Fire Ant Mound Densities in the United States and Brazil (Hymenoptera: Formicidae)

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ABSTRACT To compare fire ant populations *(Solenopsis)* in North and South America, we surveyed 102 preselected roadside sites, half in the southeastern United States and half in the state of Mato Grosso do Sul, Brazil. Fire ants were considerably more abundant in the United States. They occurred at more sites (100 versus 70%), in higher densities (170 versus 30 mounds/ha), in larger mounds (27.0 versus 13.8 liters), and they constituted a larger fraction of the local ant community (97 versus 13% of occupied baits). These data are consistent with the hypothesis that North American populations of *S. invicta* have escaped natural biological control; however, cultural and climatic factors are also likely explanations.

KEY WORDS Insecta, *Solenopsis invicta,* polygyny, invasions

THE RED IMPORTED FIRE ANT, *Solenopsis invicta* Buren, was introduced into the United States from South America ≈50 yr ago (Vinson & Greenberg 1986). Today, this exotic pest infests almost the entire southeastern United States. High densities of *S. invicta* have caused numerous environmental and economic problems (Lofgren 1986).

The introduction of exotic species into new continents usually occurs without natural biological control agents (DeBach 1974). This was certainly true for *S. invicta*. Numerous pathogens, parasites, and other potential biological control agents have been found in South America (Jouvenaz et al. 1980, Williams 1980, Jouvenaz 1986, Wojcik et al. 1987), but only a handful have been discovered in the United States (Collins & Markin 1971, Jouvenaz et al. 1977, Neece & Bartell 1981, Kathirithamby & Johnston 1992).

The absence of natural enemies can allow exotic species to reach much higher population densities in newly invaded regions than in their native habitats (van den Bosch et al. 1973, Huffaker & Messenger 1976). Some reports have suggested that the fire ant populations are much higher in the United States than in South America (Allen et al. 1974, Williams & Whitcomb 1974, Fowler et al. 1990), whereas other reports indicated that population densities are similar (Hays 1958, Wojcik 1983, Banks et al. 1985, Wojcik 1986). Most of these reports, however, were based on informal observations and none of them used uniform sampling procedures across continents.

To address this problem, we conducted a systematic survey of fire ant populations in the southeastern United States and the state of Mato Grosso do Sul, Brazil. We also assessed the frequency of polygyny and the relative dominance of *S. invicta* in local ant communities.

Materials and Methods

Techniques used in this survey were similar to those of Porter et al. (1991). We preselected 50 sites along roadsides in the state of Mato Grosso do Sul, Brazil, and another 52 in the southeastern United States (Fig. 1). Mato Grosso do Sul was surveyed because the region around the Pantanal has been proposed as the homeland of the fire ant in South America (Allen et al. 1974, Buren et al. 1974). Roadsides were used because they were appropriate fire ant habitat, they have structurally similar vegetation, they were convenient, and they helped to standardize sampling efforts between countries. Sites in both countries were generally along two-lane paved highways in rural areas. Locations of sites in both countries were carefully recorded so that they could be resampled within 50 m or less. Sampling was conducted during the spring of 1989 in both countries, with U.S. sites being sampled 11–18 March and Brazilian sites 8–19 October.

We collected four major types of information at each site: (1) habitat and environmental data, (2) estimates of mound densities, (3) foraging activity, and (4) the presence or absence of multiple-queen colonies. Habitat and environmental data included mean soil temperature (5 cm), soil moisture (dusty, damp, moist, wet), soil type,

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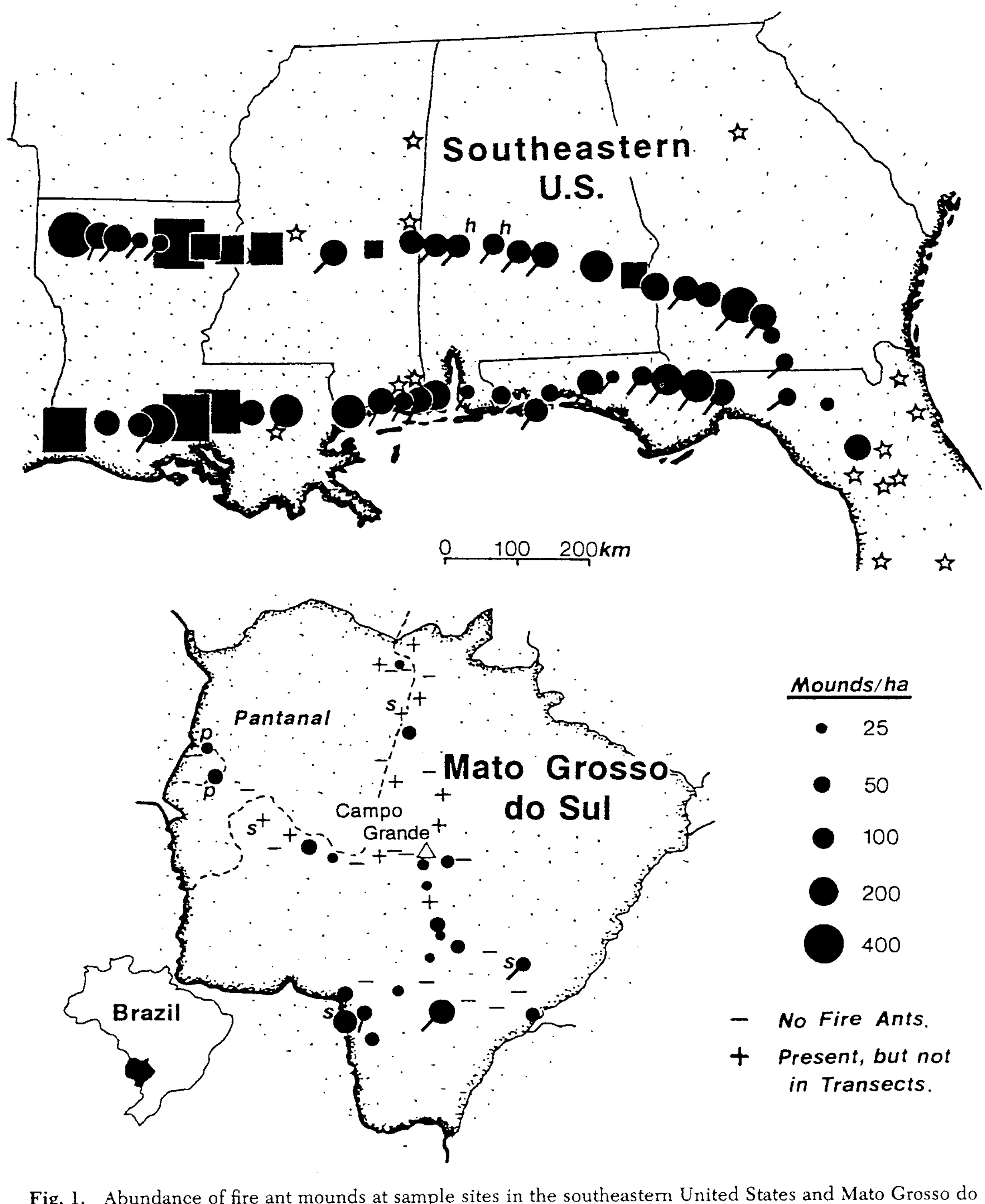

Fig. 1. Abundance of fire ant mounds at sample sites in the southeastern United States and Mato Grosso do Sul, Brazil. Areas of circles and squares are proportional to mound density. Circles indicate monogyny; diagonal tails on circles indicate confirmed monogyny. Squares indicate polygyny. All sites contained the red imported fire ant, *S. invicta*, except those indicated by "*h*" (*S. invicta* × *S. richteri* hybrid), "*p*" (*S. pusillignis*) or "*s*" (similar to *S. saevissima*). Stars show locations of previously reported polygyne populations (see Glancey et al. 1973, Fletcher 1983, Glancey et al. 1987, Glancey et al. 1989).

grade of road, percent bare ground (0, 10, 25, 50, 75, 90, 100), height of grass along roadside, height of nearby trees or shrubs, and type of vegetation adjacent to road rights-of-way.

Mound densities were determined from four belt transects, two on either side of the road. One transect on each side of the road was along the outer border of the right-of-way; the other was on the inner border adjacent to the road. Each transect was 70 paces long. All active mounds within reach of a 1.2-m stick were tallied into one of six categories according to their diameter: ≤15, ≤30, ≤46, ≤61, ≤76, and >76 cm. We also measured the height, width, and length of the first four mounds found at each site. Mound volumes (v) were calculated using the formula for half of a spheroid ($v = 2/3\pi abc$, where a is length/2, b is width/2, and c is height). The pace and reach of each investigator were determined and used to calculate the area they sampled. The average pace was 0.9 m and the average reach was 2.5 m.

Polygyne and monogyne colonies were detected by removing several shovelfuls of soil from a mound and scattering them across a plastic sorting sheet (0.7 by 1.2 m). Mound soil was carefully inspected for wingless queens; if they were present, up to six were collected from each colony. Several dozen workers were also collected from each mound by burying a 20-ml scintillation vial up to its neck in mound soil. The inside rim of this vial was coated with Fluon or talcum powder so that workers falling inside could not escape. We also rated the size of workers (small, medium, large) and the abundance of sexuals and brood in each mound. We inspected three to five mounds per site, whenever possible.

Preserved queens were later dissected to determine if their spermathecae were filled with sperm. Sites were declared to be "polygyne" if at least one colony contained two or more inseminated queens. "Confirmed monogyne" sites contained at least one colony with a single highly physogastric queen that had at least two intersegmental membranes clearly visible from above. "Probable monogyne" sites were sites where sexual production (Vargo & Fletcher 1987) and the worker size distribution (Greenberg et al. 1985) were characteristic of monogyne colonies, but no inseminated queens were recovered.

Foraging activity of the ant community was assessed at 34 of the sites in Brazil and 26 of the sites in the United States. We placed 16 baits at 10-pace intervals at each of these sites, 8 on each side of the road. Baits consisted of a quartered cross section of a beef wiener (United States) or chicken Vienna sausage (Brazil) placed approximately 30 mm inside a disposable culture tube (12 by 75 mm). Each bait tube was shaded with a 10-cm cardboard square held in place by a wire flag. Bait tubes were left out for 20 min, then plugged with cotton and placed in a plastic bag with a small amount of alcohol.

Voucher samples of fire ants have been placed in the Museu de Zoologia, Universidade de São Paulo, Brazil, and the entomology collection at Texas A&M University, College Station, Tex. Copies of data sheets are available from authors. Chi-squared tests were used for categorical variables and two-tailed t tests for continuous variables. Log transformations and arcsine transformations were used where appropriate to normalize continuous variables. Standard deviations are indicated for means unless indicated otherwise.

Table 1. Abundance of monogyne fire ants (*Solenopsis*) at preselected roadside sites in Brazil and the United States[a]

Measure of abundance	Brazil	United States[f]
Percent of sites with fire ants (*Solenopsis*)[b]		
In transects (50, 41)	42%	100%***
On baits (33, 20)	48%	100%***
Found by all methods (33, 20)	70%	100%*
Percent of sites with *S. invicta*[b]		
In transects (50, 43)	34%	95%***
On baits (33, 20)	36%	95%***
Found by all methods (33, 20)	58%	95%**
Mound density (mounds/ha ± SD)[c, d]		
All sites (50, 43)	20 ± 33	170 ± 113***
Solenopsis sites (33, 43)	30 ± 37	170 ± 113***
S. invicta sites (27, 41)	27 ± 34	173 ± 115***
Mound size, all fire ant species (±SD, n = 50, 80)[c]		
Height (cm)	9 ± 6	12 ± 8*
Mean diameter (cm)	31 ± 12	43 ± 13***
Volume (liters)[c]	13.8 ± 19.2	27.0 ± 26.1**
Percent of occupied baits with fire ants (± SD)[c, e]		
All sites (32, 17)	13 ± 19%	97 ± 4%***
Solenopsis sites (22, 17)	19 ± 21%	97 ± 4%***
S. invicta sites (18, 16)	17 ± 22%	98 ± 4%***

[a] Nine polygyne sites in the United States were eliminated from these calculations to make means comparable with those from Brazil. The number of sites is shown in parentheses for each category (Brazil, United States).
[b] Analyzed with χ^2 tests of independence.
[c] Analyzed with two-tailed t tests.
[d] Used log-transformation.
[e] Used arcsine (square root) transformation.
[f] $*P < 0.05$, $**P < 0.01$, $***P < 0.001$.

Results

Fire Ant Abundance. Fire ants were much more common at sample sites in the southeastern United States than they were in Mato Grosso do Sul, Brazil. In the United States, 100% of sites contained fire ants both in the transects and on the baits (Table 1). By contrast, only 42% of sites in Brazil contained fire ants in the transects and only 48% of sites contained fire ants on baits. When we included transects, baits, and a general search of 200–300 m of right-of-way on either side of the road, we were able to find fire ants at 70% of Brazilian sites compared with 100% in the United States. The eight sites within the Pantanal were no more likely to contain fire ants than those outside (Fig. 1). This observation agrees with the results of Whitcomb (1980), who reported that the Pantanal itself is not particularly good fire ant habitat.

We found *S. invicta* at 50 sites in the United States and 27 sites in Brazil (Fig. 1). Site percentages for *S. invicta* exclusive of other species are shown in Table 1. Two additional U.S. sites contained the *S. invicta* × *S. richteri* Forel hybrid (Fig. 1). Four sites in Brazil contained colonies similar to *Solenopsis saevissima* F. Smith and two sites contained *Solenopsis pusillignis* Trager, a newly described species in the *electra* subcomplex (Trager 1991). Altogether, we found *S. invicta* at 82% (27/33) of the Brazilian sites with fire ants. By contrast, Allen et al. (1974) reported *S. invicta* from only 19% (5/27) of their collections in Mato Grosso do Sul. This difference is primarily attributable to a broader species concept developed by Trager (1991).

Solenopsis mound densities along roadsides in the United States were almost nine times the average of all sites in Brazil (Table 1; note that polygyne sites were not included in this table). If only sites with fire ants are compared, mound densities in the United States were still almost six times those in Brazil. *S. invicta* densities considered alone were almost the same as all *Solenopsis* combined (Table 1).

Not only were fire ant mounds more abundant at sample sites in the United States, but they were also about twice the volume of those in Brazil (Table 1). The exclusion of data for non-*S. invicta* species had very little impact on average mound size. Mounds tallied in the United States were much more likely to fall into the three largest size categories than were mounds in Brazil. The percentages of mounds in the ≤15, ≤30, ≤46, ≤61, ≤76, and >76-cm size categories were, respectively, 6, 22, 35, 24, 10, and 3% (n = 396) in the United States compared with 25, 33, 34, 5, 3, and 0% (n = 61) in Brazil. Most authors agree that fire ant mounds in the United States are usually larger (Allen et al. 1974, Williams & Whitcomb 1974, Wojcik 1983, Banks et al. 1985), although quantitative comparisons have not been provided. Mound size is not always well correlated with colony size. However, the magnitude of the difference we observed in this study suggests that colonies at sites in the United States are generally more populous than those in Brazil.

In Brazil, ants (all species) occupied 71 ± 27% ($\bar{x}$ ± SD) (n = 34) of baits per site compared with 61 ± 22% (n = 20) in the United States. Fire ants accounted for an average of 13% of occupied baits in Brazil compared with 97% in the United States (Table 1). Even after we excluded all Brazilian sites without fire ants, *S. invicta* and the other *Solenopsis* species still accounted for <20% of occupied baits. (Three sites in the United States and three sites in Brazil were excluded from bait comparisons because <35% of the baits at these sites were occupied, primarily due to extreme temperatures.)

Approximately half of our sites in Brazil had termite mounds. Sixty-four of these mounds were cracked open with a rock pick. Ants were found in 25 (39%) mounds, but only 5 (20%) of these mounds contained fire ants, a frequency very similar to the frequency of fire ants at baits (Table 1). Wojcik (1986) also reported that fire ants were not particularly common in termite mounds.

Polygyny and Monogyny. We found polygyny at nine of the sample sites (17%) in the southeastern United States, but none of the sites in Brazil (Fig. 1). All but one of the U.S. polygyne sites were located in the western half of the study area. Sixty-seven percent of the 43 mounds inspected at polygyne sites were confirmed as polygyne by the presence of multiple-inseminated queens. Two of the polygyne sites also appeared to contain monogyne colonies based on the large size of workers and the large numbers of sexuals in several colonies.

Polygyne sites averaged 544 ± 346 mounds/ha compared with 170 ± 113 for the monogyne sites. The percentage distribution of polygyne mounds in the previously defined six size classes was 7, 47, 30, 9, 4, and 3% (n = 267).

The presence of at least one mound with a single highly physogastric queen confirmed monogyny at 67% of the U.S. and 14% of the Brazilian monogyne sites. The low percentage of confirmed sites in Brazil is attributable to the smaller number of mounds available at each site and less favorable environmental conditions. The mother queen had apparently died recently in about 5% of the 166 mounds inspected in U.S. monogyne areas because these colonies contained numerous uninseminated dealate queens with degenerated wing muscles. Nearly 17% of the 36 monogyne colonies with physogastric queens contained additional dealate queens, but none of these queens were inseminated or had degenerated wing muscles. Apparently, these queens had dealated recently, either naturally or as a result of the nest excavation. These data also indicate that inseminated replacement queens (Tschinkel & Howard 1978) are not common in colonies with a functioning monogyne queen.

Of 74 mounds inspected in Brazil, 75% contained worker brood, 54% contained winged females, 31% contained winged males, and 45% contained sexual brood. Equivalent figures for U.S. colonies were 70, 33, 17, and 63%, respectively. Basically, South American colonies contained more winged adults and less sexual brood because they were sampled further into the spring season.

We found sexuals of a small parasitic *Solenopsis* (=*Labauchena*) species in 3 of the 77 mounds inspected in Brazil (4%). This rate was similar to that reported for *S. richteri* in Argentina but higher than the 0.2% reported for the Mato Grosso region by Jouvenaz et al. (1981). The three parasitized mounds were all at different sites and all were associated with *S. invicta* colonies. Other nearby *S. invicta* colonies did not appear to be parasitized by this ant.

Environmental Conditions. Sites in Brazil and the United States were all sampled during the spring. Weather conditions in the United States were generally good for finding fire ants because mounds were warmer than the surrounding soil. Conditions in Brazil were good at southern and central sites because of recent rains. However, some of the northern and western sites in Brazil were drier than desirable, as were some sites in the United States. Our estimates of soil moisture at sites in Brazil were not significantly different from sites in the United States ($\chi^2 = 1.6$, df = 3, $P > 0.05$). Soil temperatures in Brazil averaged 28 ± 7°C (range, 16–47°C) compared with 20 ± 3°C (range, 12–26°C) in the United States (t = 6.53, df = 100, $P < 0.0001$).

The average height of the grass along roadsides in the United States was 15 ± 10 cm compared with 45 ± 48 cm in Brazil. The mean for Brazil dropped to 30 ± 16 cm after eliminating five sites with grass over >1 m high, but the grass was still significantly higher in Brazil (t = 5.69, df = 93, $P < 0.0001$). About 36% of Brazilian sites had grass that was 20 cm or less in height. No correlation was found between height of grass and mound density among sites within either country. The percentage of bare ground at Brazilian sites averaged 13% compared with 3% at U.S. sites ($\chi^2 = 39.5$, df = 3, $P < 0.0001$). Basically, grass in Brazil was taller but with more bare ground around clumps. Trees and bushes along roadsides in Brazil were considerably shorter than those in the United States (2.4 ± 2.6 versus 8.1 ± 3.6 m).

In Brazil, forest, rangeland, bushes and trees, tall grass, cultivated fields, and swamp accounted for, respectively, 0, 51, 24, 14, 6, and 4% of vegetation types immediately adjacent to the roadside sample sites. By comparison, forest, rangeland, bushes and trees, tall grass cultivated fields, and swamp accounted for 39, 32, 18, 0, 5, and 2% of sites in the United States, respectively. Soil at Brazilian sites was mostly silt or silt–clay. Soils at U.S. sites were much more diverse and fairly evenly distributed among the different soil combinations. We correlated fire ant mound densities with the various habitat and environmental variables from each country, but no significant relationships were found.

Discussion

Fire Ant Abundance. Fire ants *(Solenopsis)* are common and widely distributed in Brazil. In selected areas, population densities can be as great as those in the United States (Fig. 1) (Wojcik 1983, Banks et al. 1985). Nevertheless, results of this survey indicate that fire ants are much more common along roadsides in the United States than they are in central Brazil. Monogyne fire ants in the southeastern United States occurred at more sites, in higher densities, and in larger mounds than their counterparts in Mato Grosso do Sul, Brazil (Fig. 1, Table 1). Furthermore, fire ants constituted only 13% of local Brazilian ant communities compared with 97% in the southeastern United States (Table 1). Altogether, fire ant mounds were almost an order of magnitude more abundant in the United States than they were at sites in Brazil. Our sample sites included ≈10–20% of *S. invicta*'s core range; consequently, density estimates are needed from other areas to determine the importance of regional variation.

The abundance of *S. invicta* alone was, of course, less than that of all *Solenopsis* species combined (Table 1), but for the purposes of intercontinental comparisons, it is probably simpler and more accurate to consider fire ant species as ecological equivalents. While this assumption is not entirely correct, it seems likely that South American *Solenopsis* species are at least somewhat interchangeable; that is, elimination of one species should result in proportional increases by others.

Polygyny and Monogyny. We found polygyny at 17% of sites in the southeastern United States but at none of the sites in Brazil (Fig. 1). The absence of polygyne fire ants in our Brazilian samples was in accord with Jouvenaz et al. (1989), who reported having examined over 1,500 mounds from numerous sites in the Mato Grosso region of Brazil without finding polygyny. Porter et al. (1991) reported polygyny at 54% of sites in Texas. Jouvenaz et al. (1989) reported polygyny in 16 of 295 (5%) *Solenopsis quinquecuspis* Forel and *S. richteri* colonies collected from 8 of 33 sites (24%) in Argentina. Trager (1991) observed polygyne *S. quinquecuspis, S. richteri*, and *S. invicta* colonies in Argentina. In short, polygyny is common in certain parts of the United States and perhaps Argentina but apparently not in the Mato Grosso region of Brazil.

We do not yet know the reasons why polygyny is more common in one region than another. Comparisons with standard habitat, climate, and historical factors have so far proved of little value (Porter et al. 1991). One possibility is that the occurrence of polygyny is linked to the absence of biological control agents. The extremely high nest densities associated with polygyny plus the frequent sharing of workers among nests would seem to make this form especially susceptible to pathogens and other biological agents.

Mound densities at U.S. polygyne sites were 3.2 times those at U.S. monogyne sites (544 versus 170 mounds/ha). This difference is consistent with a previous study in Texas where densities at polygyne sites were 2.3 times those at monogyne

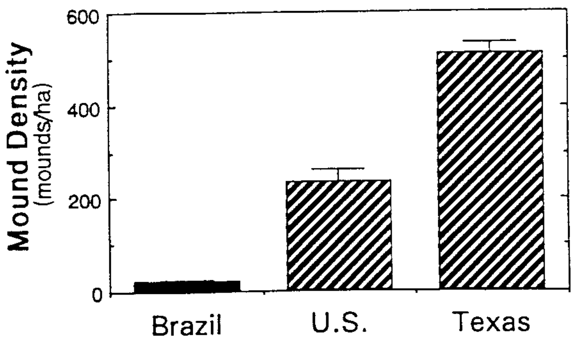

Fig. 2. Comparison of fire ant mound densities at roadside sites in Brazil (n = 50), the southeastern United States (n = 52), and Texas (n = 377) (see Porter et al. 1991). Both polygyne and monogyne sites are included in these figures. Standard errors are plotted above each bar.

sites (680 versus 295 mounds/ha, Porter et al. 1991). High mound densities at polygyne sites are attributable to the lack of territorial boundaries and the presence of interconnected supercolonies (Bhatkar & Vinson 1987).

Polygyne sites were excluded from Table 1 to eliminate polygyny as a factor in these calculations. Inclusion of polygyne sites, however, provides a more complete comparison of intercontinental population differences (Fig. 2). The 35-fold difference in mound densities between Brazil and Texas is particularly striking; this difference is at least partially attributable to the high frequency of polygyny in Texas (Porter et al. 1991).

Causes of Low Fire Ant Densities in Brazil. Low densities of fire ants in Brazil are consistent with the hypothesis that natural enemies limit fire ant populations in their native habitat. Certainly, biological control agents (pathogens, parasites, predators) are much more common in Brazil than they are in the United States. So far, researchers have found eight or nine specific pathogens that together infect 10–20% of all Brazilian fire ant colonies (Jouvenaz et al. 1981, Jouvenaz 1986, Wojcik 1986, D. P. Jouvenaz, USDA–ARS, personal communication); this compares with one endoparasitic (nonpathogenic) yeastlike fungus (Hyphomycetes) that occurs in about 9% of U.S. colonies (Jouvenaz et al. 1977, Jouvenaz & Kimbrough 1991). More than 20 species of parasites have been found in South America (Williams 1980) compared with only one or two in the United States (Wojcik 1990, Kathirithamby & Johnston 1992). Fire ants in Brazil are also under competitive pressure from numerous species of ants. Only 13% of the baits with ants contained fire ants, and only 2 of the 32 sites (6%) had a majority of baits occupied by fire ants. Other reports also indicate that fire ants generally comprise a minority of the total ant community in Brazil (Allen et al. 1974, Whitcomb 1980, Fowler et al. 1990). In contrast, fire ants accounted for practically all of the occupied baits at our U.S. sample sites. Abundant competitors, together with numerous parasites and various pathogens, make natural enemies prime suspects for the lower densities of fire ants observed in Brazil. Nevertheless, it has not yet been demonstrated that any of these agents actually reduce South American fire ant populations (Jouvenaz 1983).

Two cultural explanations for our results also need to be evaluated. The first is that heavy pesticide use in Brazil may have resulted in long-term reductions of fire ant populations. This might be true in some regions of the country, but only 5 of our 50 sample sites were adjacent to cultivated fields where such chemicals might have been used. Fire ants were present at two of these sites. Furthermore, the use of most chlorinated hydrocarbons has been prohibited in Brazil for almost a decade.

A second cultural practice is that roadsides in Brazil are generally not mowed; consequently, grass at sites in Brazil was about twice as high as it was in the United States. We found no correlation between mound density and grass height within either country; however, mowing or burning can make grass height much more variable than mound density. Grass at 36% of Brazilian sites was within normal height range for the United States. Most Brazilian sites appeared to be suitable fire ant habitat; however, tall grass clearly limited populations at some locations.

Differences in the availability or types of food resources are another factor that could affect fire ant populations in North and South America. This possibility has not been carefully investigated and deserves further attention; however, S. *invicta* is very general in its feeding habits (Tennant & Porter 1991).

Climatic differences are another important consideration. Mean winter and summer temperatures are respectively 17–21°C (July) and 24–27°C (January) in Mato Grosso do Sul compared with 7–13°C (January) and 27–28°C (July) for sites in the United States (NOAA, Monthly Climatic Data for the World, National Climatic Data Center, Federal Building, Asheville, North Carolina, U.S.A. 28801-2696). In other words, sites in Brazil were warmer in the winter and almost as hot in the summer. Annual precipitation in Mato Grosso do Sul ranges between 100 and 160 cm, which is very similar to the 120–170 cm of rain for the sites in the United States. An important difference is that Mato Grosso do Sul has dry winters (June–August), during which only 9–20 cm of rain falls. By contrast, our sample sites in the United States averaged 23–43 cm of rain during winter months (December–February). This difference is substantial, but its significance is not clear because monogyne areas around San

Antonio, Tex., average only 10–15 cm of rain during winter months and still have roadside fire ant densities of about 200 mounds/ha (Porter et al. 1991).

In conclusion, fire ants were much more abundant at sample sites in the United States than they were in Brazil. The primary reason for this difference is not known; however, climatic differences, cultural practices, and the relative dearth of biological control agents in the United States are likely factors that deserve further attention.

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