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**Research article**

# Multivariate analyses of the factors affecting the distribution, abundance and social form of Louisiana fire ants, *Solenopsis invicta*

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**Abstract.** We surveyed 165 sites to determine the ecological factors influencing the distribution, abundance, and occurrence of polygyny in the red imported fire ant (*Solenopsis invicta)* in Louisiana. On average, sites had 220 nests/ha, 14 % of mounds were polygyne, and 22 % of sites had $\geq$ one polygyne mound. The density of nests and ants per site both increased with the proportion of mounds that were polygyne and the organic and phosphorous content of the soil but decreased with longitude, latitude, and the silt: clay, calcium and sodium content of the soil. Ant density also declined with ambient relative humidity. These multivariate models explained ~ 25 % of the variation in nest and ant density per site. Mean mound size per site increased with the phosphorous content of the soil and the number of nests at the site suggesting that prospective queens may select sites that are conducive to produce large mounds. Mean nest size, however, decreased with the proportion of nests that were polygyne and soil potassium while mounds in forests were typically larger than those in residential areas. Overall, this model accounted for 29 % of the variation in mean nest size per site. Polygyne sites were patchily distributed across Louisiana. The probability of a site being polygyne declined with mean monthly temperature for 1999 – 2003 and distance to the nearest commercial waterway suggesting that shipping activities may have played a role in the introduction of polygyne colonists to an area. Forested sites were also less likely to be polygyne than those in residential areas. Finally, the density of polygyne nests and ants increased with latitude whereas that of the monogyne form generally declined with latitude. The abundance of both social forms was also greater when they occurred alone. These data are consistent with the hypothesis that monogyne and polygyne *S. invicta* compete with one another.

*Keywords: Solenopsis invicta*, nest density, nest size, polygyny, commercial waterway.

## Introduction

Understanding the factors that determine the distribution and abundance of plants and animals is a problem that has long fascinated biologists (e.g., Lack, 1954; Andrewartha and Birch, 1960; Connor and Simberloff, 1979; Connell, 1980; Atauri and de Lucio, 2001; Symonds et al., 2006). In particular, the ecological factors that influence the distribution of ants have attracted considerable attention for two reasons. First, ants represent a substantial fraction of the biomass and are a major force structuring communities (Hölldobler and Wilson, 1990). Second, the ecology, demography and social structure of ants including the number of reproducing queens per nests (or polygyny) are believed to be tightly intertwined (e.g., Hölldobler and Wilson, 1990; Herbers, 1993; Bourke and Franks, 1995). Theoretical and empirical studies suggest that high population densities coupled with ecological constraints that increase the costs of queens dispersing from their natal mounds and/or establishing nests solitarily should promote the adoption of queens into existing nests and favor the evolution of polygyny (e.g., Herbers, 1986; Nonacs, 1988; Keller, 1991; Pamilo, 1991; Heinze, 1993; Bourke and Heinze, 1994; Seppä et al., 1995; Pedersen and Boomsma, 1999a; Ingram, 2002; Foitzik et al., 2004). Keller (1995) proposed that studying populations with varying numbers of queens per nest may provide insight into the determinants of polygyny.

The red imported fire ant (*Solenopsis invicta*) is a South American native that was accidentally released in Alabama, US in the late 1930's and since then has spread to 15 states and Puerto Rico. There are two forms of *S. invicta* mounds, apparently determined by variation at a single gene, *Gp-9* (Ross and Keller, 1998; Krieger and Ross, 2002). Monogyne mounds are always headed by a single fertile queen of genotype $Gp\text{-}9^{BB}$ while polygyne ones always have multiple queens of genotype $Gp\text{-}9^{Bb}$ (Ross and Keller, 1998). *Gp-9* may also affect the population biology of *S. invicta* by influencing the agonistic behavior of workers. Workers from neighboring polygyne nests exhibit little to no territorial behavior towards one another and this may allow nests to occur closer and polygyne populations to attain higher mound densities than monogyne ones (e.g., Porter et al., 1991; Macom and Porter, 1996; Fuxa et al., 2005). Mirenda and Vinson (1982), Greenberg et al., (1985), Porter et al. (1988; 1991), and Fritz and Vander Meer (2003) further observed that populations generally consist of predominantly one social form and proposed that the two forms cannot coexist. Keller and Ross (1998) showed that young queens of genotype BB introduced into polygyne mounds were attacked and killed by workers.

The abundance of *S. invicta*, which is a function of the number and size of mounds, and the distribution of the two social forms have been studied in both the native and introduced ranges. Porter et al. (1991) conducted an extensive survey of over 450 sites in Texas and showed fire ants reaching densities of ~ 400 mounds/ha with 54 % of sites having at least one polygyne nest. Their results also suggest that the proportion of nests that were polygyne was the single, most important predictor of *S. invicta* mound densities at a site. Porter (1992) conducted another, albeit more limited, survey of 85 sites located across part of Florida and found that nest densities (262 mounds/ha) and polygyny rates (15 % of sites) there were lower than in Texas. Finally, Porter et al. (1992; 1997) sampled 50–65 sites in South America and 5 to 30 sites in each of Texas, Louisiana, Mississippi, Alabama, Georgia, Florida and Puerto Rico to compare the demography of *S. invicta* in native and introduced ranges. They found that mound densities and polygyny rates were lower in South (40–60 mounds/ha; 0–12 % of sites polygyne, respectively) than North America (170–215 mounds/ha; 17–20 %of sites polygyne, respectively). Although these studies suggest interesting demographic differences between native and introduced *S. invicta* ranges and within the United States, they must be interpreted with caution because (1) only one type of habitat (roadside) was sampled and the sites were often preselected; and (2) apart from Porter et al. (1991), they include a relatively small number of sites considering the size of the area sampled.

While social form is likely to be an important determinant of *S. invicta* abundance, there are several other factors that may affect its demography. Climate is believed to be critical in limiting fire ant expansion within the US (Pimm and Bartell, 1980; Korzukhin et al., 2001; Sutherst and Maywald, 2005) but its impact on *S. invicta* abundance at finer geographical scales is more equivocal. Porter et al. (1991; 1997) found that temperature and precipitation were at best weakly related to *S. invicta* population density. Many studies have shown that the abundance and composition of ant communities vary across habitat type (e.g., Fisher, 1997; Pfeiffer et al., 2003; Sackmann and Farji-Brenner, 2006). Specifically, forests often have low fire ant densities, and *S. invicta* seems to prefer mesic habitats with high water tables over more xeric ones (Tschinkel, 1988a). Porter et al. (1991) found that the density of *S. invicta* was higher on grazing lands than on lawns while Russell et al. (2001) observed more fire ant nests on roadbeds than in adjacent pastures. More generally, soil attributes also appear to affect ant abundance (Fisher, 1997; Bestelmeyer and Wiens, 2001; Wang et al., 2001; Boulton et al., 2005; Rios-Casanova et al., 2006). Clay-rich soils may have greater moisture retention and have been associated with better alate survival in *Pogonomyrmex rugosus* and *P. barbatus* (Johnson, 2000). Ant abundance was higher in sandy soils (Rios-Casanova et al., 2006) perhaps because they are easier to tunnel. *S. xyloni* abundance in serpentine soils was positively correlated with pH and the organic matter, zinc, potassium, copper, boron and sodium content of the soil (Boulton et al., 2005). Soil coarseness affected the density of *S. invicta* mounds in North America but not in Brazil or Argentina (Porter et al., 1997). The effect of soil chemistry on *S. invicta* abundance has not yet been investigated. Finally, human activity played a key role in the introduction of *S.invicta* and it may also be an important determinant of its distribution and abundance within the US (e.g., Vinson, 1997; Forys et al., 2002). In particular, human-mediated dispersal of mated queens or nest fragments may be of significant importance to the polygyne form because of its limited dispersal ability (Ross and Keller, 1995).

The goals of this study were four-fold: first, to establish a more comprehensive account of the distribution and abundance of *S. invicta* in Louisiana. Second, to determine the effect of social form, climate, habitat type, geography, soil attributes and human activity on *S. invicta* abundance. As far as human activity, we focused on the effect of shipping and movement of goods along commercial waterways. Louisiana has many of the most important deep water and inland ports and typically leads the US in total cargo tonnage (United States Army Corps of Engineers, 2003). Third, to ascertain the occurrence, distribution and ecological correlates of S. *invicta* polygyny in Louisiana. Fourth, to compare the abundance of monogyne and polygyne *S. invicta* at sites with a single social form to that where both forms occur.

## Methods

### *Selection of sites*

The state of Louisiana was divided into 55 quadrats of approximately 900 square miles. Three longitudinal and latitudinal coordinates were randomly selected within each quadrat, and the nearest road-accessible point was designated as the site to be sampled. The roads used to access these sites included highways (interstate and state highway), city streets, and service roads on farms, oil fields, hunting clubs, wildlife management areas, state parks, logging areas and National Forests.

### *Sampling methods*

Once at a site, we walked a random number of paces in a random direction and used that point as the center of our study plot. The plot was 0.05 hectare and was searched for approximately 30 minutes for *S. invicta* mounds. The size of each colony was determined by slightly disturbing the mound and scoring the number of workers seen on a scale of 1 to 5 (1 = ≤ 100 workers 2 = 101 – 1,000 workers; 3 = 1,001 – 10,000 workers; 4 = 10,001 – 50,000 workers; 5 = > 50,000 workers) that was based on Lofgren and Glancey (1982). The presence of brood was also recorded, and an ant sample for each of up to 10 mounds per site (mounds determined at random when there were more than 10) was taken by placing a Teflon coated vial at disturbed nests (see Fuxa et al., 2005). The ant samples were kept in a cooler and returned to the laboratory where they were placed at –4°C until further analysis. Soil and vegetation samples were taken from the center of the plot and at least 1 m away from the nearest nest (soil and vegetation sample were not taken from 10 sites). Temperature and relative humidity at the time of collection were also recorded. Sites were sampled in the spring (27 March 2003 – 5 May 2003) when fire ants are most active in their mounds (Porter et al., 1991), and only when it did not rain or was not unusually cold (mean ± SD conditions at sampling: 25.9 ± 6.4°C and 52 ± 16.6% RH).

### *Soil attributes and climate data*

Soil characteristics (see below) were determined by standard analytical techniques at the department of Agronomy at Louisiana State University. Monthly climate data (mean temperature and total precipitation) were obtained from the Louisiana Office of State Climatology for the weather station closest (mean ± SD distance: 17.4 ± 5.1 km) to each fire ant sampling site for 1 January 1999 to 27 March 2003.

### *Nest social form*

*S. invicta* social form was determined by purifying DNA from a group of 30 ants per nest and conducting two separate polymerase chain reactions (PCR) using the primers and conditions of Valles and Porter (2003). The first PCR detected the $Gp\text{-}9^B$ allele and served as a positive control as virtually all individuals carry this allele (Krieger and Ross, 2002). The second one was specific to the $Gp\text{-}9^b$ allele and thus was used to identify polygyne mounds (Krieger and Ross, 2002).

### *Dependent and independent variables*

There were four dependent variables: number of mounds (square root transformed to meet assumption of normality), mean nest size, ant density (= number of mounds per site x mean size of mounds; square root transformed to meet assumption of normality), and presence/absence of ≥ 1 polygyne nests per site.

To meet the assumption of linearity, independent variables expressed as percentages were arcsine square root transformed while soil chemistry variables were square root transformed (Sokal and Rohlf, 1981). The independent variables fall under five headings: first, habitat characteristics ($n = 4$): four dummy variables (Habitat Variable 1 to 4) were used to denote the type of habitat in which a site was found: fields used in agriculture, for grazing, or crops were respectively assigned 1, 0, 0, 0: forests: 0, 1, 0, 0; highway shoulders, ditches and right-of -ways: 0, 0, 1 and 0; river/stream banks and marsh edges: 0, 0, 0 and 1; and lawns on public or private property: –1, –1, –1 and –1. Second, geographic characteristics ($n = 4$): latitude, longitude (expressed as negative values because Louisiana is West of the Prime Meridian), distance to the nearest one of the top six Louisiana commercial waterways (see below), and distance to the nearest port. Third, ant nest characteristics ($n = 1$ or 2): percent polygyne nests at a site (arcsine square root transformed) was used as an independent variable in the analyses of number of mounds, mean mound size, and ant density. The number of nests (square root transformed) at a site was also used as an explanatory variable in the analysis of nest size. Fourth, soil characteristics ($n = 9$): pH; % organic matter (arcsine square root transformed) ; % sand, % silt and % clay expressed as log (% sand / % clay) and log (% silt / % clay) because % sand + % silt + % clay = 1 (see Sokal and Rohlf, 1981); and, calcium, magnesium, phosphorus, potassium, and sodium concentration (all square root transformed). Fifth, climate characteristics ($n = 2$): mean monthly temperature and precipitation averaged across 1 January 1999 to 27 March 2003. Air temperature and relative humidity at the time a site was surveyed were also included in the analyses of mound size and ant density as they may affect nest rating (Pranschke and Hooper-Bui, 2003).

Climate means were calculated using data from the 5 years preceding the survey. Yearly mean temperature and precipitation were generally intercorrelated (data not shown) suggesting that five-year means should thus be representative of longer-term as well as recent past conditions at a site.

The six busiest commercial waterways in Louisiana are the Mississippi River, the Calcasieu shipping channel, the Sabine River, the Intracoastal Waterway, the Red River, and the Atchafalaya River (see Fig. 1). The top imported cargoes moving along these waterways are petroleum products, iron, steel, metal ores, methanol, coffee, forest products, fertilizers, molasses, and bulk chemicals. The top cargoes bound for export include farm products (grains and machinery), petroleum products, iron, steel, metal ores and scrap, coke, and pipe. Domestic cargoes include many of the previously listed goods plus limestone, gravel, and sand. All waterway statistics were obtained from the US Army Corps of Engineers (2003).

### *Statistical analyses*

Data were analysed with uni- and multivariate statistics. Pearson correlation, simple logistic, and multiple linear and logistic regressions were used to examine the effect of continuous predictors on a dependent variable while 1-way ANOVA, and contingency tables were used for categorical predictors. Multiple linear and logistic regressions were used to examine the joint effect of predictors on the dependent variables and were built using backward variable selection. This approach starts with all predictors in the model and removes the independent variable that explains the least variation. The process is repeated until the change in explained variance (usually controlled by F-value) becomes significant. We chose this method because adding any single predictor, as in stepwise selection, may have little effect and cause the construction of the model to stop, possibly overlooking many models that better fit the data (Graham, 2003). Residual analyses of the models selected did not suggest that the assumptions of regression were violated. All analyses were conducted using SAS (2003).

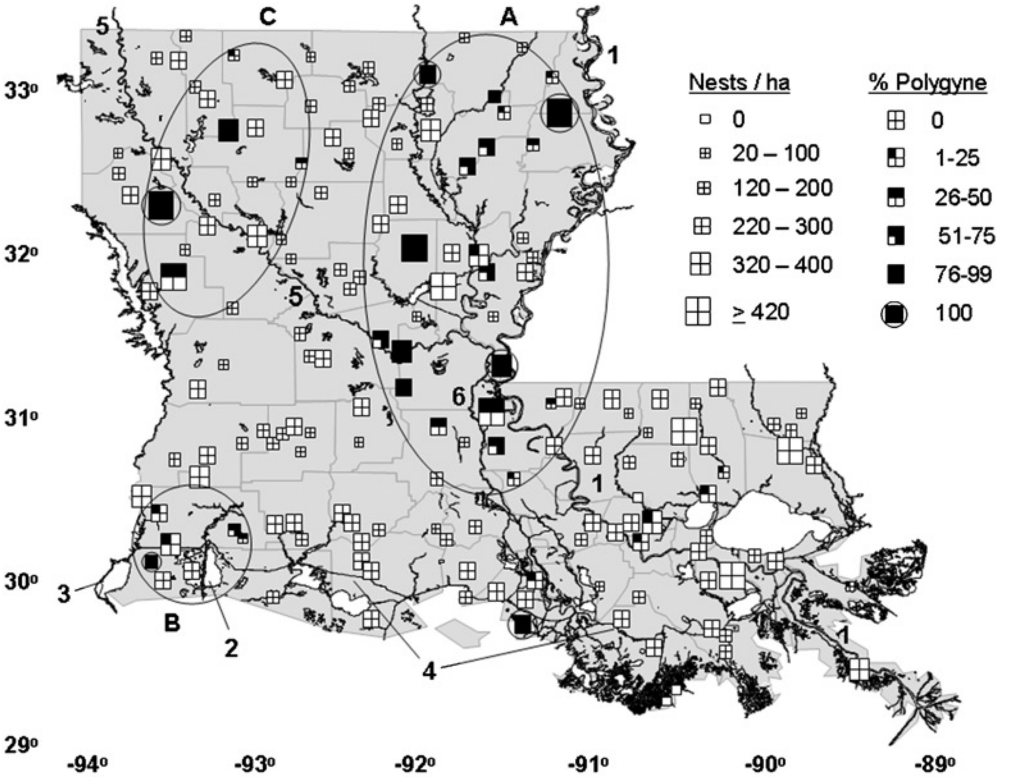

**Fig. 1.** Number of mounds per hectare and percent nests that were polygyne at 165 Louisiana sites surveyed between 27 April and 5 May 2003. 1 = Mississippi River; 2 = Calcassieu Shipping Channel; 3 = Sabine Shipping Channel; 4 = Intracoastal Waterway; 5 = Red River; 6 = Atchafalaya River.

## Results

### *General*

*S. invicta* mounds were found at 98 % (162/165) of sites, and in all 55 Louisiana parishes (Fig. 1). On average, there were 11.0 (SD = 0.6) nests per site (= 220 nests/ha) with a mean nest size of 3.0 (SD = 0.6). The majority (86 %; 1128/1313) of *S. invicta* mounds screened were monogyne, and only 14 % (185/1313) were polygyne. Polygyne sites (sites with ≥ 1 polygyne mound: mean ± SE: 15.5 ± 2.1) had 57 % more nests than monogyne ones (mean ± SE: 9.9 ± 0.4; t = –2.56, d. f. = 39, P = 0.014). The majority (65 %; 120/185) of polygyne mounds occurred at sites where they were intermingled with monogyne mounds. Overall, 76 % (125/165) of sites had monogyne nests only, 18 % (30/165) had both social forms, and 4 % (7/165) consisted exclusively of polygyne mounds (3 sites had no fire ants).

### *Nest and ant density*

A one-way ANOVA showed that mound and ant density were independent of habitat category (both $F \leq 1.4$, d.f. = 4,160, and $P \geq 0.24$; Table 1). Simple (Pearson) linear correlations showed that the number of mounds and the density of *S. invicta* ants both increased with the proportion of nests that were polygyne (number of mounds: r = 0.294; ant density: r = 0.207, N = 165, both $P < 0.008$) and decreased with the sodium content of the soil (number of mounds: r = –0.195, P =0.02; ant density: r = 0.172, P = 0.03, both N = 155).

Multivariate analyses showed that the density of *S. invicta* nests (NEST) and ants (ANT) per site increased with the proportion of mounds that were polygyne (POLY); and the organic matter (OM) and phosphorus ($P^{5+}$) content of the soil. Both density indices also decreased with longitude (LONG; from west to east); latitude (LAT; from south to north); and the silt: clay (SILT: CLAY), calcium ($Ca^{2+}$) and sodium ($Na^{+}$) content of the soil. Percent ambient relative humidity (RH) was also retained in the ant density model. The two models

$$\begin{aligned}\mathrm{NEST} = {} & 0.02(\mathrm{POLY}) + 0.13(\mathrm{OM}) + 0.07(\mathrm{P}^{5+}) - 0.29(\mathrm{LONG}) \\ & - 0.24(\mathrm{LAT}) + 0.49(\mathrm{SILT{:}CLAY}) - 0.01(\mathrm{Ca}^{2+}) - 0.07(\mathrm{Na}^{+}) \\ & + 15.69\end{aligned}$$

$$\begin{aligned}\mathrm{ANT} = {} & 0.02(\mathrm{POLY}) + 0.24(\mathrm{OM}) + 0.10(\mathrm{P}^{5+}) - 0.54(\mathrm{LONG}) \\ & - 0.37(\mathrm{LAT}) - 1.04(\mathrm{SILT{:}CLAY}) - 0.02(\mathrm{Ca}^{2+}) - 0.11(\mathrm{Na}^{+}) \\ & - 0.020(\mathrm{RH}) - 30.37\end{aligned}$$

explained about the same proportion of variance (nest density model: $R^2 = 0.25$, F = 6.09, d.f. = 8,146 and $P < 0.001$; ant density model: $R^2 = 0.24$, F = 5.07, d.f. = 9, 145 and $P < 0.001$). Interestingly, the relationships with latitude appear to vary across social form. The density of polygyne nests and ants per site *increased* with latitude (polygyne nest density = number of nests at site x percent polygyne nests: Pearson r = 0.183; polygyne ant density = polygyne nest density x mean size of polygyne

**Table 1.** Mean (SE) number of mounds, nest size, and ant density (= number of mounds x mean mound size) per site ( = 0.05 ha) in relation to type of habitat category. Means followed by the same letter are not significantly different ($P > 0.05$) by ANOVA followed by a Tukey test.

| | Habitat Category | | | | |
|---|---|---|---|---|---|
| | Agriculture ($n = 52$) | Forest ($n = 42$) | Highway-ROW ($n = 28$) | Marsh ($n = 9$) | Residential ($n = 31$) |
| Mean Number Mounds | 11.7 (0.9)a | 9.3 (1.1)a | 10.8 (1.2)a | 9.1 (1.8)a | 12.8 (2.1)a |
| Mean Nest Size | 2.9 (0.1)ab | 3.2 (0.1)b | 2.9 (0.1)ab | 3.0 (0.4)ab | 2.6 (0.1)a |
| Mean Ant Density | 34 (2.5)a | 29.5 (3.2)a | 30.3 (2.9)a | 30.6 (6.7)a | 34.6 (5.1)a |
| Observed (Predicted)[1] Monogyne: Polygyne Sites | 37:15 (40.1:11.9) | 38:4 (32.4:9.6) | 22:6 (21.6:6.4) | 7:2 (6.9:2.1) | 21:10 (23.9:7.1) |
| Observed (Predicted)[1] Monogyne: Polygyne Nests | 390:52 (379.7:62.3) | 278:20 (256:42) | 180:42 (190.7:31.3) | 54:19 (62.7:10.3) | 226:52 (238.8:39.2) |

[1] Predicted number of nests or sites assuming that social form and habitat type are independent of each another.

*Note:* Three sites had no *S. invicta* nests and were omitted from the analyses.

nests: Pearson $r = 0.184$, both $P = 0.009$ and $N = 165$) whereas the reverse was generally observed for monogyne mounds and ants (monogyne nest density = number of nests at site x (1-percent polygyne nests): $r = -0.123$, $P = 0.057$; monogyne ant density = monogyne nest density x mean size of monogyne nests: $r = -0.147$, $P = 0.03$, both $N = 165$).

### Nest size

One-way ANOVA showed that mean nest size per site varied across habitat category (Table 1: $F = 3.6$, d.f. = 4,160, $P = 0.008$). Mounds in forests were larger than those in residential areas (Table 1). Simple linear correlation showed that mean nest size was also related to the number of mounds at the site ($r = 0.271$, $N = 165$, $P < 0.001$); the proportion of nests that were polygyne ($r = –168$, $N = 165$, $P = 0.031$); and to the sand: clay ($r = 0.224$, $N = 155$, $P = 0.005$), magnesium ($r = -0.294$, $N = 155$, $P < 0.001$), potassium ($r = -0.282$, $N = 155$, $P < 0.001$) and sodium ($r = -0.271$, $N = 155$, $P < 0.001$) content of the soil.

Multiple regression analysis showed that nest size (NEST SIZE) increased with the density of nests at the site (NEST) and the phosphorus concentration of the soil. It, however, declined with the proportion of nests that were polygyne and soil potassium ($K^+$) content. Habitat Variable 2 (HV2) was also retained in the model suggesting that mounds in forests were larger than those in residential areas. This model

$$\text{NEST SIZE} = 0.18(\text{NEST}) + 0.03(P^{5+}) - 0.005(\text{POLY}) - 0.04(K^+) + 0.30(\text{HV2}) + 2.36$$

explained 29 % ($F = 12.42$, d.f. = 5,149, $P < 0.001$) in mean mound size per site.

### Polygyny

The majority of polygyne sites found during this study (20/37; 54 %) were located in the eastern part of the upper half of the state starting near the elbow in the Louisiana-Mississippi state line and extending up to Arkansas (Patch A; Fig. 1). Furthermore, the majority of sites within this area (20/39; 51 %) were polygyne. There appeared to be a second, smaller clump in the southwest corner near Lake Charles, LA and perhaps an even looser one in the northwest close to Shreveport, LA (Patches B and C, respectively; Fig. 1).

Simple logistic regression analyses showed that the probability of a site being polygyne increased with the potassium (simple logistic regression coefficient = 0.088, $\chi^2 = 4.77$, d. f. = 1, $P = 0.03$) and magnesium content of the soil (simple logistic regression coefficient = 0.056, $\chi^2 = 4.88$, d. f. = 1, $P = 0.03$). Polygyne sites (= sites with $\geq 1$ polygyne mound) were independently distributed across habitat category (Table 1: $\chi^2 = 6.88$, d.f. = 4, $P = 0.14$). Polygyne nests were not distributed at random across habitat type (Table 1; $\chi^2 = 31.1$, d. f. = 4, $P < 0.001$). Forests had less than half while habitats along marsh edges and waterway banks had 84 % more polygyne mounds than expected by chance (Table 1).

Multivariate analyses showed that the probability of a site having at least one polygyne nest declined with distance to the nearest commercial waterway (DISTWATERWAY), and with mean monthly temperature across 1999 to 2003 (TEMP99–03). Habitat Variable 2 was also included in the model suggesting that sites in residential habitats were more likely to be polygyne than those in forests (Tables 1 and 2). The goodness-of-fit test that compared the three variable model

$$\text{logit (POLY)} = -0.01(\text{DISTWATERWAY}) - 0.32(\text{TEMP99–03}) - 0.72(\text{HV2}) + 20.27$$

with just the constant was significant ($\chi^2 = 10.1$, d. f. = 3, $P < 0.0019$).

**Table 2.** Mean (SE) number of nests, nest size and ant density of each social form per site (0.05 ha) with monogyne nests only, polygyne nests only, or both social forms.

| | Monogyne Nests Only (N = 125) | Monogyne and Polygyne Nests (N = 30) | Polygyne Nests Only (N = 7) | % Difference[1] |
|---|---|---|---|---|
| Mean No. Monogyne Nests | 9.9 (0.4) | 8.0 (1.6) | | –19 |
| Mean No. Polygyne Nests | | 7.0 (0.5) | 17.7 (3.9) | –60 |
| Mean Size Monogyne Nests | 3.0 (0.05) | 3.0 (0.1) | | 0 |
| Mean Size Polygyne Nests | | 2.6 (0.1) | 2.6 (0.1) | 0 |
| Mean Ant Density of Monogyne Nests | 31.2 (1.5) | 24.8 (5.4) | | –21 |
| Mean Ant Density of Polygyne Nests | | 18.7 (3.8) | 44.3 (8.2) | –58 |

[1] with monogyne or polygyne nests only.

### *Mixed sites*

About 80 % (30/37) of sites designated as polygyne also had monogyne mounds. Overall, there was a near even proportion of nests of each social form at these 30 mixed sites (monogyne: 53.8 % (140/260); polygyne: 46.2 % (120/260)).

The density of polygyne mounds and ants at mixed sites was about 60 % lower than that at sites with only polygyne mounds (Table 2: mounds: F = 10.4; ants: F = 8.6; both d.f. = 1, 35, *P* = 0.001 and 1-tail tests). Similarly, there were approximately 20 % fewer monogyne nests and ants at mixed sites than at those with monogyne nests only, but the difference just failed significance in both cases (Table 2: mounds: F = 2.50: ants: F = 2.45; both d.f. = 1, 153; *P* = 0.058 and P = 0.059 respectively; 1-tail tests). The mean sizes of monogyne and polygyne mounds at mixed sites did not differ from those from sites with a single social form (Table 2: size of polygyne mounds: F ≃ 0, d.f. = 1, 35: size of polygyne nests: F = 1.1, d.f. = 1, 153, both *P* > 0.30).

## Discussion

### *General*

*S. invicta* was found at 98 % of sites with an average of 220 mounds/ha/site. Porter (Porter, 1992) and Porter et al. (1992; 1997) reported similar findings in their fire ant surveys of the southeast US and Puerto Rico (170 – 262 mounds/ha). In neighboring Texas, however, *S. invicta* occurred at about twice those densities (~400 mounds/ha/visited site) (Porter et al., 1991). Seasonality and differences in habitats sampled cannot explain this discrepancy. All four surveys were conducted in early spring to early summer. A comparison limited to sites along highways shows that mounds were still more than twice as numerous in Texas than Louisiana (10.8 nests per 0.05 ha = 216 nests/ha see Table 1). Polygyny is one factor that may account, if only partially, for lower nest densities in Louisiana. Polygyne sites (with ≥ 1 polygyne mound) typically have greater nest densities (e.g., Porter et al., 1991; Macom and Porter, 1996; Fuxa et al., 2005) and were more than twice as frequent in Texas (54 %; Porter et al., 1991) than in this study (22 %; 37/165) or in Porter et al., (1992; 1997: US polygyny rates = 17 and 20 %, respectively).

### *Nest and ant density*

Social form also appears to be a key determinant of *S. invicta* population densities *within* Louisiana. The density of nests and ants per site increased with the proportion of mounds that were polygyne corroborating the results of many studies on *S. invicta* (e.g., Porter et al., 1991; Ross and Keller, 1995; Fuxa et al., 2005) and other species (e.g., Seppä et al., 1995; Pedersen and Boomsma, 1999b; Ingram, 2002).

Our multivariate analyses suggest that other variables may also influence *S. invicta* abundance in Louisiana. First, ant and nest density declined with longitude (west to east; Table 1). Porter et al., (1991) also observed that mound densities covaried with longitude in Texas but they found that it increased with longitude. Our finding could be the result of (a) the shape of the state and (b) polygyne sites which typically have higher nest densities mainly occurring in northern Louisiana (Fig. 1). Within the top or bottom half of the state (above/below 31°, respectively), there appears to be little indication that nest densities vary with longitude.

Second, ant and nest density decreased with increasing latitude (from south to north). Several measures of abundance (population density, species abundance and/or diversity) have been shown to decline with latitude in a variety of ant species (Gustavo et al., 1994; Weseloh, 1995; Majer et al., 2001; Gotelli and Ellison, 2002; Kilpelainen et al., 2005). The effect of latitude observed in this study may, however, vary across social form and will be discussed below.

Third, several soil attributes (organic matter +; phosphorus +; silt: clay –; calcium –; sodium –) were associated with *S. invicta* nest and ant abundance. The organic content of the soil maintains the soil in a loose, friable condition and supplies many essential nutrients for plant growth such as phosphorus (Ashman and Puri, 2002). Phosphorus is involved in plant respiration, photosynthesis and is part of nucleic acids and cell membranes (Salisbury and Ross, 1992). The organic matter and phosphorus content may thus reflect soil fertility and vegetation composition, a cue that may be simple enough for prospective queens to use when choosing nesting sites. Several studies have reported positive correlations between ant species richness and plant community attributes (e.g., Quiroz-Robledo and Valenzuela-González, 1995; Torres and Snelling, 1997; Rios-Casanova et al., 2006). Prospective queens may prefer sites with luxurious vegetation because they support an abundant and diverse guild of herbivores that *S. invicta* can prey upon. On the hand, soils with high silt content are easily compacted, poorly aerated, impervious and allow puddles to form (Ashman and Puri, 2002). Calcium is another important plant nutrient but high soil calcium concentrations can interfere with the uptake of magnesium, a component of chlorophyll (Street and Kidder, 1997). Soils rich in sodium tend to be hard, crust when dry and to have poor drainage, germination and plant growth (Ashman and Puri, 2002). Sites with soils rich in silt, calcium and sodium may be poor nesting sites for *S. invicta* because of poor plant growth (and food availability) and heightened risk of mounds drowning during heavy rainfalls. Alternatively, instead of soil chemistry influencing fire ant abundance, *S. invicta* presence may be *responsible* for these relationships. Several studies have shown that ants, including *S. invicta*, can alter physico-chemical properties of the soil and that conditions inside nests differ from those adjacent to the mound (e.g., Herzog et al., 1976; Green et al., 1999; Dostal et al., 2005; Frouz et al., 2005; Lafleur et al., 2005; Wagner and Jones, 2006). It has further been proposed that these effects may be transmitted to the entire landscape as mounds relocate.

The density of ants at a site also declined with percent ambient relative humidity when a site was surveyed. Pranschke and Hooper-Bùi (2003) proposed that low soil relative humidity may increase working dessication and cause them to move deep below ground where moisture may be higher thus causing the size of nests to be underestimated.

Finally, our regression models explained only ~25 % of the variation in *S. invicta* ant and nest density indicating that other variables may influence fire ant abundance. Monogyne nests can live up to 7 years (Tschinkel, 1987) and polygyne mounds perhaps even longer because they (1) have multiple queens and (2) can adopt newly mated ones (Glancey and Lofgren, 1988; Vander Meer and Porter, 2001). The distribution and abundance of *S. invicta* at the time of this survey may thus have been influenced by historical and stochastic events having occurred up to a decade earlier.

### *Nest size*

The mean size of mounds at a site declined with the proportion of nests that were polygyne (Table 1). This result is consistent with many other findings including Porter et al., (1991), Keller and Ross (1995) and Macom and Porter (1996). Nest size, however, increased with the number of nests per site. This may initially appear counter intuitive because areas with high nest densities tend to be polygyne and should have smaller mounds. Instead, this result may indicate that once the effect of polygyny and other variables in the model are controlled, sites with high nest densities also produce large mounds.

Nest size was also related to many soil characteristics. Multiple regression analyses showed that the average size of mounds at a site increased with the phosphorus but decreased with the potassium content of the soil. Phosphorus levels may reflect prey abundance (see above) and sites with greater food resources may be able to support larger nests. The potassium relationship may be the by-product of (a) the probability of a site being polygyne increasing with soil potassium content and (b) polygyne mounds typically being smaller than monogyne ones. The relevance of other soil characteristics (magnesium, –; sodium, –; sand: clay, +) in determining nest size is a bit more ambiguous because these variables were only related to mound size in simple but not in multivariate analyses.

Habitat variable 2 (HV2) also entered the multivariate model indicating that mounds in forests were larger than those in residential habitats. This finding might be the result of forest habitats having the fewest polygyne sites and nests (Table 1).

Overall, our five variable (% polygyne nest, number of nests per site, $P^{5+}$, $K^+$ and HV2) regression model explained 29 % of variation in nest size. Nest age (Tschinkel, 1988b), disease, predation/parasitic intensity, intra- and interspecific competition with other ant/arthropod species, number of queens per polygyne nests are some other variables that may affect nest size but were not quantified in this study.

### *Polygyny*

Only 14 % of screened mounds were polygyne, and only 22 % of sites had one or more polygyne nest. As previously mentioned, the proportion of polygyne sites in Louisiana was less than half that of Texas but similar to the rest of the southeast US. Also, in contrast to Texas, the distribution of polygyne sites within Louisiana did not follow a mosaic pattern (Porter et al., 1991). Instead, polygyne sites appeared clumped in space and mainly occurred in three patches (Fig. 1). In particular, more than half of all polygyne sites were located in the eastern portion of the top half of Louisiana (Patch A; Fig. 1). Polygyne patches B and C (Fig. 1) probably represent the eastern range of the polygyne distribution observed in

Texas and the gap between these patches coincides with the area in Texas that is dominated with forests and where there were no polygyne nests (see Fig. 2 of Porter et al., 1991). The areas between Patches B and C, and between C and A in Louisiana (Fig. 1) includes 5 stands of the Kitsatchie National Forests and 9 wooded management areas further suggesting that forests may be an important barrier impeding the dispersal of polygyne queens.

The six Louisiana sites that Porter et al. (1992) found to be polygyne more than a decade earlier were all located in the vicinity of our polygyne sites. Porter et al., (1991) revisted a sample of their Texas sites 12 months following their initial survey and found that the majority of them had retained their initial designation i.e. monogyne and polygyne. Together, these findings suggest that site social form may be quite static.

The probability of a site being polygyne varied across habitat type. Forests were less likely to have polygyne sites than residential areas. Tsuji and Tsuji (1996) argued that ant populations were controlled by density dependent factors in forests and that this favored monogyny whereas density independent processes were more prevalent in open areas favoring polygyny. To support their hypothesis, Tsuji and Tsuji (1996) used the data of Yamauchi and Ogata (1995) and showed that 68% of the ant species on Okinawa Island whose main habitat were forests were monogyne whereas 77% of those nesting predominantly in open areas were polygyne.

The probability of a site being polygyne declined with mean monthly temperature for 1999 – 2003. This is probably a reflection of most polygyne sites being located in the northern half of the state. Three explanations may account for our finding. First, the polygyne form is adapted and prefers colder climates. To date, there is no evidence to support this hypothesis. Second, the polygyne form is relegated to colder habitats because it is an inferior competitor to the monogyne form. Third, the initial colonists to these areas were polygyne and because of their limited ability to disperse and establish mounds claustrally (Ross and Keller, 1995) have not yet been able to move to warmer habitats.

The probability of a site being polygyne decreased with distance to the nearest commercial waterway. This suggests that shipping activities may have played an important role in the introduction of polygyne colonists to an area and perhaps also in their subsequent spread from there. Mounds may have accidentally been brought with cargo or ballast. Mated queens are attracted to shinny reflective surfaces (Vinson, 1997) such as cargo containers and may have been carried long distances aboard ships. Their dispersal inland may be more dependent on their limited flight capabilities and may explain why the probability of a site being polygyne declines as distance to the nearest waterway increases.

The probability of a site being polygyne increased with the magnesium and potassium content of the soil in simple but not multiple regression analyses thus making it difficult to assess their relevance. Magnesium is part of chlorophyll while potassium is required in many plant enzymatic reactions and carbohydrate metabolism (Salisbury and Ross, 1992). Hence, as with phosphorus, the magnesium and potassium content of the soil may reflect fertility and be an indicator of prey availability. Food abundance may be of particular importance to prospective polygyne queens because of the greater caloric demands of the polygyne form relative to the monogyne one (Macom and Porter, 1996).

### *Mixed sites*

At individual sites, the abundance (mound and ant density) of polygyne *S. invicta* was lower when the other form was present (mixed sites). There also were 20% fewer monogyne mounds and ants at mixed sites than at pure monogyne ones but the differences just missed significance. The size of monogyne and polygyne mounds, however, was not influenced by the presence of the other form suggesting that the interactions between the two forms may be greatest when mounds are founded.

At the level of the state of Louisiana, monogyne and polygyne sites appear segregated in space (Fig. 1). The density of polygyne mounds and ants per site increased with latitude whereas the reverse was generally observed in the case of the monogyne form. Overall, these data are consistent with the hypothesis that monogyne and polygyne *S. invicta* adversely affect each others' demography. This could be the result of (a) agonostic, territorial behavior between workers of different forms or (b) more benign, passive processes. Sites have a fixed carrying capacity and the presence of one form should limit the amount of space and resources available to the other. Hence, even in the absence of antagonistic interaction between monogyne and polygyne *S. invicta*, one might expect the abundance of both forms to be lower at mixed than pure sites. The distribution of the two social forms at the state level may also simply reflect the initial invasion locations of the two forms or that monogyne and polygyne *S. invicta* have different habitat requirements, in which case, the conditions at mixed sites may have been intermediate and suboptimal for each social form. At this time, however, we are not aware of any evidence supporting this hypothesis.

### *Limitations*

In this study, we used regression analyses to identify the variables that might affect the distribution and abundance of *S. invicta* in Louisiana. Interpreting the parameter estimates of multivariate regression models from any observational study can be very challenging (e.g., Sokal and Rohlf, 1981). The problem is even more acute when models contained several predictors. Furthermore, as with any other observational study, our findings do not imply causality. Future work should thus attempt to experimentally manipulate the predictors we identified to confirm their effect on fire ant abundance and social form.

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