

Comparison of Polygyne and Monogyne Red Imported Fire Ant (*Hymenoptera: Formicidae*) Population Densities

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ABSTRACT Polygyne or multiple-queen colonies of red imported fire ant, *Solenopsis invicta* Buren, are reported to be a substantially greater environmental and economic problem than monogyne or single-queen fire ants because of much higher population densities associated with polygyny. This study compared population densities of polygyne and monogyne fire ant colonies using measures of mound density, worker number, ant biomass, metabolic consumption, and standing caloric energy of ant biomass. We began the experiment by counting and measuring mounds at 14 polygyne and 14 monogyne sites located within a 35-km radius of Gainesville, FL. Average mound densities were 3.03 times larger at polygyne sites than at monogyne sites (470 versus 155 mounds per hectare). To adjust for differences in mound size, 22 monogyne and 21 polygyne mounds of various sizes were excavated from 16 of the experimental sites. Colony size and biomass were regressed on mound volume. These regressions then were used to estimate colony size and colony biomass from the mound volumes measured at the 28 field sites. The estimated colony sizes and colony biomasses at each site were summed and used to estimate field population densities. Polygyne populations contained 1.94 times more workers per unit area (35 million versus 18 million workers per hectare) and 1.86 times more biomass (27.7 versus 14.9 kg wet weight per hectare) than monogyne populations. Energy usage and standing energy of the ants per hectare were, respectively, 2.30 and 1.90 times higher in polygyne populations. Overall, this study indicates that polygyne population densities are ≈ 2 times larger on average than monogyne population densities.

KEY WORDS *Solenopsis invicta* colony size, respiration, polygyny, metabolism, mounds

THE RED IMPORTED fire ant, *Solenopsis invicta* Buren, was introduced into the United States from South America ≈ 60 yr ago (Vinson and Greenberg 1986). Fire ants currently occupy most of the southeastern United States and are continuing to spread northward and westward (Lofgren 1986). The aggressive nature, high densities, and irritating sting of the red imported fire ant have made them serious environmental, agricultural, and urban pests (Lofgren 1986).

Solenopsis invicta occurs in 2 distinct forms: the monogyne or single-queen form and the polygyne or multiple-queen form. Fire ant populations in the United States and South America are predominantly monogyne except in Texas (Porter et al. 1991, 1992; Porter 1992). *S. invicta* was believed to be a monogynous species until the early 1970s when the 1st polygyne populations were reported (Glancey et al. 1973, Hung et al. 1974). In the last 20 yr, polygyne populations have been found at more and more sites throughout the southeastern

United States (Porter et al. 1991, 1992; Porter 1992).

In addition to the number of queens per mound, monogyne and polygyne fire ants differ in other important aspects of their biology. For example, polygyne colonies consist of individuals with varying degrees of relatedness, whereas the monogyne colonies consist of a single family unit (Ross and Fletcher 1985). Polygyne queens are less fecund than monogyne queens (Fletcher et al. 1980, Vargo 1990, Vander Meer et al. 1992). Polygyne colonies reproduce primarily by budding (Vargo and Porter 1989, Porter et al. 1991), whereas monogyne colonies reproduce through claustral founding (Markin et al. 1973). Monogyne colonies have a higher rate of sexual production than do polygyne colonies (Vargo and Fletcher 1987). Polygyne workers are 16% smaller on average (Greenberg et al. 1992) and are less aggressive toward non-nestmate conspecifics than monogyne workers (Obin et al. 1993). This lack of aggression with conspecifics apparently creates a situation where nests become interconnected into supercolonies (Bhatkar and Vinson 1987). Presumably, interconnected colonies allow polygyne populations to cover a field completely and consume most of the available resources, whereas territorial behavior in monogyne

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colonies may reduce resource access and use. The net result is that polygyne populations occur in larger densities than monogyne populations (Lofgren and Williams 1984, Bhatkar and Vinson 1987, Glancey and Lofgren 1988, Porter et al. 1988). The exchange of food and workers between nests in polygyne populations can make the definition of colony as it pertains to polygyne populations unclear. For the purpose of this article, we consider individual polygyne nests to be colonies despite of their interconnections, because they are fully functional units that are spatially isolated from each other.

The discovery of more and more polygyne populations has caused great concern, because the ecological and economic damage of fire ants should be correlated with their population densities (Porter and Savignano 1990). Our study was designed to compare field population densities of monogyne and polygyne forms of *S. invicta* in Florida. Most of the previous work on fire ant populations has been based upon mound counts. The problem with using mound counts to compare monogyne and polygyne populations is that polygyne colonies tend to be smaller (Porter et al. 1991, Porter 1992), contain smaller workers (Greenberg et al. 1985, Porter 1992), and produce fewer sexuals (Vargo and Fletcher 1987). To account for these differences, we calculated population densities based on worker number, number of individuals, colony biomass, metabolic rates, and the caloric energy of ant biomass.

Materials and Methods

Mound Densities and Sizes. Field surveys were conducted from mid-February to mid-March 1994. Fourteen monogyne and 14 polygyne sites were selected from a 35-km radius around Gainesville, FL. All sites consisted of ≥ 5 ha of cleared pasture land that was used for grazing for at least 5 yr before the beginning of this study. The sites were selected from different geographic locations and from several different soil types. The sites were selected by the owners based on convenience rather than on fire ant abundance. Queens collected from each site were dissected and their spermatheca examined to determine if they were inseminated. Sites were classified as polygyne when ≥ 2 inseminated queens were found in ≥ 4 colonies and little or no aggression was observed between non-nestmate conspecifics (Tschinkel et al. 1995). Sites were determined to be monogyne by the presence of mounds with a single large physogastric queen and strong aggression between non-nestmate conspecifics. Several sites ($n = 6$) that appeared to have mixed populations were excluded from this study.

Each site contained 3 circular plots each with a radius of 15.9 m (0.08 ha). Plots were ≥ 20 m apart. All the mounds in each plot were counted and measured. The 1st plot was placed in the center

of the field. Locations of the other 2 plots were preselected by direction and distance from the 1st plot. Mound area (A) was calculated using the formula for an ellipse, $A = \pi ab$, where a is the length/2 and b is the width/2. Mound volume (V) was calculated using the formula for half a spheroid, $V = 2/3 \pi abc$, where a is the length/2, b is the width/2, and c is the height (Porter 1992). All of the mound areas and volumes for each test site were summed to obtain the total mound area and total mound volume per hectare.

Mound Excavations. Mound excavations were conducted between mid-March and mid-April. Colonies were sampled in early spring when they are usually near their largest size (Tschinkel 1993). Two or 3 mounds were selected from each of 8 monogyne sites and 8 polygyne sites. Altogether, 46 colonies were censused. Three of these colonies were discarded because they lacked worker brood and did not appear healthy. Special care was made to include both large and small colonies to increase the predictive power of the regression model.

Colony populations were determined using a subsampling method developed by S.D.P. and later used by Tschinkel (1993). Colonies were excavated into 19-liter (5-gal) buckets. Baby powder was applied to the inside rims of each bucket to stop the fire ants from escaping. The contents of the buckets were weighed and placed into a large bin, also with a rim of baby powder around the top to stop the ants from escaping. The dirt and ants were thoroughly mixed and 5 samples of ≈ 100 g each were collected for processing. If >2 buckets were required to excavate the colony, we removed a 10% sample from the bin after the contents of each 2 buckets were mixed. When the colony was completely excavated, all the 10% samples were mixed together, and 5 subsamples of ≈ 100 g each were taken. Adult and brood stages were separated from the subsamples and counted and weighed. Almost all the workers and large brood in the subsamples were counted because they were conspicuous and easy to retrieve. Unfortunately, the estimates for total individuals were low because early instars were hard to find and the eggs were not counted.

Colony populations were estimated by multiplying the numbers and wet weights of the adult and brood stages by the ratio obtained by dividing the total soil weight by the weight of each subsample. The average standard error for the estimates of colony size, worker number, colony weight, and worker weight were 12% of the mean. Worker number, total individuals, and total biomass were calculated for each colony and regressed against mound area and mound volume. These regression equations were used to estimate worker number, total individuals, and colony biomass from volumes of the mounds that were counted and measured at each of the field plots. Colony population estimates were then summed across plot and used to esti-

mate population densities per square meter or per hectare.

Respiration Rates. Previous studies have demonstrated that smaller ants have higher metabolic rates (Jensen and Nielsen 1975, Porter and Tschinkel 1985). Polygyne colonies contain smaller workers on average (Greenberg et al. 1985, Porter 1992) and therefore should have higher metabolic rates than the monogyne form. Respiration rates were measured and used to compare relative energy expenditures of polygyne and monogyne colonies. These rates were determined using "closed system" metabolic chambers (Vlek 1987) consisting of 60 ml (60-cc) syringes fitted with a 3-way valve as described by Anderson (1993) and an O_2 analyzer and sensor. Measurements were made on 0.25 g samples of workers and brood the morning after they were collected from the field. Samples and controls were placed in an incubator at 28°C for 3 h. Metabolic calculations were made at 28°C to simulate the field temperature during the summer. Oxygen levels in the syringes did not decrease by >3% during the experiment. Rates of oxygen consumption (VO_2) were calculated using the equation:

$$VO_2 = 1,000 \times STP \times V(F_I O_2 - F_E O_2) / (1 - F_E O_2)h,$$

where STP is the standard temperature and pressure at atmospheric conditions at the time of the experiment (Vlek 1987); V is the initial volume of dry, CO_2 -free air in the syringe at STP; $F_I O_2$ and $F_E O_2$ are the O_2 fractions within the syringe at the start and end of the incubation period; and h is the incubation time in hours. The samples were then killed, dried, and weighed. The results were used to calculate $\mu l O_2/h \cdot mg$ colony dry weight. Oxygen consumption rates were converted to metabolic rates using the conversion factor 0.0048 cal/ $\mu l O_2$ (Elliot and Davidson 1975). Energy consumption rates per square meter were then calculated using the estimates of biomass per square meter from the field surveys.

Energy Content of Ant Tissue. Fat content in *S. invicta* has been demonstrated to increase as worker size and as colony size increases (Ricks and Vinson 1972, Porter and Tschinkel 1985, Tschinkel 1993). Polygyne colonies are smaller on average (Greenberg et al. 1985, Porter et al. 1991, Porter 1992) and contain smaller workers (Greenberg et al. 1985, Porter 1992) and therefore should be expected to contain less energy per gram. Samples for the fat extractions (1.0–0.5 g), which included both workers and brood, were randomly selected from 10 monogyne and 10 polygyne colonies from the mound excavations. Two subsamples were selected from each colony and placed into extraction thimbles (10 by 50 mm), covered with glass wool, and placed in a Soxhlet extractor. The extraction was carried out over 12 h using methylene chloride. Previous experiments showed no significant weight loss in sample weight of the ants after 12

Table 1. Comparisons of mound dimensions and mound densities at sites infested with monogyne and polygyne fire ants

	Monogyne sites	Polygyne sites
Mound dimensions		
Ht, cm ^a	11.6 ± 0.4	9.5 ± 0.9*
Length, cm ^a	49.2 ± 2.6	38.6 ± 2.4**
Width, cm ^a	39.8 ± 1.9	31.5 ± 1.5**
Area, cm ^{2a}	1,700 ± 165	1,100 ± 136**
Vol, liters ^a	14.7 ± 1.5	7.6 ± 1.4**
Mound densities		
Density, mounds/ha ^b	155 ± 11	470 ± 64***
Total area, m ² /ha ^b	25.0 ± 2.1	51.0 ± 10.1*
Total vol, m ³ /ha ^b	2.1 ± 0.21	3.5 ± 0.71

Data are means ± SE from 14 monogyne and 14 polygyne sites. *, $P < 0.05$; **, $P < 0.005$; ***, $P < 0.0001$.

^a Tested using 1-way ANOVA.

^b Tested using Mann-Whitney *U* test.

h. After the extraction, the samples were dried and reweighed. The difference between the pre- and postextraction dry mass was used to compute the mean lipid and percentages lipid dry weight. This method does not distinguish body lipid from oil stored in the crop (Tschinkel 1993). The remaining weight of the ant was considered lean body weight. Energy content of the ants was calculated from the lipid and lean weight (lipid 9.40 Kcal/g; lean matter 4.50 Kcal/g) (Peakin 1972).

Data Analysis. Descriptive statistics, regressions, and nonparametric statistical tests were calculated using the statistical package Statview Student (Abacus Concepts 1991), and analyses of variance (ANOVA) tests were calculated using SuperANOVA (Abacus Concepts 1989). The data were log or square-root transformed when necessary to equalize the variance and normalize the distribution. Voucher specimens of fire ants have been placed in the Florida State Collection of Arthropods, Florida Department of Agriculture and Consumer Service, Division of Plant Industry, Gainesville. Standard errors are displayed with means. All biomass measurements are expressed as dry weights unless otherwise specified.

Results

Mound Densities and Sizes. Monogyne mounds were 22% taller, 26% wider, and 27% longer on average than polygyne mounds (Table 1). Mounds at monogyne sites averaged 55% larger in area and 90% larger in volume than the average polygyne mounds (Table 1). The largest mound, however, was a polygyne mound that measured 99.5 liters, almost 10 liters larger than the largest monogyne mound at 89.7 liters.

The average mound density at polygyne sites was 3.03 times greater than at monogyne sites (Table 1). The large variance in mound numbers could not be equalized through log or square-root transformation; therefore, a nonparametric statistical test was used to compare the population den-

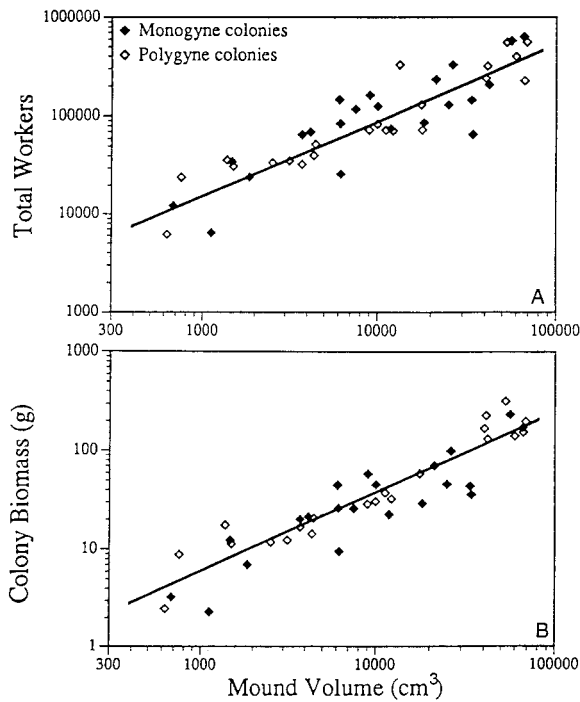


Fig. 1. Relationship between colony and mound size. (A) Relationship between worker number and mound volume of 21 polygyne colonies and 22 colonies ($R^2 = 0.80$, $y = 99.41x^{0.750}$). (B) Relationship between colony biomass and mound volume ($R^2 = 0.85$, $y = 0.021x^{0.812}$).

sities (Mann-Whitney U ; $Z = -4.323$; $n = 14, 14$; $P < 0.0001$). The average total mound base area of all mounds at polygyne sites was 2.04 times higher than at monogyne sites (Table 1; Mann-Whitney U ; $Z = -2.297$; $n = 14, 14$; $P = 0.0216$). Total mound volume of all mounds at polygyne sites was 1.67 times greater than at monogyne sites (Table 1; Mann-Whitney U ; $Z = -1.378$; $n = 14, 14$; $P = 0.1681$).

Correlation of Mound Size with Colony Size.

As colonies grow, they usually increase their living space to accommodate the increase in the number of individuals. The living space available in the nests should be related to colony size. Indeed, mound area and mound volume of the excavated colonies were both strongly correlated with worker number, total number of individuals, worker biomass, and colony biomass (Fig. 1; Table 2). A dummy variable was used to test for differences in the slope and y-intercept of regressions for monogyne and polygyne colonies. No significant differences were found; therefore, the results of the regressions for the polygyne and monogyne colonies were combined (Fig. 1). Mound volume explained 77–85% of the variation present, whereas mound area explained 71–76% of the variation present (Table 2). Soil in our sample areas averaged $85 \pm 9\%$ sand (range, 66–94%) and $8 \pm 7\%$ clay (range, 2–25%). Differences in soil texture among areas were not correlated with differences in the volume of excavated mounds after accounting for the size

Table 2. Regressions of 4 colony size variables (worker number, number of individuals, worker biomass, and colony biomass) versus 2 measures of mound size.

Colony variable, y	Mound variable, x	Equation	R^2
No. workers	Volume	$y = 99.41x^{0.750}$	0.81
	Area	$y = 13.07x^{1.226}$	0.74
No. individuals	Volume	$y = 165.34x^{0.715}$	0.77
	Area	$y = 23.17x^{1.177}$	0.71
Worker biomass	Volume	$y = 0.016x^{0.816}$	0.84
	Area	$y = 0.0019x^{1.328}$	0.76
Colony biomass	Volume	$y = 0.021x^{0.812}$	0.85
	Area	$y = 0.0025x^{1.320}$	0.76

$P < 0.0001$ for all interactions.

of the colony that built them (multiple regressions, $P > 0.4$)

The equations obtained from the regressions with mound volume were used to estimate number of workers, number of total individuals, and colony biomass for each mound at the field sites. These estimates of colony size for each mound were summed across plot and converted to estimates of population density per square meter. After using the regressions to convert mound size to colony size (Table 3), polygyne sites had an estimated 1.94 times more workers and 1.86 times more individuals per square meter than monogyne sites (Mann-Whitney U ; number of workers; $Z = -2.022$; $n = 14, 14$; $P = 0.043$; total individuals $Z = -2.16$; $n = 14, 14$; $P = 0.031$). Polygyne sites

Table 3. Population densities of polygyne and monogyne fire ants in terms of numbers, biomass, metabolic rates, and caloric content

Parameters	Monogyne sites	Polygyne sites
Field estimations ^a		
Workers, No./m ²	1,800 ± 140	3,500 ± 650*
Total individuals, No./m ²	2,200 ± 130	4,100 ± 480*
Total colony biomass, g/m ²	0.70 ± 0.06	1.30 ± 0.25 ^b
Metabolic rates ^c		
Rate per unit biomass, $\mu\text{l O}_2/\text{h}\cdot\text{g}$	2,400 ± 152	2,900 ± 106*
Metabolic rate, cal/h·g	11.5 ± 0.7	13.9 ± 0.5*
Metabolic usage, cal/h·m ²	8.0 ± 0.7	18.3 ± 3.5*
Caloric energy of ant biomass		
Caloric value of value, Kcal/g	6.37 ± 0.13	6.47 ± 0.12
Caloric density of ant biomass, Kcal/m ²	4.5 ± 0.38	8.4 ± 1.62*

Data are mean ± SE from 14 monogyne and 14 polygyne sites. *, $P < 0.05$.

^a Estimated from mound volumes using equations in Table 2.

^b Approaching significance; $P = 0.0536$.

^c Estimations based on respiration experiment conducted at 28°C.

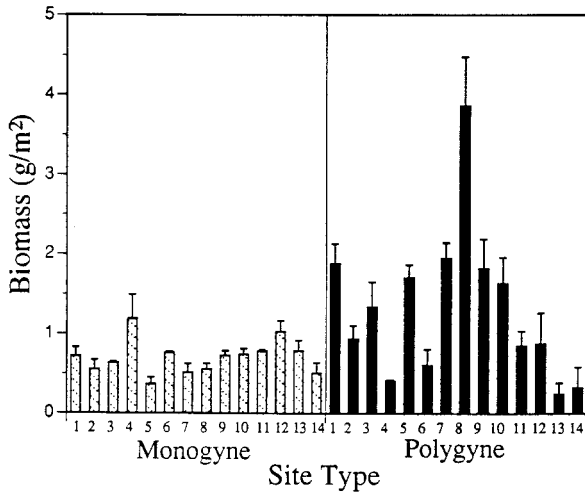


Fig. 2. Average biomass per square meter for polygyne and monogyne populations. Each bar is the average of 3 plots in a test site. Standard errors are indicated for each bar. Site numbers are indicated below each bar.

also contained 1.86 times more biomass per square meter than monogyne sites (Table 3). Total colony biomass approached significance (Fig. 2; Mann-Whitney U ; $Z = -1.93$; $n = 14, 14$; $P = 0.054$), but large variability among the polygyne samples kept this test from being significant (Fig. 2). The largest biomass density estimated at a polygyne site was 3.25 times larger than the largest biomass estimated at a monogyne site. However, the lowest total biomass estimated at a polygyne site was 0.67 times smaller than the lowest total biomass estimated at a monogyne site.

Metabolic Rates. Metabolic rates of polygyne colonies per gram dry weight were 17% higher than metabolic rates for monogyne colonies (Table 3; ANOVA, $F = 6.54$; $df = 1, 26$; $P = 0.016$). These results indicate that polygyne colonies use more energy and are more costly to maintain per gram than monogyne colonies. Respiration rates per unit area were determined for monogyne and polygyne populations by multiplying the estimated biomass per square meter by the respiration rates per gram for each form. Metabolic energy usage per square meter was 2.29 times higher at polygyne sites than monogyne sites (Table 3; Mann-Whitney U ; $Z = -3.79$; $n = 14, 14$; $P = 0.0132$).

Caloric Energy of Ant Biomass. Fat content was used to calculate the standing caloric energy content of tissue in fire ant populations. Percentage body fat was not significantly different between monogyne and polygyne colonies ($38.1 \pm 2.0\%$ versus $40.1 \pm 1.9\%$; ANOVA; $F = 0.491$; $df = 1, 18$; $P = 0.49$; Table 3). This information was combined with the estimates of biomass to calculate the caloric energy of the ants at each site (Table 3).

Colony Composition. The excavated colonies were broken down into workers, worker brood, sexuals, and sexual brood. The relative proportion of the number of individuals of each caste and stage was estimated from the total of all the excavations. Numerically, in early spring, polygyne colonies consisted of 80.2% workers, 19.6% worker brood, 0.0% sexuals, and 0.2% sexual brood, whereas monogyne colonies consisted of 82.7% workers, 15.6% worker brood, 0.1% sexuals, and 1.7% sexual brood. Biomass comparisons between polygyne and monogyne colonies showed that polygyne colonies contained 79.8% workers, 17.4% worker brood, 0.0% sexuals, and 2.8% sexual brood, whereas monogyne colonies consisted of 76.6% workers, 10.5% worker brood, 0.5% sexuals, and 12.4% sexual brood. Colony compositions were similar to what Markin et al. (1973, 1974) reported for monogyne colonies at this time of the year. The major difference in colony composition was that polygyne colonies contained 75% more worker brood, whereas monogyne colonies contained 4 times more sexual brood as a percentage of colony weight. Average worker dry weight was almost 40% greater in monogyne colonies than in polygyne colonies (0.36 ± 0.02 mg versus 0.26 ± 0.04 mg dry weight; t -test; $t = 4.079$, $df = 41$, $P = 0.0002$). Worker weights were comparable to those found by Porter (1992) after adjusting for fat content.

Discussion

Field Population Density Estimates. Polygyne populations in the United States have been reported to occur in much higher densities than monogyne populations (Lofgren and Williams 1984, Porter et al. 1988). This has caused concern because ecological and economic damage increases as population densities increase (Porter and Savignano 1990). Polygyne populations in this study were 3.03 times more dense than monogyne populations based upon the number of mounds (470 versus 155 mounds per hectare) (Table 1). This was close to the 2.3, 3.2, and 2.3 ratios reported respectively by Porter (1992) for Florida, by Porter et al. (1992) for the Southeast, and by Porter et al. (1991) for Texas.

Mound counts, however, are not a good way to compare monogyne and polygyne fire ant population densities because polygyne colonies are usually smaller than monogyne colonies (Table 1). Worker numbers, number of total individuals of all caste and developmental stages, and total biomass per square meter were calculated to account for differences in mound size and worker size. Polygyne populations contained ≈ 1.94 times more workers per square meter than monogyne populations. On average, this works out to be ≈ 35 million workers per hectare for polygyne populations and 18 million workers per hectare for monogyne populations. The highest density we observed was

99.8 million workers per hectare estimated at a polygyne site. Brood and sexuals (minus eggs and small larvae) were added to the number of workers to obtain the total number of individuals per square meter. Total individuals per square meter was 1.86 times greater in polygyne populations than in monogyne populations (41 million versus 22 million individuals per hectare). The highest density was 123.4 million individuals per hectare at the same polygyne site mentioned above.

We compared the regression of colony biomass and mound volume to Tschinkel's (1993) results. In general, biomass in this study was somewhat higher than Tschinkel (1993) reported for the same-sized mounds. We found that colony biomass increased more rapidly than mound volume, whereas, Tschinkel (1993) showed only a slight tendency in this direction. These differences could be a result of differences in season, rainfall, or soil composition. Tschinkel's data were collected over many months, whereas ours was collected only during late winter and early spring when fire ant colonies are generally at their largest. Tschinkel's data were also collected from a single site with much clay, whereas most of our sites contained sandy soils. Soils at our sample sites contained 66–94% sand; however, we did not find any correlation between soil texture and the size of mound built by a colony of a particular size.

Field Estimates of Total Biomass. In addition to larger mounds, monogyne fire ants have larger workers (Greenberg et al. 1985, 1992) and produce more sexuals (Vargo and Fletcher 1987). Total colony biomass per square meter was estimated to adjust for these differences. Polygyne populations contained ≈ 1.86 times more biomass per square meter than monogyne populations. Biomass for polygyne populations was 13 kg of ants (dry weight) per hectare, whereas monogyne populations averaged 7 kg of ants per hectare. When converted to live weight assuming 53% water content (Porter and Tschinkel 1985), polygyne populations averaged 27.7 kg/ha and monogyne populations averaged 14.9 kg/ha.

The difference of almost 2 times in worker number, total individuals, and total biomass between polygyne and monogyne fire ants was substantial but considerably less than the 3-fold difference in mound densities between polygyne and monogyne fire ants. Several studies have reported that polygyne fire ants can reach mound densities 6–10 times larger than monogyne fire ants (Lofgren and Williams 1984, Bhatkar and Vinson 1987, Glancey and Lofgren 1988, Porter et al. 1988). Differences of this magnitude were probably a result of comparing extremely high polygyne mound densities with average monogyne mound densities.

Metabolic Comparisons. Up to this point in the study, population densities have been based on numbers and weights. Another interesting way to look at a population is the way it uses energy. Metabolic rates are useful in comparing populations,

especially for estimating their potential environmental impact. Polygyne colonies used 17% more energy per gram dry weight than monogyne colonies. This was probably because of larger numbers of small workers in the polygyne colonies, which are more costly to maintain (Porter and Tschinkel 1985, Calabi and Porter 1989). Respiration rates were $\approx 25\%$ higher than Calabi and Porter (1989) predicted. This could be a result of different measuring techniques and differences in test samples. Calabi and Porter (1989) measured workers of a particular size to estimate respiration rates, whereas we measured mixed worker sizes together with brood and sexuals.

Caloric Content of Ant Biomass. Caloric content of ant biomass showed no significant difference between monogyne and polygyne fire ants at this time of year. Consequently, the difference in caloric density of ant tissue between the polygyne and monogyne populations is almost the same as the difference reported for the biomass (Table 3). We expected monogyne colonies to contain a slightly larger percentage of fat body, because worker fat content usually increases with worker size (Porter and Tschinkel 1985) and with colony size (Tschinkel 1993). Monogyne colonies might also have been less food stressed if they defended relatively larger territories. These effects, if they exist, are apparently more subtle than the normal variability associated with the colonies we collected.

Possible Reasons For Larger Polygyne Populations. Polygyne populations were considerably larger in every estimate of population density in this study. How do polygyne colonies at these sites reach and maintain such high densities compared with monogyne populations? The following 3 possibilities exist: First, polygyny in the fire ant has led to the collapse of territorial boundaries and the elimination of intraspecific competition (Bhatkar and Vinson 1987, Vargo and Fletcher 1987, Obin et al. 1993). Presumably, this lack of aggression has reduced the area between territories (Hölldobler and Wilson 1990) and allowed fire ants to make more thorough use of sporadically distributed food resources. Monogyne colonies have a defined territory that they actively defend. Monogyne colonies probably defend more territory than they need for normal growth and maintenance. This would ensure that the colony would have sufficient resources for growth during periods of reduced resource availability. This defense would not only limit access of unused resources to other colonies but also create areas of unexploited resources between colonies. Polygyne colonies do not defend territory against conspecifics and therefore may allow more of the potential resources to be used. Again, more complete use of available resources in polygyne populations presumably would allow larger populations to exist.

Second, monogyne colonies put between 16 and 30% of their available resources into producing

Table 4. Population and biomasses of several ant species compared with polygyne and monogyne fire ant population densities

Species	Mean no. individuals/m ²	Mean biomass, g dry wt/m ²	Source
<i>Formica pratensis</i> (Retzius) ^a	12–45	0.06–0.232	Jensen (1978)
<i>Formica rufa</i> L. ^a	—	12.0	Markovsky (1962)
<i>Lasius alienus</i> (Foerster)	900–2,000 ^b	0.960–2.09	Nielsen and Jensen (1975)
<i>Lasius flavus</i> (F.)	700–9,200	1.4–16.5	Odum and Pontin (1961), Nielsen (1986), Jensen (1978)
<i>Lasius niger</i> (L.) ^a	785 ^b	1.06	Nielsen (1974)
<i>Myrmica rubra</i> (L.) ^a	430 ^b	0.93	Jensen (1978)
<i>Myrmica ruginodis</i> Nylander ^a	230 ^b	0.16	Jensen (1978)
<i>Myrmica schencki</i> Emery ^a	47	0.034	Jensen (1981)
<i>Pogonomyrmex badius</i> (Latreille)	13.5	0.084	Golley and Gentry (1964)
<i>Pogonomyrmex californicus</i> (Buckley) ^a	2.4	0.0034	MacKay (1981)
<i>Pogonomyrmex montanus</i> MacKay	0.5–4.3	0.001–0.010	MacKay (1981)
<i>Pogonomyrmex rugosus</i> Emery ^a	0.8–19.4	0.006–0.137	MacKay (1981)
<i>Pogonomyrmex subnitidus</i> Emery	0.6–5.3	0.002–0.016	MacKay (1981)
<i>Solenopsis invicta</i> Buren			
Monogyne	2,200	0.70	This article
Polygyne	4,100	1.30	This article
Polygyne ^a	2,230	1.0	Vargo and Porter (1989)
<i>Tetramorium caespitum</i> (L.)	241–440	0.160–0.232	Brian et al. (1967)

^a Estimates based on 1 or 2 populations only.

^b Estimated numbers based on dry weights of workers (Jensen 1978).

sexuials (Markin et al. 1974, Tschinkel 1993), whereas polygyne colonies put only 3.5–6.6% of their available resources into sexual production (Vargo and Fletcher 1986). This reduction in sexual production should increase the polygyne colony's ability to produce and maintain more workers by an equivalent percentage.

Third, dense polygyne populations are generally associated with reduced species diversity (Porter and Savignano 1990, Hölldobler and Wilson 1990). A combination of the discussed above effects together with their natural aggressiveness, apparently drives out competitors (Porter and Savignano 1990, Morris and Steigman 1993) opening additional resources and allowing still higher fire ant populations.

Population Comparisons with Other Genera.

The information in this study can be used to compare population estimates of the fire ant with other ant genera (Table 4). *S. invicta* had a higher biomass per square meter than that reported for most other genera. Fire ant densities were considerably larger than most of the *Myrmica*, *Pogonomyrmex*, *Tetramorium*, and some *Formica* species. *Formica rufa* (L.), *Lasius alienus* (Foerster), *L. flavus* (F.), *L. niger* (L.), and *Myrmica rubra* (L.) had reported densities greater than the fire ant. When comparing populations, one must consider the extremely high population densities a species can reach in the environment. Several population densities from other genera were measured from a single site that was selected probably because they contained unusually large densities of the ants being studied. The maximum densities of fire ants in this study (Fig. 2) were equal to or greater than the maximum densities reported for all ant genera except

E. rufa (12.0 g dry weight/m²) and *L. flavus* (1.4–16.5 g dry weight/m²).

Food Flow. Our population estimates also can be used to calculate the amount of food flowing into populations of fire ants. Macom and Porter (1995) determined the average caloric intake of polygyne colonies at 29°C was 3.46 ± 0.17 Kcal/wk · g dry weight. Monogyne colonies would probably require ≈17% less food per gram because of lower metabolic rates (Table 3). Based upon this information, an average monogyne population in this study would need to collect ≈1.9 Kcal/wk · m², whereas an average polygyne population would require ≈4.5 Kcal/wk · m² (Macom and Porter 1995) to sustain themselves in the summer. For monogyne populations, this is equivalent to about 3.5 kg of insects (live weight) per week per hectare plus ≈13 liters of a 1M sugar solution per week per hectare (Tennant and Porter 1991, Macom and Porter 1995). For polygyne populations, this energy requirement would be equivalent to 8.2 kg of insects (live weight) per week per hectare and ≈30 liters of a 1 M sugar solution per week per hectare. Clearly, fire ants play a substantial role in the food webs of North Florida pastures.

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References Cited

- Abacus Concepts.** 1991. Statview. Abacus Concepts, Berkeley, CA.
1989. SuperANOVA. Abacus Concepts, Berkeley, CA.
- Anderson, J. F.** 1993. Respiratory energetics of two Florida harvestman. *Comp. Biochem. Physiol. A. Comp. Physiol.* 105: 67-72.
- Bhatkar, A. P., and S. B. Vinson.** 1987. Colony limits in *Solenopsis invicta* Buren, pp. 599-600. In J. Eder and H. Rembold [eds.], *Chemistry and biology of social insects*. Peperny, Munich.
- Brian, M. V., G. Elmes, and A. F. Kelly.** 1967. Populations of the ant *Tetramorium caespitum* Latreille. *J. Anim. Ecol.* 36: 337-342.
- Calabi, P., and S. D. Porter.** 1989. Worker longevity in the fire ant *Solenopsis invicta*: ergonomic considerations of correlations between temperature, size and metabolic rates. *J. Insect Physiol.* 35: 643-649.
- Elliott, J. M., and W. Davison.** 1975. Energy equivalents of oxygen consumption in animal energetics. *Oecologia (Berl.)* 19: 195-201.
- Fletcher, D.J.C., M. S. Blum, T. V. Whitt, and N. Temple.** 1980. Monogyny and polygyny in the fire ant, *Solenopsis invicta*. *Ann. Entomol. Soc. Am.* 73: 658-661.
- Glancey, B. M., and C. S. Lofgren.** 1988. Adoption of newly-mated queens: a mechanism for proliferation and perpetuation of polygynous red imported fire ants. *Solenopsis invicta* Buren. *Fla. Entomol.* 71: 581-587.
- Glancey, B. M., C. H. Craig, C. E. Stringer, and P. M. Bishop.** 1973. Multiple fertile queens in colonies of the imported fire ant, *Solenopsis invicta*. *J. Ga. Entomol. Soc.* 8: 237-238.
- Golley, F. B., and J. B. Gentry.** 1964. Bioenergetics of the southern harvester ant, *Pogonomyrmex badius*. *Ecology (New York)* 45: 217-225.
- Greenberg, L., D.J.C. Fletcher, and S. B. Vinson.** 1985. Differences in worker size and mound distribution in monogynous and polygynous colonies of the fire ant *Solenopsis invicta* Buren. *J. Kans. Entomol. Soc.* 58: 9-18.
- Greenberg, L., S. B. Vinson, and S. Ellison.** 1992. Nine-year study of a field containing both monogyne and polygyne red imported fire ants (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* 85: 686-695.
- Hölldobler, B., and E. O. Wilson.** 1990. *The ants*. Belknap, Cambridge, MA.
- Hung, A.C.F., S. B. Vinson, and J. W. Summerlin.** 1974. Male sterility in the red imported fire ant, *Solenopsis invicta*. *Ann. Entomol. Soc. Am.* 67: 909-912.
- Jensen, T. F.** 1978. Annual production and respiration in ant (Formicidae) populations. *Oikos* 31: 207-213.
1981. Distribution and density of nests of *Myrmica schencki* Emery in a sandy heath area in Jutland, Denmark. *Nat. Jutl.* 19: 67-72.
- Jensen, T. F., and M. G. Nielsen.** 1975. The influence of body size and temperature on worker ant respiration. *Nat. Jutl.* 18: 21-25.
- Lofgren, C. S.** 1986. History of imported fire ants in the United States, pp. 36-47. In C. S. Lofgren and R. K. Vander Meer [eds.], *Fire ants and leafcutting ants: biology and management*. Westview, Boulder, CO.
- Lofgren, C. S., and D. F. Williams.** 1984. Polygynous colonies of the red imported fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae) in Florida. *Fla. Entomol.* 67: 484-486.
- MacKay, W. P.** 1981. A comparison of the nest phenologies of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). *Psyche* 88: 25-74.
- Macom, T. E., and S. D. Porter.** 1995. Food and energy requirements of laboratory fire ant colonies (Hymenoptera: Formicidae: *Solenopsis invicta*). *Environ. Entomol.* 24:387-391
- Marikovskiy, P. I.** 1962. On intraspecific relations of *Formica rufa* L. (Hymenoptera, Formicidae). *Entomol. Rev. (Engl. Transl. Entomol. Obozr.)* 41: 47-51.
- Markin, G. P., J. H. Dillier, and H. L. Collins.** 1973. Growth and development of colonies of the red imported fire ant, *Solenopsis invicta*. *Ann. Entomol. Soc. Am.* 66: 803-808.
- Markin, G. P., J. O'Neal, J. H. Dillier, and H. L. Collins.** 1974. Regional variation in the seasonal activity of the imported fire ant, *Solenopsis saevissima richteri*. *Environ. Entomol.* 3: 446-452.
- Morris, J. R., and K. L. Steigman.** 1993. Effects of polygyne fire ant invasion on native ants of a blackland prairie in Texas. *Southwest. Nat.* 38: 136-140.
- Nielsen, M. G.** 1986. Ant nests on tidal meadows in Denmark. *Entomol. Gen.* 11: 191-195.
1974. Number and biomass of worker ants in a sandy heath area in Denmark. *Nat. Jutl.* 17: 91-95.
- Nielsen, M. G., and T. F. Jensen.** 1975. Okologiske studier over *Lasius alienus* (Forst.) (Hymenoptera, Formicidae). *Entomol. Med.* 43: 5-16.
- Obin, M. S., L. Morel, and R. K. Vander Meer.** 1993. Unexpected, well-developed nestmate recognition in laboratory colonies of polygyne imported fire ants (Hymenoptera: Formicidae). *J. Insect Behav.* 6: 579-589.
- Odum, E. P., and A. J. Pontin.** 1961. Population density of the underground ant *Lasius flavus* L. as determined by tagging with 32P. *Ecology* 42: 186-189.
- Peakin, G. J.** 1972. Aspects of productivity in *Tetramorium caespitum* L. *Ekol. Pol.* 20: 55-63
- Porter, S. D.** 1992. Frequency and distribution of polygyne fire ants (Hymenoptera: Formicidae) in Florida. *Fla. Entomol.* 75: 248-257.
- Porter, S. D., and D. A. Savignano.** 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology (New York)* 71: 2095-2106.
- Porter, S. D., and W. R. Tschinkel.** 1985. Fire ant polymorphism (Hymenoptera: Formicidae): the ergonomics of brood production. *Behav. Ecol. Sociobiol.* 16:323-336.
1987. Foraging in *Solenopsis invicta* (Hymenoptera: Formicidae): effects of weather and season. *Environ. Entomol.* 16: 802-808.
- 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. Am.* 81: 913-918.
- Porter, S. D., A. P. Bhatkar, R. Mulder, S. B. Vinson, and D. J. Clair.** 1991. Distribution and density of polygyne fire ants (Hymenoptera: Formicidae) in Texas. *J. Econ. Entomol.* 84: 866-874.
- Porter, S. D., H. G. Fowler, and W. P. Mackay.** 1992. Fire ant mound densities in the United States and Brazil (Hymenoptera: Formicidae). *J. Econ. Entomol.* 85: 1154-1161.
- Ricks, B. L., and S. B. Vinson.** 1972. Changes in nutrient content during one year in workers of the imported fire ant. *Ann. Entomol. Soc. Am.* 65: 135-138.

- Ross, K. G., and D.J.C. Fletcher. 1985.** Comparative study of genetic and social structure in two forms of the fire ant *Solenopsis invicta* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 17: 349–356.
- Tennant, L. E., and S. D. Porter 1991.** Comparison of diets of two fire ant species (Hymenoptera: Formicidae): solid and liquid components. *J. Entomol. Sci.* 26: 450–465.
- Tschinkel, W. R. 1993.** Sociometry and sociogenesis of colonies of the fire ant *Solenopsis invicta* during one annual cycle. *Ecol. Monogr.* 63: 425–457.
- Tschinkel, W. R., E. S. Adams, and T. E. Macom. 1995.** Territory area and colony size in the fire ant *Solenopsis invicta*. *Anim. Ecol.* 64:473–480
- Vander Meer, R. K., L. Morel, and C. S. Lofgren. 1992.** A comparison of queen oviposition rates from monogyne and polygyne fire ant, *Solenopsis invicta*, colonies. *Physiol. Entomol.* 17: 384–390.
- Vargo, E. L. 1990.** Social control of reproduction in fire ant colonies, pp. 158–172. *In* R. K. Vander Meer, K. Jaffe, and A. Cedeno [eds.], *Applied myrmecology: a world perspective*. Westview, Boulder, CO.
- Vargo, E. L., and D.J.C. Fletcher. 1986.** Queen number and the production of sexuals in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). *Behav. Ecol. Sociobiol.* 19: 41–47.
- 1987.** Effect of queen number on the production of sexuals in natural populations of the fire ant, *Solenopsis invicta*. *Physiol. Entomol.* 12: 109–116.
- Vargo, E. L., and S. D. Porter. 1989.** Colony reproduction by budding in the polygyne form of *Solenopsis invicta* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* 82:307–313.
- Vinson, S. B., and L. Greenberg. 1986.** The biology, physiology, and ecology of imported fire ants, pp. 193–226. *In* S. B. Vinson [ed.], *Economic impact and control of social insects*. Praeger, New York.
- Vlek, D. 1987.** Measurement of oxygen consumption, carbon dioxide production, and water vapor production in a closed system. *J. Appl. Physiol.* 62: 2103–2106.

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