

## Distribution and Density of Polygyne Fire Ants (Hymenoptera: Formicidae) in Texas

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**ABSTRACT** Multiple-queen or "polygyne" *Solenopsis invicta* Buren colonies are a serious economic and environmental concern because they occur in much higher densities than the monogyne form. Polygyne colonies have been found at numerous locations in the United States; nevertheless, the frequency and distribution of this form are poorly known. Almost 700 roadside sites in 168 Texas counties were surveyed. Polygyny was discovered at 54% of the infested sites. Polygyne populations were scattered in a mosaic across Texas. The frequency of polygyny varied somewhat with geographic region, but the pattern was generally unrelated to habitat and environmental conditions. Polygyne sites averaged more than twice as many mounds per hectare as monogyne sites. Populations of monogyne and polygyne forms were slightly lower in cooler and drier portions of the state. Mounds of both forms were about the same size. Polygyny was correlated with lower rates of sexual production and reduced numbers of native ants. The high frequency of polygyny in Texas indicates that the fire ant problem in the state is much greater than previously realized.

**KEY WORDS** Insecta, polygyny, mound density, *Solenopsis invicta*

MOST RED IMPORTED FIRE ANT (*Solenopsis invicta* Buren) colonies are apparently monogynous; that is, they contain a single fertile queen (Lofgren et al. 1975). In many areas of Texas, *S. invicta* colonies contain dozens of fertile queens (Miranda & Vinson 1982, Vargo & Fletcher 1989). Multiple-queen or "polygyne" colonies have been discovered at numerous sites throughout the Southeast (Ross et al. 1987). Their origin remains a mystery, but they appear to be spreading (Glancey et al. 1987). This spread is particularly unfortunate because polygyne supercolonies occur in very dense concentrations of 300-2,000 mounds per hectare (Lofgren & Williams 1984, Glancey & Lofgren 1988, Porter et al. 1988, Bhatkar & Vinson 1987) compared with only 40-80 mounds per hectare for monogyne colonies (Vinson & Sorensen 1986, Porter & Tschinkel 1987). Such high densities are a problem in parks, campgrounds, yards, and some agricultural crops (Lofgren 1986). The presence of polygyne colonies also appears to have a serious effect on the diversity of native animals including arthropods (Porter & Savignano 1990) and vertebrates (Lofgren 1986, Masser & Grant 1986, Sikes & Arnold 1986).

The objective of this survey was to study the distribution and abundance of polygyne *S. invicta* colonies. We were particularly interested in the extent and pattern of this distribution in relation

to geography and habitat. Information concerning the distribution and abundance of polygyne colonies aids management programs because the presence of polygyne colonies can affect the type of control, the duration of control, and rates of bait application (Glancey et al. 1987, Drees & Vinson 1990). This survey also establishes a base line that will eventually allow us to determine if the polygyne form is spreading in Texas and how rapidly this change might be occurring. It also provides a basis for comparing *S. invicta* populations in North and South America (S. D. Porter, H. G. Fowler & W. P. MacKay; unpublished data).

### Materials and Methods

This project was a joint activity of the Texas Department of Agriculture, the University of Texas, and Texas A&M University. The Texas Department of Agriculture provided the field inspectors, and the two academic institutions cooperated in project design, training, and data analysis.

**Site Selection.** This survey included 122 Texas counties within the fire ant quarantine area as well as 46 uninfested counties along the western front and in western Texas. Four sites were surveyed in each of the infested counties (one in each corner). Five sites were surveyed in each of the uninfested counties (one in the middle and one in each corner). Nonurban sites were selected in advance using county maps. Generally, they were 0.32 km (0.2 mi) from a major intersection. If a preselected site proved inappropriate (e.g., a parking lot or a bridge), the inspectors moved 0.32 km farther down the road and tried again. Sample sites were marked on a map with appropriate directions so that the gen-

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eral area could be revisited. Samples were taken along the rights-of-way of public roads. Rights-of-way were used because they were appropriate *S. invicta* habitat, they had structurally similar vegetation, they were convenient, and they helped to standardize sampling efforts from county to county. Before the survey, the inspectors spent 3 h learning to collect data in a standard manner and another 2 h doing a practice field survey. To further aid consistency, inspectors worked in teams of two for the first week so they could check each other's methods.

**Habitat Data.** Inspectors collected habitat information for each site on a standard data sheet. Vegetation in the surrounding area was categorized into 13 vegetational types: swamp (0.1% of sample sites), forest (9.9%), mixed bushes and trees (26.3%), tall bushes (0.4%), low bushes (0.9%), tall grass (1.3%), rangeland (17.6%), pasture (27.4%), cultivated field (10.5%), residential (2.1%), parkland (0.5%), commercial (2.4%), and other (0.5%). The average height of grass along the rights-of-way was estimated at  $17 \pm 10$  cm ( $\bar{x} \pm SD$ ). (Means are shown  $\pm SD$  unless otherwise indicated.) About 80% of the sites had at least some trees nearby with an average height of  $9.3 \pm 4.8$  m. The percentage of bare ground along roadsides was tallied into seven categories: 0, 10, 25, 50, 75, 90, and 100%. Most sites had a heavy ground cover; 93% had 10% or less bare ground. Inspectors rated the grade of the road as level at 22% of sites, slight at 54%, moderate at 22%, and hilly at only 3% of sites. Several soil characteristics were measured. The inspectors rated soil at 25% of the sites as dry (0), 43% as slightly moist (1), 22% as moist (2), and 10% as wet (3). Thirty-six percent of sites had no rocks, 54% had small rocks (<5.1 cm) and 10% had larger rocks. Inspectors rated 17% of sites as sandy, 25% as sandy loam, 15% as clay, and 12% as clay-loam. Almost 20% were rated as loam and 7% as sandy clay. Soil determinations should be considered approximate because the inspectors were not formally trained in soil tests. Also, it should be pointed out that soil along rights-of-way is frequently hauled in during construction. Weather data for each county were obtained from the Texas almanac (Anonymous 1987).

**Mound Densities.** Mound densities were determined from four belt transects, two on either side of the road. One transect on each side was along the outer border of the mowed area; the other was on the inner border adjacent to the road. Each transect was 70 paces long. All active mounds within reach of a 1.2-m stick were tallied according to their approximate diameter ( $\leq 30$ ,  $\leq 60$ ,  $> 60$  cm). The pace and reach of each inspector were determined and used to calculate the area they sampled. The average inspector had a reach of 2.6 m and a pace of 0.70 m, which averaged 127 m<sup>2</sup> per transect or 0.051 ha per site. Repeat measurements of each inspector's pace and reach indicated that areas sampled varied by  $13 \pm 11\%$ .

**Polygyny and Monogyny.** Polygyne colonies were detected by removing several shovels of dirt from a mound and scattering them across a plastic sorting sheet (1.2 by 0.7 m). Mound soil was carefully inspected for wingless queens. If they were present, three to six were collected and preserved in alcohol. For each mound, the abundance of female alates, male alates, sexual brood, and worker brood were scored using four categories: 0, none; 1, few; 2, moderate; 3, abundant. Scores for each group were averaged to produce abundance indices. Several dozen workers were collected from each mound by burying a 20-ml scintillation vial up to its lip in mound soil. The inside rim of this vial was coated with Fluon (ICI United States, Wilmington, Del.) so that workers falling inside could not escape. If wingless queens were not found in the first three mounds inspected, two or three additional mounds were also examined at each site. If at least three mounds were not available at the sample site, this was noted and the inspectors searched another mile or so down the road to find *S. invicta* mounds.

Preserved queens were later dissected to determine if their spermathecae were filled with sperm. Sites were declared to be polygyne if at least one colony contained two or more inseminated queens. Previous studies have repeatedly demonstrated that almost all inseminated queens in polygyne colonies lay viable eggs (Vargo & Ross 1989) and contribute to brood production (Ross 1988). Sites were considered possibly monogyny if all colonies contained zero or only one inseminated queen. The designation of monogyny was more difficult because the single mother queen is more difficult to find.

**Foraging Activity.** Baits provided an estimate of general *S. invicta* activity and its effect on the native ant community. The bait survey was conducted by setting out 16 baits (sliced hotdogs) at 10-pace intervals, 8 on each side of the road. Locations of the baits were marked with wire plot flags. Baits were left out for 40–60 min, then were inspected for the presence of imported fire ants and native ants. Native ants were not identified to species, but the inspectors did estimate how many "kinds" of ants they observed at a site. Inspectors were trained to distinguish imported fire ants from native ants. A laboratory test indicated that their determinations were >95% accurate. The number of ants on each bait was tallied into approximate categories (e.g., 0, 5, 10, 20, 50, 100, or 200 individuals). Ground temperature (5 cm deep) was measured at two locations for each site so that foraging activity could be adjusted for temperature (Porter & Tschinkel 1987).

**Sample Periods.** The main sampling period was between mid-March and July 1988. To improve the chances of finding queens, sampling was not conducted on rainy days or during unusually cold periods. Each site required  $\approx 80$  min. We attempted to do most of the sampling in the spring because this is the season when fire ants are most active in their mounds. Eighty percent of the counties were

sampled by the end of May. After the end of May, hot, dry soil conditions often make sampling less than ideal. To evaluate the reliability of the main sample, we resampled 14 counties during the fall of 1988 (October–December) and another 30 in the spring of 1989 (March–May). We also sampled 22 outlying locations missed during the main sampling period.

Statistical analyses were done using StatView 512 (Feldman et al. 1987) computer software. Data were analyzed using a combination of linear regression, multiple regression, one-way ANOVAs, contingency tables, and a paired *t* test.

Preserved samples from each site have been deposited in the entomology collection at Texas A&M University, College Station (main samples), and Brackenridge Field Laboratory, Austin, Tex. (resamples). Copies of all maps, data sheets, dissection tallies, and computer data files (90-mm floppy disks) have been deposited at both institutions. These data and specimens are freely available for future studies should the need arise.

## Results

**Density and Distribution.** Imported fire ants infest approximately the eastern third of Texas (Fig. 1). They were ubiquitous within the central core of this infestation from Panola (A) to Kerr (B) to Nueces (C) counties. Infested sites in Texas averaged  $510 \pm 440$  mounds per ha. Two bands of high density are evident in Fig. 1: One band runs northeast from Guadalupe County (D) to Panola County (A); the other band runs parallel along the coast. Two pockets of low density are evident: One is north of Beaumont around Tyler, Jasper, and Newton counties (E). The other pocket (F) is along the southwestern front between San Antonio and Corpus Christi. Densities appear to be relatively low in the Dallas–Fort Worth area (G) in spite of the fact that *S. invicta* has been in this area for more than 30 yr. We compared the distribution of fire ants shown in Fig. 1 with USDA quarantine maps for the years 1953, 1958, 1959, 1964, 1972, 1975, 1982, 1987, and 1988 (also see Cokendolpher & Phillips 1989). The pattern of occupied sites roughly corresponded to the 1982 map, indicating that after a county is quarantined, a number of years are required before roadsides become generally infested.

About 117 sites without *S. invicta* were found inside the quarantine area, primarily along the northern and western borders. None of the 215 sites outside the quarantine area contained imported fire ants. Native fire ants were collected at 35 (11%) of the uninfested sites. Northern and western *Solenopsis* collections were mostly *S. xyloni* McCook; the extreme southern ones were probably *S. geminata* (F.). Native fire ants were found at only 3 (0.8%) of the 376 infested sites and all were along the outer margin of the infestation (Fig. 1). No native fire ants were found in the central core of

the infestation, even though they were formerly common in this region (Hung & Vinson 1978).

Mound densities at infested sites were weakly correlated (simple regression) to several climatic, geographic, and habitat variables; significance levels were  $P < 0.001$  or better because of the large sample size ( $n \geq 360$ ). Positive correlations included: mean annual precipitation ( $r^2 = 0.038$ ), longitude ( $r^2 = 0.031$ ), mean minimum temperature in January ( $r^2 = 0.071$ ), and length of growing season ( $r^2 = 0.085$ ). Mound densities were negatively correlated with soil temperature at 5 cm ( $r^2 = 0.113$ ), rock size ( $r^2 = 0.044$ ), mean maximum air temperature in July ( $r^2 = 0.030$ ), and the percentage of bare ground ( $r^2 = 0.042$ ).

A stepwise multiple regression of mound density (*y*) on the presence of polygyny and the variables described above explained 39% of the variation between sample sites ( $R^2 = 0.389$ ;  $F = 58.2$ ;  $df = 4, 355$ ;  $P < 0.0001$ ):  $\log y = 1.09 + 0.34a + 0.012b + 0.004c - 0.007d$ . Polygyny (*a*) was by far the most important factor, explaining 26% of the variation, followed by an additional 6% for precipitation (*b*), 6% for plant growing season (*c*), and 1% for soil temperature (*d*). The addition of precipitation to the model eliminated the significance of other variables associated with western locations including longitude, rock size, and mean maximum temperature in July. Growing season had a similar effect on the value of mean minimum temperature in January. Soil temperature added a small amount to the model, probably because mound densities tend to decline somewhat during hot weather.

Several factors were not correlated with mound density (simple regression,  $P > 0.05$ ) including: "height of grass along the right-of-way" ( $r^2 = 0.0$ ), grade of the road ( $r^2 = 0.001$ ), soil moisture ( $r^2 = 0.017$ ), and latitude ( $r^2 = 0.007$ ). Similarly, mound density did not vary significantly with soil type (ANOVA;  $F = 0.5$ ;  $df = 5, 347$ ;  $P = 0.75$ ). Within sites, we found that mound densities along the edge of the road were not significantly different from those along the outer border of the mowed area (Paired *t* test;  $t = 1.55$ ;  $df = 117$ ;  $P = 0.12$ ; spring 1989 only). Also, the direction of the road did not affect the total number of mounds at a site or how many mounds were on one side of the road or the other (ANOVA on difference between sides;  $F = 2.24$ ;  $df = 3, 94$ ;  $P = 0.09$ ; spring 1989 only). In other words, gross differences in solar exposure resulting from changes in direction were not found to affect the density of *S. invicta* mounds along Texas roadsides.

**Polygyny.** Polygyne *S. invicta* colonies were very common in Texas (Fig. 2). Polygyny was confirmed at 54% of the preselected sample locations that were infested; the remaining locations were designated monogyne (44%) or were eliminated because of questionable data (2%). Polygyny was scattered from one end of Texas to the other, including several outlying sites in western Texas. The areas around Atascosa County (A) and Jasper County (B)

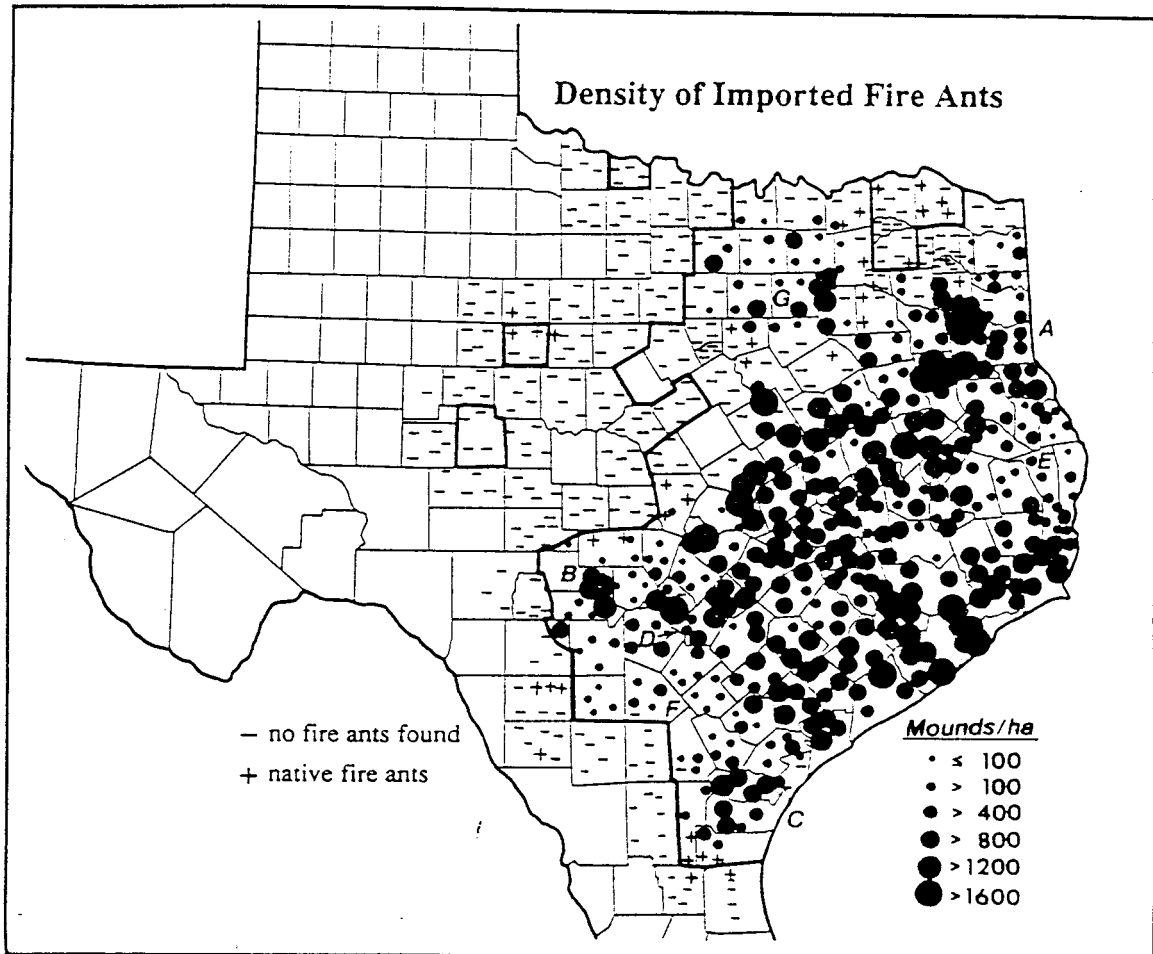


Fig. 1. Density of *S. invicta* at  $\approx 700$  preselected sites in Texas. The area of the circles is proportional to mound density. The heavy black line encloses counties included in the 1988 quarantine area. Capital letters are explained in results section.

were primarily monogyne. We also discovered polygyne *Solenopsis xyloni* colonies at 2 of 14 sites where colonies were examined (Hunt and Taylor counties).

Polygyny in *S. invicta* was associated with much higher nest densities (Fig. 3). Approximately 60% of polygyne sites contained 500 or more mounds per ha compared with only 10% of monogyne sites. Overall, polygyne sites averaged  $680 \pm 475$  mounds per ha, whereas monogyne sites averaged  $295 \pm 240$  mounds per ha (ANOVA:  $F = 131$ ;  $df = 1, 518$ ;  $P < 0.0001$ ; data were normalized with a log transformation). Comparison of Fig. 1 and 2 shows that areas of high mound density were generally polygyne, whereas areas of low mound density were frequently monogyne. The size distributions of mounds in polygyne and monogyne areas were very similar (Fig. 4), although polygyne sites had a slightly higher percentage of small mounds (ANOVA:  $F = 6.9$ ;  $df = 1, 518$ ;  $P = 0.009$ ).

Mound densities at polygyne sites were well

within the range reported in other studies (Lofgren & Williams 1984, Glancey & Lofgren 1988, Porter et al. 1988); however, densities at monogyne sites were considerably higher than generally reported for the monogyne form (e.g., Vinson & Sorenson 1986, Porter & Tschinkel 1987). Part of the reason for this difference is that some sites designated as monogyne were probably polygyne (see resamples). A second reason is that fire ants are probably naturally dense along roadsides because of an edge effect. A third reason is that our sampling method may have overestimated roadside densities if colonies tend to aggregate along borders of rights-of-way. Although such a bias would not affect the internal consistency of this study, care should be taken when comparing this study with those using different sampling methods.

Colonies at polygyne sites appeared to contain considerably fewer winged queens (Fig. 5; ANOVA:  $F = 79.7$ ;  $df = 1, 500$ ;  $P < 0.0001$ ) and winged males (ANOVA:  $F = 54.6$ ;  $df = 1, 499$ ;  $P < 0.0001$ ),

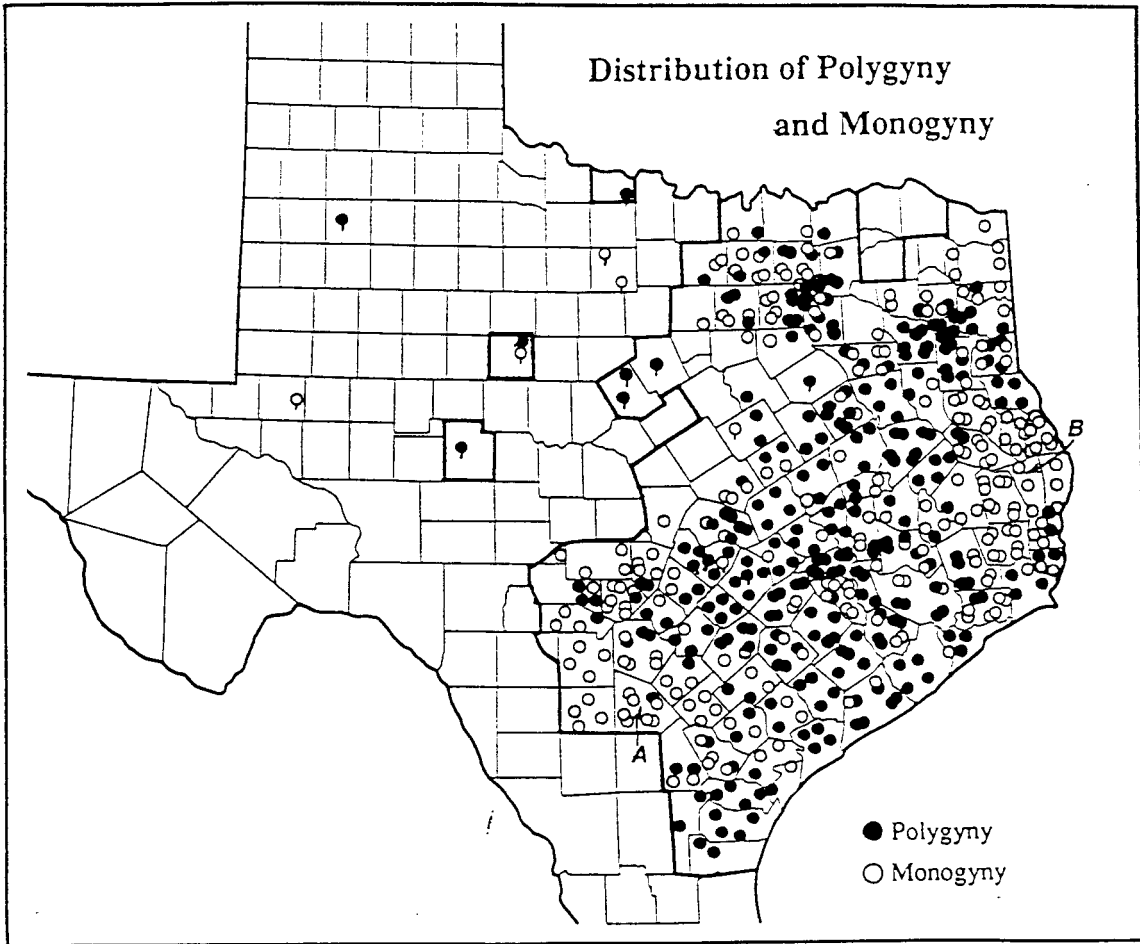


Fig. 2. Distribution of sites with polygyne and monogyne colonies of *S. invicta* in Texas. "Underlapping" circles indicate results from fall 1988 or spring 1989 resamples. Capital letters indicate concentrations of monogyny. Circles with a tail are supplemental samples, mostly from isolated infestations missed by the general sampling procedure (Fig. 1).

a phenomenon previously reported by Vargo & Fletcher (1987). In contrast, worker brood was rated less abundant in monogyne colonies (ANOVA;  $F = 20.6$ ;  $df = 1, 505$ ;  $P < 0.0001$ ), indicating that sexual production may be achieved at the expense of worker production.

Polygyne colonies were not associated with any particular types of habitat except they were 50% less common than expected along roadsides surrounded by forests ( $\chi^2 = 16$ ;  $df = 1$ ;  $P < 0.001$ ). This negative association was restricted to forests in far eastern Texas (Fig. 2, location B). Polygyny was not significantly correlated with longitude, latitude, precipitation, maximum temperature in July, or the height of grass along the right-of-way. However, polygyne areas did tend to have a slightly longer plant growing season ( $256 \pm 2$  ( $\bar{x} \pm SE$ ) versus  $267 \pm 2$  days; ANOVA;  $F = 23.2$ ;  $df = 1, 362$ ;  $P < 0.0001$ ). The distribution of polygyne fire ants (Fig. 2) was compared with old USDA quar-

antine maps, maps of past eradication efforts, as well as vegetational maps and soil maps for the state of Texas. No general patterns could be discerned between these maps and the distribution of polygyne *S. invicta* colonies.

Dealate queens collected in fall 1988 and spring 1989 resamples were dissected to determine what percentage were inseminated and what percentage had intact wing muscles (Table 1). Almost all of the inseminated queens had degenerated wing muscles. Most of the uninseminated queens in polygyne colonies also had degenerated wing muscles, indicating that they had not been adopted into the colony recently. At least some of the uninseminated queens with intact wing muscles were dealated mechanically during excavation; however, others may have dealated naturally. The designation of polygyne sites was generally quite certain. We obtained two or more polygyne colonies from 72% of the polygyne sites that were sampled. Overall, 80

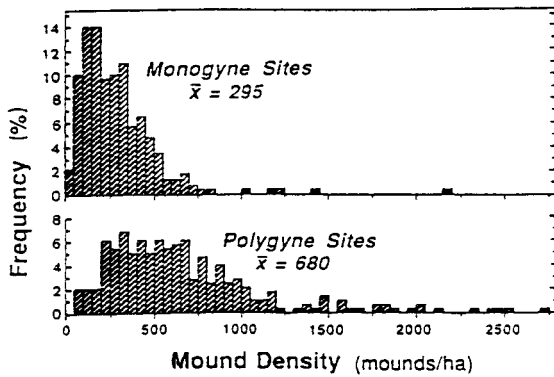


Fig. 3. Frequency distribution of *S. invicta* mound densities at monogyne sites ( $n = 236$ ) and polygyne sites ( $n = 284$ ).

$\pm 20\%$  of colonies at polygyne sites were confirmed as polygyne.

The designation of monogyne sites was less certain. The inspectors were not able to discover dealate queens in  $\approx 70\%$  of 350 colonies examined at monogyne resample sites. A single inseminated queen was found in 15% of the colonies. Uninseminated queens with degenerated wing muscles were collected from 5% of colonies at monogyne sites. None of these colonies contained an inseminated mother queen, indicating she may have died, thus permitting the winged virgin queens in the colony to dealate (Fletcher & Blum 1983). About 10% of colonies contained uninseminated dealate queens with intact wing muscles. The origin of these queens may be similar to those in polygyne colonies. Two inseminated queens with intact muscles were found in what was probably a monogyne mound; their origin is uncertain, but they may have been accidental captures of claustral founding queens.

**Baits.** Imported fire ants thoroughly dominated baits at the infested sites, accounting for  $90 \pm 22\%$  of the occupied baits. The more mounds present, the greater the dominance of occupied baits ( $\log(y + 1) = 6.3 + 32x; r^2 = 0.31; F = 155; df = 1, 349; P < 0.0001$ ); for example,  $97 \pm 8\%$  of occupied baits at sites with  $>400$  mounds per ha were *S. invicta*. The percentage of baits occupied by ants *invicta* was much higher in infested areas than in uninfested areas ( $81 \pm 1$  versus  $39 \pm 4\%$ ; ANOVA;  $F = 164; df = 1, 452; P < 0.0001$ ). Within infested areas, higher mound densities also resulted in higher percentages of baits being occupied ( $\log(y + 1) = 21 + 23x; r^2 = 0.12; df = 1, 354; F = 47; P < 0.0001$ ). The average number of ants estimated on occupied baits in infested areas  $\pm SE$  was about  $100 \pm 3$  compared with  $60 \pm 7$  in uninfested areas (ANOVA;  $F = 20; df = 1, 418; P < 0.0001$ ). High densities of *S. invicta* mounds were also associated with a reduction in the number of other kinds of ants visiting the baits (Fig. 6;  $r^2 = 0.18; F = 85; df = 1, 399; P < 0.0001$ ).

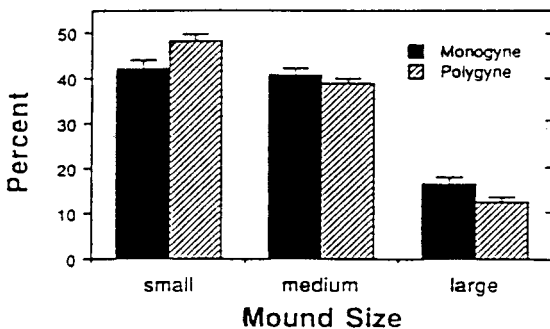


Fig. 4. Percentage distribution of small ( $\leq 30$  cm), medium ( $\leq 60$  cm), and large ( $> 60$  cm) *S. invicta* mounds among monogyne sites and polygyne sites. Error bars show standard errors of the mean.

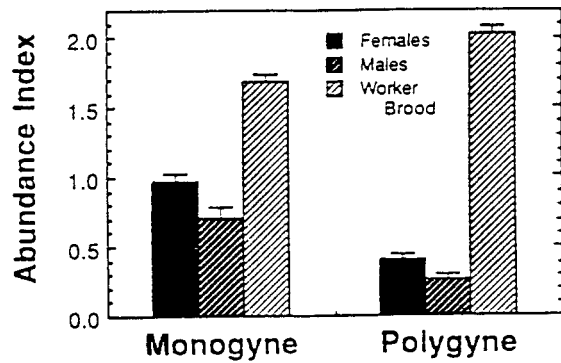


Fig. 5. Abundance index of male reproductives, female reproductives, and worker brood in monogyne and polygyne colonies of *S. invicta*. Error bars show standard errors of the mean. The index for colonies at each site was the average score of four categories: 0, none; 1, a few; 2, moderate; and 3, abundant.

**Resamples.** We resampled a total of 142 sites in 44 counties. Sample sites were not permanently marked, and directions to these sites were not always as specific as desirable; consequently, most resamples were not taken at exactly the same site as the original sample. Inspection of locality records indicated 50 resamples were "near"; that is, they were taken within 0.16 km (0.1 mi) of the original site. Another 35 resamples were "distant"; that is,

Table 1. Percentage of dealate queens collected from the 96 polygyne sites (892 queens) and 70 monogyne sites (176 queens) displayed according to insemination status and condition of wing muscles, fall 1988 and spring 1989

Sites	Inseminated		Uninseminated	
	% De-generated wing muscles	% Intact wing muscles	% De-generated wing muscles	% Intact wing muscles
Polygyne	82.3	0.6	14.0	3.1
Monogyne	30.1	1.1	18.8	50.0

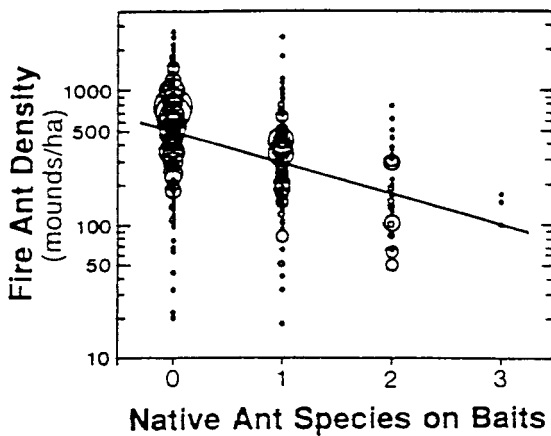


Fig. 6. Association between the number of kinds of native ants (species) found near baits and the abundance of *S. invicta* mounds at infested sites. Note that mound densities are plotted on a log scale. The size of circles is proportional to the number of observations: ( $n = 224$  (0 species),  $n = 128$  (1 species),  $n = 45$  (2 species),  $n = 3$  (3 species)).

they were taken at locations 1.6–8.0 km (0.5–5.0 mi) from the original site. The remainder of the resamples (57) were within several miles of the original site, but exactly how close was difficult to determine.

For the "near" resamples, we found that 77% of monogyne sites (20/26) and 87% of polygyne sites (21/24) did not switch categories ( $\chi^2 = 20.9$ ;  $df = 1$ ;  $P < 0.0001$ ). In other words, there was a strong tendency to retain the original designations upon resample. Nevertheless, 18% of sites did switch designations, apparently due to small differences in sample location or errors in designating sites as monogyne. More sites switched from monogyne to polygyne (six) than the converse (three), but this was not significant ( $\chi^2 = 0.77$ ;  $df = 1$ ;  $P > 0.10$ ). "Distant" sites also had a significant tendency to retain their original designation; 65% of monogyne sites (15/23) and 85% of polygyne sites (11/13) did not switch ( $\chi^2 = 8.3$ ;  $df = 1$ ;  $P < 0.004$ ). In other words, distant sites were about as likely to switch designations as near sites, probably because of regional consistency in the frequency of polygyne. For near resamples, mound density in the first sample predicted 56% of the variation in mound density of the second sample ( $F = 62.9$ ;  $df = 1, 49$ ;  $P < 0.0001$ ), but this correlation dropped to only 5% for distant resamples ( $P > 0.05$ ).

### Discussion

Most of Texas roadsides (54%) were infested by the polygyne form of the *S. invicta* (Fig. 2). Polygyne is about three times as common in Texas as it is in the other southeastern states (S.D.P., unpublished data). The reason Texas has so many polygyne sites is currently unknown. Perhaps the

original stock of ants invading the state was primarily polygyne, or perhaps the polygyne form is in the process of a secondary invasion. It is also possible that environmental conditions in Texas naturally favor polygyne. Certainly, polygyne is common among native Texas fire ants (Summerlin 1976; Porter et al. 1988; also see results section). Whatever the reason, the high frequency of polygyne in Texas is a matter of serious economic and environmental concern (Porter & Savignano 1990).

Monogyne and polygyne fire ants appear to form a mosaic across the state (Fig. 2). Local sites generally contain only one form or the other rather than an interspersed mixture of both (Mirenda & Vinson 1982, Greenberg et al. 1985, Porter et al. 1988). The two forms are probably incompatible because polygyne supercolonies overwhelm neighboring monogyne colonies and absorb or kill founding monogyne queens. Explaining the patchwork nature of the mosaic on a larger scale is more difficult. One possibility is that the mosaic has resulted from numerous independent switches from monogyne to polygyne or even the reverse. However, most *S. invicta* populations in the United States have remained exclusively monogyne for  $\geq 30$  yr; in other words, the change from one form to the other does not occur sufficiently frequently in most areas to account for the mosaic. A second possibility is that the two forms are segregated according to habitat type. Polygyne colonies were less common than expected along roadsides surrounded by forests, but this was only in one area of the state (Fig. 2, location B); in other areas of the state, the frequency of polygyne was not associated with the surrounding vegetation. Similarly, we did not find associations between polygyne and soil type, climatic conditions, topography, percentage ground cover, and solar orientation. In short, environmental factors measured in this survey were not useful in predicting the overall distribution of polygyne and monogyne populations in Texas. The third, and perhaps most likely, explanation is that the mosaic is a historical result of the invasion process. The patchwork distribution of the two forms may have resulted from haphazard natural dispersal and human transport back and forth across the state.

Hölldobler & Wilson (1990) propose that polygyne ant species are usually associated with ephemeral nest sites, scarce nest sites, or stable habitats with a patchy distribution. Polygyne fire ants in Texas do not fit any of these categories. Suitable nesting sites are definitely neither ephemeral nor scarce. Polygyne fire ants do occupy stable habitats, but their distribution in Texas is much more expansive than patchy. Distributions in other states are patchy but they are not associated with unusually stable habitats. Distributional patterns of polygyne fire ants in South America have not been determined.

Long-term population trends of the polygyne form in Texas are unknown. Populations around

Austin, Tex., have probably been polygyne since the original invasion  $\approx 10$  yr ago. However, the general impression of researchers in College Station is that polygyne colonies have become more common in their area over the past 10–15 yr. Researchers in Gainesville, Fla., also report that polygyny is becoming more common in certain parts of their state (Glancey et al. 1987). Future surveys will be necessary to determine if polygyne populations in Texas are still increasing or if they have stabilized.

Mounds of monogyne and polygyne forms were slightly less dense in the drier and the cooler portions of Texas (see stepwise regression), but the correlation was very weak. In other words, climatic conditions in Texas do not appear to be a major stress factor for fire ant populations, at least for sites that are already infested.

Colonies at polygyne sites exhibited a number of characteristics commonly associated with polygyny. For instance, the frequency of winged sexuals was much lower in polygyne colonies (Fig. 5). Apparently, large numbers of fertile queens in polygyne colonies suppress the development of sexual brood (Vargo & Fletcher 1986). We also found that 17% of the dealate queens in polygyne colonies were not inseminated (Table 1), a figure somewhat lower than the 25–30% reported by Vargo & Fletcher (1989) but almost the same as those reported by Miranda & Vinson (1982). Glancey & Lofgren (1988) reported that large numbers of newly inseminated queens appear in colonies shortly after mating flights. Only a small fraction of inseminated queens in our samples had intact or largely intact wing muscles (0.6%), perhaps because these queens were taken before and after the normal season for mating flights (i.e., March–April and October–December).

High mound densities were the most important characteristic of polygyne sites. Polygyne sites averaged more than twice as many mounds per ha as monogyne sites (Fig. 3). This difference might have been even greater except that some sites designated as monogyne may actually have been polygyne (see resamples). We found that the size distribution of mounds in polygyne and monogyne areas was quite similar (Fig. 4). In other words, the high densities of mounds at polygyne sites were not simply a result of polygyne mounds being smaller and more numerous.

Polygyne fire ants are a serious environmental concern because high densities of this form threaten native animal communities (Porter et al. 1988). We found that imported fire ants thoroughly dominated baits at infested sites. The more *S. invicta* mounds present at sample sites, the more baits that were occupied and the fewer kinds of native ants that were present (Fig. 6). The overall effect of a polygyne invasion can be rather severe. Porter & Savignano (1990) reported that polygyne fire ants decimated the native ant community at a research station in central Texas. They also reported that the total number of fire ants at infested sites was

10–30-fold greater after the invasion than all of the native ants had been before the invasion.

Polygyne fire ants can also disrupt human activities. Polygyne colonies can cause considerably more problems in recreational areas and peoples' back yards simply because they are so abundant. Increased damage should also be true for crops and livestock. However, polygyne fire ants may benefit sugarcane (Long et al. 1958) and cotton production (Jones & Sterling 1979) by providing more effective control of major arthropod pests. Polygyny probably also provides more thorough control of the lone star tick (Harris & Burns 1972, Fleetwood et al. 1984).

The presence of polygyne colonies is important information for designing effective management programs. Mound-by-mound control efforts (e.g., drenches and mechanical devices) are not very effective with polygyne colonies because high mound densities make their use extremely time consuming and not very cost-effective (Drees & Vinson 1990). Furthermore, mound-by-mound treatments usually miss the cryptic satellite colonies associated with polygyne colonies (Bhatkar & Vinson 1987). Polygyne colonies may also require higher application rates of poison baits to achieve satisfactory control (Glancey et al. 1987) (note that label restrictions should be heeded). Another problem is that polygyne colonies spread primarily by budding (Porter et al. 1988, Vargo & Porter 1989). This means that attempted control of polygyne fire ants in small areas (<0.2 ha) may be rather difficult because small areas may be quickly reinvaded by buds produced from surrounding untreated colonies. On the other hand, control of large polygyne areas (>5 ha) may actually be more effective because polygyne colonies appear less capable of independent colony foundation (Porter et al. 1988), and reinvasion by budding would be relatively slow. Another problem is that polygyne colonies are probably more likely to be spread in sod or nursery stock because colony fragments and satellite colonies are much more likely to contain fertile queens. A final consideration is that landowners in Texas with monogyne fire ants might want to consider living with their problem rather than risk the possibility of a polygyne reinvasion.

In summary, polygyne *S. invicta* colonies were very common throughout Texas. The frequency of polygyny varied somewhat in different regions of the state, but polygyny was poorly correlated with environmental conditions. As expected, polygyne sites had very high mound densities. The higher the density of fire ants, the greater the potential for environmental and economic damage. The high frequency of polygyny in Texas indicates that large areas of this state have especially severe fire ant problems.

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