies of the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol.* 3:297–310.
- . 1983. Pleometrotic colony foundation in the fire ant, *Solenopsis invicta*. *Behav. Ecol. Sociobiol.* 12:103–13.
- TSCHINKEL, W. R. and S. D. PORTER. 1988. The efficiency of sperm use in queens of the fire ant, *Solenopsis invicta* Buren. *Ann. Entomol. Soc. Amer.* 81:777–81.
- WILSON, N. L., J. H. DILLIER and G. P. MARKIN. 1971. Foraging territories of imported fire ants. *Ann. Entomol. Soc. Amer.* 64:660.