

Sympatry of Polygyne and Monogyne Colonies of the Fire Ant *Solenopsis invicta* (Hymenoptera: Formicidae)

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ABSTRACT The polygyne form of the red imported fire ant, *Solenopsis invicta* Buren, is thought to occur primarily in discrete populations embedded within areas composed of monogyne colonies. This distribution implies that polygyne colonies compete with monogyne colonies and subsequently create a population homogenous in social form. Because polygyne colonies produce mostly sterile males, opportunities for insemination of female alates might be minimal at the centers of large polygyne areas. To test for homogeneity in social form, a large polygyne population described in northcentral Florida was examined for the presence of single queen colonies. Forty-six to 51 colonies were sampled from each of six sites located along an east-west transect through the middle of the polygyne area in Marion County and a site at the northernmost limit of the polygyne area, Gainesville, FL. Several hundred workers from each nest were collected along with nest material. The social form of each sample was determined by an aggression test of workers to the introduction of non-nestmates and by the dissection of males for sterility. Both social forms of *S. invicta* were present at all collection sites and 103 of 333 (30.93%) colonies sampled were determined to be monogyne colonies. Among the collection sites, the percentage of colonies that were monogyne ranged from 3.9 to 57.4%. The polygyne region in northcentral Florida is more accurately described as an area where relatively high frequencies of polygyne colonies are interdispersed with single queen colonies.

KEY WORDS *Solenopsis invicta*, red imported fire ant, sympatry, distribution, polygyne

THE RED IMPORTED FIRE ANT, *Solenopsis invicta* Buren, is thought to have been introduced into the United States during the late 1930s via ballast discharges from ships arriving to the port of Mobile, AL, from South America (Lofgren et al. 1975, Lofgren 1986). Within 20 yr after its introduction, *S. invicta* became the dominant ant species in this region (Lofgren 1986). Concurrently, the ant was spread throughout most of the Southeast via transport by humans (e.g., nursery stock), where it has become the dominant species in many areas (Ross et al. 1987; Porter et al. 1988, 1991; Porter 1992; Wojcik 1994). Numerous studies on the basic biology, behavior, and control of the red imported fire ant followed its introduction, and the only social form reported for this species was single queen colonies ("monogyne") (Wilson 1951, 1962, 1971; Wilson and Brown 1958; Lofgren et al. 1975; Lofgren 1986). In the early 1970s, however, multiple queen colonies (polygyne) were reported from Mississippi and Georgia (Glancey et al. 1973, 1975; Hung et al. 1974). Within approximately a decade after these reports, patches of polygyne colonies were found in many other areas of the Southeast, including Louisiana, Florida, Arkansas, Alabama, Oklahoma, and Texas

(Fletcher et al. 1980; Mirenda and Vinson 1982; Lofgren and Williams 1984; Ross and Fletcher 1985a; Glancey et al. 1987, 1989).

The relatively sudden appearance of multiple, disjunct patches of polygyne colonies in the Southeast suggest that this social form of *S. invicta* is quite vagile. Studies on the density and distribution of polygyne colonies in the Southeast have implied or stated that certain areas are now exclusively inhabited by polygyne colonies (Porter et al. 1991, Porter 1992, Ross and Fletcher 1985a, Ross and Shoemaker 1997). Although both forms differ substantially in behavior, physiology, and growth rates, monogyne and polygyne colonies appear to occupy identical ecological niches. Thus, the subsequent "expansion" of polygyne populations over broad geographic regions soon after this social form was first reported in the mid-1970s has implied a concomitant reduction of monogyne colonies (Fletcher et al. 1980, Glancey et al. 1987, Porter et al. 1991). The manner in which polygyne colonies establish in a particular region and whether polygyne populations truly expand their range appreciably through time is not clear. Genetic studies indicate low vagility for this social form (Ross and Shoemaker 1997), and the only long-term studies that have monitored polygyne distribution indicate that polygyne patches expand too slowly to account for their present distribution (Porter et al. 1988, Greenberg et al. 1992, Porter 1993).

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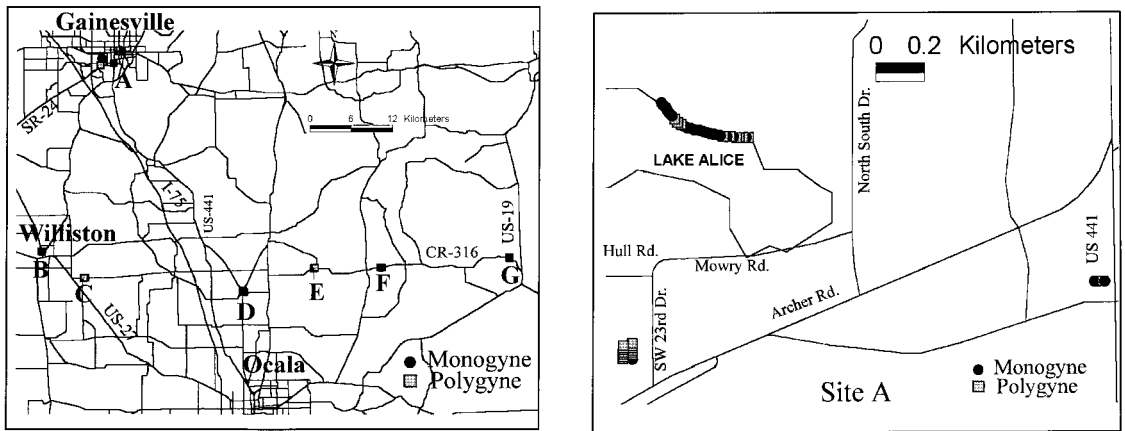


Fig. 1. Location of seven collection sites of *S. invicta* in northcentral Florida. Sites B through G were located along an east-west transect bisecting the center of the polygyne population. Three locations where colonies were collected in site A are shown at right; shaded squares and filled circles show colony distribution for each social form.

The first report of polygyne colonies in Florida was at the University of Florida, Horse Research Center located in Marion County, 16 km north of Ocala (Lofgren and Williams 1984). Three years later, Glancey et al. (1987) reported polygyne colonies in seven other counties including Marion, Alachua, and Levy in northcentral Florida. This region of Florida was subsequently shown to include one of the largest polygyne patches of the red imported fire ant in the United States (Porter 1992, 1993), encompassing $\approx 2,900 \text{ km}^2$. Porter (1992) designated colonies as polygyne, if more than two inseminated queens could be found, or monogyne, if a single highly physogastric queen was found (Porter 1993). If no queens could be found at a site, then sites were classified as probable monogyne or polygyne based on worker size (Greenberg et al. 1985) and amount of sexual brood (Vargo and Fletcher 1987). A maximum of five colonies were sampled per site, but sampling was halted if the first two colonies sampled were determined to be polygyne (site classified polygyne) or if the first two colonies (Porter 1992) or one colony (Porter 1993) sampled were designated as monogyne (site classified monogyne). Porter (1992, 1993) concluded that the geographic pattern of *S. invicta* occurrence in northcentral Florida was a mosaic of discrete polygyne and monogyne populations. A similar exclusion of monogyne colonies from polygyne areas has been noted in Texas (Porter et al. 1991) and Georgia (Ross and Fletcher 1985a, Ross and Shoemaker 1997).

Empirical evidence from allozymes (Ross 1992) suggests that polygyne populations depend on fertile males from monogyne colonies (Ross and Shoemaker 1993, Shoemaker and Ross 1996). In Georgia, where the population dynamics of both social forms has been examined extensively, the relatively small polygyne population is devoid of monogyne colonies, but receives fertile monogyne males from adjacent areas (Shoemaker and Ross 1996, Ross and Shoemaker 1997). It is not clear, though, how very large and

allegedly pure polygyne populations such as those reported in Texas (Porter et al. 1991) and Florida (Porter 1992, 1993) persist without an influx of monogyne males. If these large areas are indeed devoid of monogyne colonies, it suggests that some mechanism other than monogyne males can maintain polygyne.

Although the sampling method used by Porter (1992, 1993) facilitated the designation of almost 200 sites sampled throughout the Southeast as monogyne or polygyne, it did not provide information about the within site monogyne/polygyne structure. The purpose of this study was to determine whether the large polygyne region of Florida was exclusively polygyne, as indicated by Porter (1992, 1993), or harbored low frequencies of monogyne colonies as well. We examined the distribution of both social forms along an east-west transect through the center of the polygyne patch in northcentral Florida.

Materials and Methods

Collection Sites. Six collection sites (sites B through G) were established along an east-west transect in north-central Florida (Fig. 1). This particular transect was chosen for three reasons: (1) it bisected the center of the largest polygyne region known in Florida, (2) it included the eastern and western limits of the known distribution of polygyne nests in this region (Porter 1992), and (3) the collection sites were the same locations as those sampled by Porter (1992, 1993) in his survey of polygyne colony distribution in northcentral Florida (S. Porter, personal communication). A seventh collection site (site A, Gainesville, FL) was sampled at the northernmost edge of the polygyne patch.

Sample Collection. Forty-six to 51 separate colonies of *S. invicta* were sampled at each collection site during the month of July 1999 (Figs. 1 and 2). A total of 285 colonies was sampled among sites B through G and

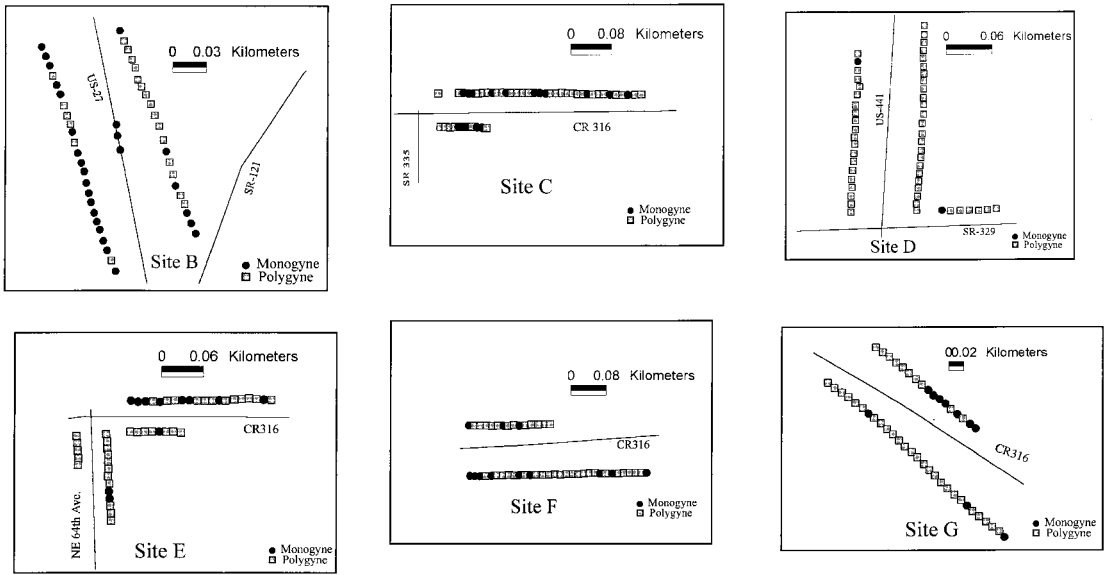


Fig. 2. Location and identity (polygyne or monogyne) of colonies of *S. invicta* collected at six sites in northcentral Florida. Shaded squares and filled circles show colony distribution for each social form.

48 colonies were sampled in areas of southwest Gainesville (site A, Fig. 1; Table 1). Because polygyne colonies may sprawl and form satellite colonies, samples were only considered to be from separate colonies if the distance between mounds was at least 10 m (Vargo and Porter 1989, Macon and Porter 1996). The top portion of a colony was removed using a shovel and ≈ 0.5 liter of soil, including portions of the colony gallery and several hundred workers, were collected from each colony. All workers, together with soil from each nest, were placed in plastic containers (1 liter) and transported to the laboratory for behavioral assays. When males were observed, these were collected and later dissected for the presence of spermatozoa. Sixty males were collected from 20 colonies in six sites.

Table 1. Monogyne and polygyne colonies collected at seven sites in northcentral Florida

Site	Location	Specific area	Monogyne	Polygyne
A	Gainesville	USDA Grounds	1	13
		Rush Lake Motel	4	1
B	Williston	Lake Alice	20	9
		E Highway 27	6	15
		W Highway 27	18	6
C	State Road 316	Median	3	0
		North 316	11	25
D	Hwy 441 & State Rd. 329	South 316	5	6
		North 329	1	6
E	SR 316 & SR 64	West 441	1	19
		East 441	0	24
		South 316	1	8
		North 316	8	12
F	SR 316, Ft. McCoy	West 64	0	5
		East 64	2	10
		South 316	9	23
		North 316	3	12
G	SR 316, Kerr City	South 316	3	26
		North 316	7	10

Determination of Social Form. Social form was determined by an assay quantifying the aggressive behavior of workers toward non-nestmate intruders. A number of studies have demonstrated that workers from polygyne colonies are relatively nonaggressive to conspecifics from foreign colonies, whether intruders originate from polygyne or monogyne colonies (Mirenda and Vinson 1982, Morel et al. 1990, Obin et al. 1993). Morel et al. (1990) demonstrated that this phenomenon was a reliable behavioral means of determining the social form of *S. invicta* colonies collected in the field. In our study, field collected samples of *S. invicta* were tested in an aggression bioassay within 24 h of field collection according to a protocol modified from Morel et al. (1990). All workers and colony material were transferred to porcelain trays (30 by 20 by 5 cm) whose sides were painted with Fluon (ICI, Wilmington, DE). Ants in each tray were then allowed to "settle" for at least 2 h at 26–28°C before testing. The nestmate recognition bioassay (Obin 1986) measured aggression in the context of nest defense. Individual workers (intruders) were allowed to walk onto a pair of forceps and were then allowed to walk off the forceps into trays containing "resident" colonies. Intruder ants for each trial were obtained from several feral polygyne nests (independently confirmed for social form). All polygyne intruders were collected on the same day that they were used, because maintenance of polygyne colonies in the laboratory leads to heightened aggression levels (Obin et al. 1993). In this way, we maximized the difference between the monogyne and polygyne resident responses. Intruder ants were discarded if they showed disturbed behavior before their introduction into the resident colony. Observations were made by an observer wearing a particle or surgical mask to

Table 2. Behavioral units and aggression scores used to assess nestmate recognition (see Obin and Vander Meer 1988)

Score	Behavior response
9	Immediate lunge, grab and sting
8	Opponent surrounded and "held" in mandibles; appendages pulled/bitten off; eventual stinging.
7	Opponent held (as in #8) but released; biting; abdomen-curling (stinging position), but no stinging.
6	As in # 7, but no abdomen-curling.
5	Alarm (running, abdomen elevation and vibration) and recruitment.
4	Mandible gaping; rapid antennation; "sidling" (maintaining a lateral orientation to and slowly circling opponent).
3	Rapid antennation with antennae extended for more than 2 s.
2	Antennation for less than 2 s. If mobile, opponent is followed slowly for several cm; if opponent stationary, worker stops.
1	As in # 2, but opponent does not induce following nor stop.

minimize disturbance by exhalation on the ants. Individual intruders were removed from resident colonies immediately after testing. Additional intruder introductions into any one resident group were spaced at least 15 min apart to allow resident workers to recover from the potential disturbance of the previous introduction.

The resident colony response to each intruder was scored on a scale of increasing aggression behavior (Table 2, Obin and Vander Meer 1988). Because of individual variability of response, we recorded only the most aggressive response observed during an intruder's interaction with 10 resident ants. The 10 interactions usually occurred within 10 min of the intruder's appearance. The observations were terminated if the highest level of aggression was observed before the tenth interaction. Colony workers giving aggression scores of ≥ 7 were designated monogyne, and scores ≤ 4 were designated polygyne. If the aggression score was in an ambiguous range (5-6), the bioassay was repeated. The result of the second aggression bioassay was used to assign colony type (see Morel et al. 1990); in no cases, however, were both scores ambiguous. The observer did not know the collection history of the colony subunits being evaluated.

Because males were encountered during the collection of workers from some colonies, these were dissected for gonadal development as a coarse means of confirming social form assessed by the aggression assay. Sixty males were collected from 20 colonies in six collection sites (one to eight males/colony). Males were dissected to expose the intact aedeagal bladder, accessory glands, seminal vesicles, and testis (Ball and Vinson 1984). Testicular lobes do not develop in sterile diploid males, thus the vasa deferentia is always transparent and devoid of sperm (Hung et al. 1974). Therefore, regardless of the age of the male, it was possible to determine if it was fertile or sterile. Because only polygyne colonies are thought to have high frequencies of sterile diploid males (Ross and Fletcher 1985b, 1986), their presence in a colony was inter-

preted as confirmation of polygyny; colonies with only fertile males could not be determined.

Results

Determination of Social Form. The distribution of initial aggression scores (see Table 2) was bimodal (Fig. 3). There were 22 colonies, however, that initially scored in between the monogyne criteria (≥ 7) and the polygyne criteria (≤ 4). When these 22 colonies were retested, four scored in the monogyne range and the remaining 18 scored in the polygyne range. These combined results were used to designate colonies as either monogyne or polygyne (see Table 2).

For the most part, the dissection of males from 20 colonies was consistent with the determination of social form by the behavioral bioassay. Nine of these colonies were determined to be monogyne based on the aggression test and all but one of the males ($n = 35$) from these colonies were fertile. Seven of the 11 colonies scored as polygyne by the aggression test had one or more sterile males (12 of 25 sterile).

Frequency of Single Queen and Polygyne Colonies. Both social forms of *S. invicta* were present at all collection sites (Table 1; Figs. 1 and 2) and 103 of 333 (30.93%) colonies were determined to be monogyne. Except for site D, in which only 2/51 sampled colonies were monogyne, the percentage of monogyne colonies among the sites ranged from 21.7 to 57.4%.

Sympatry of Single Queen and Polygyne Colonies. Because previous studies have implied that polygyne colonies have an exclusionary effect on the presence of monogyne colonies, we examined within site distribution of both social forms at a gross level. There were sufficient numbers of colonies sampled at two

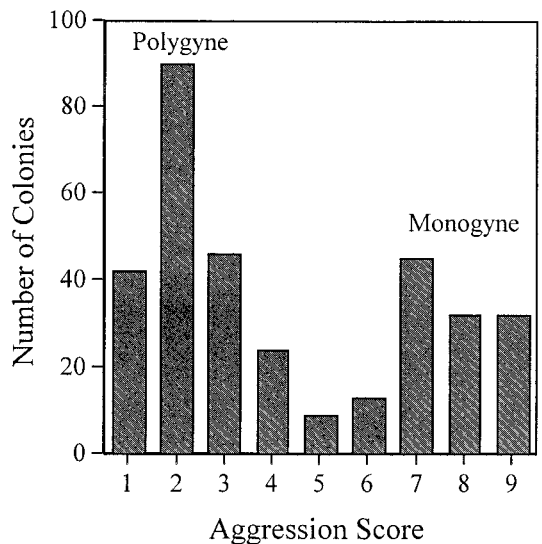


Fig. 3. Frequency histogram of the aggression score for colonies of *S. invicta* sampled in northcentral Florida. Scores ≥ 7 indicate monogyne and scores ≤ 4 indicate polygyne.

Table 3. Contingency chi-square analysis of the frequency of two social forms of *S. invicta* collected from different areas within a collection site

Site	Location	Specific Area	Obs. M	Obs. P	Cont. Chi-Sq.	Prob.
A	Gainesville	USDA	1	13	14.47	<0.01
		Grounds				
B	Williston	Lake Alice	20	9	10.38	<0.01
		E Highway 27	6	15		
C	SR 316	W Highway 27	18	6	0.84	>0.70
		North 316	11	25		
F	Ft. McCoy	South 316	5	6	0.14	>0.70
		South 316	8	21		
G	Kerr City	North 316	3	12	5.94	<0.05
		South 316	3	26		
		North 316	7	10		

M, monogyne; P, polygyne.

distinct locations (e.g., opposite sides of a highway) within five collection sites (A, B, C, F, and G) to test for significant differences in the frequency of both social forms. At three of these sites (A, B, and G), the frequency of single queen colonies differed significantly from one collection location to another (Table 3). In Gainesville, FL, for example, all but one of the colonies sampled around the grounds of the USDA were polygyne. Conversely, colonies sampled at the botanical gardens near Lake Alice (University of Florida, ≈ 1 km from the USDA) were primarily monogyne. A significant difference in the frequency of both social forms was also observed on opposite sides of highways at sites B and G (Table 3).

Discussion

Our data demonstrate that the transect across north Marion County, FL, bisects an area that is primarily polygyne, as expected from previous surveys (Porter 1992, 1993). However, the number of monogyne colonies found at each site was unexpected. Monogyne colonies were found at every site along the transect and comprised $\approx 25\%$ or more of the colonies encountered at five of the six sites. Although the aggression test may have misclassified some polygyne colonies, the high frequency of monogyny in most sites indicates that polygyny does not inevitably lead to the complete displacement of monogyne colonies in a particular region. After 13 or more years of a significant polygyne presence in this part of Florida, monogyne colonies are still common and persist interspersed within the polygyne population, at least along the roadsides.

The presence of monogyne colonies throughout the polygyne population suggests that the former are simply remnants of the monogyne population that presumably existed in the area before the presence and spread of polygyne forms (Vargo and Porter 1989). Colony longevity, however, would preclude this possibility because the two sampling times (Porter 1992 and our samples in 1999) are spread beyond the normal life expectancy of monogyne colonies (Tschinkel 1987). Nevertheless, some monogyne colonies might

persist well beyond the typical longevity expected for this social form; when colonies lose their queen, workers become nonaggressive and can adopt a single queen-derived newly mated queen (Vander Meer and Alonso, 2002). Most likely, though, monogyne colonies persist in polygyne areas by foundress queens originating from local monogyne colonies or from those in adjacent areas. Because newly mated queens from polygyne colonies have relatively small fat reserves, single foundresses are not successful (Porter et al. 1988; Keller and Ross 1993, 1995), and polygyne colonies are thought to spread primarily by budding (Vargo and Porter 1989). Although the literature on *S. invicta* implies that polygyne forms have a negative effect on the presence and density of monogyne forms, the proximate reasons for such an effect are not known, and the relationship remains speculative. If there is a competitive interaction between both social forms in Florida, the vagility of single queen forms probably helps maintain their presence in available habitat.

Large areas that are exclusively polygyne may result in limited insemination opportunities for female alates. The production of male and female sexuals has been negatively correlated with queen number in *S. invicta* (Vargo and Fletcher 1986), and therefore polygyne colonies produce significantly fewer sexuals per unit time than those with single queens (Vargo and Fletcher 1987). In addition to fewer sexuals, polygyne colonies primarily produce sterile males (Hung et al. 1974, Ross and Fletcher 1985b). Polygyne colonies appear to use the same environmental cues as single queen colonies to initiate mating flights, because males from monogyne colonies are thought to account for $\approx 80\%$ of inseminations of polygyne queens (Ross 1997). Because alates mate only once (Hung and Vinson 1976, Ball and Vinson 1983), polygyne-derived female alates appear to depend primarily on monogyne colony-derived males for successful mating. Therefore, polygyne colonies that are far removed from sources of monogyne males may have difficulty maintaining numbers of fertile queens by queen adoption or difficulty expanding their territory through budding. Such large tracts of polygyne colonies have been reported for both Texas (Porter et al. 1991) and Florida (Porter 1992, 1993); our data suggest that such tracts may not be as homogenous as previously thought and that in northcentral Florida the frequency of polygyne females fertilized by monogyne males is probably high.

Although polygyne colonies of *S. invicta* are common in many areas of the southeastern United States, this social form is uncommon in South America and the structure of these colonies differs markedly from United States polygyne populations (Ross et al. 1996). In South America, each polygyne colony has few queens that are closely related. In the United States, polygyne colonies have large numbers of unrelated queens, suggesting that the mechanism to polygyny in the United States is different from that in the native habitat of *S. invicta*. We have demonstrated that monogyne colonies can be found in close association with

polygyne *S. invicta* populations, which probably maintains the reproductive and genetic dynamics between both social forms as reported Ross and Fletcher (1985a), Ross et al. (1996), and Ross (1997).

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