BIOLOGICAL CONTROL

Intercontinental Differences in the Abundance of *Solenopsis* Fire Ants (Hymenoptera: Formicidae): Escape from Natural Enemies?

SANFORD D. PORTER, DAVID F. WILLIAMS, RICHARD S. PATTERSON, AND
HAROLD G. FOWLER[1]

Center for Medical, Agricultural and Veterinary Entomology, USDA–ARS, P.O. Box 14565, Gainesville, FL 32604

ABSTRACT The absence of natural enemies often allows exotic pests to reach densities that are much higher than normally occur in their native habitats. When *Solenopsis* fire ants were introduced into the United States, their numerous natural enemies were left behind in South America. To compare intercontinental fire ant densities, we selected 13 areas in South America and another 12 areas in North America. Sample areas were paired with weather stations and distributed across a broad range of climatic conditions. In each area, we measured fire ant densities at 5 preselected roadside sites that were at least 5 km apart. At each site, we also measured foraging activity, checked for polygyne colonies, and recorded various kinds of environmental data. In most areas, we also measured fire ant densities in lawns and grazing land. Fire ant populations along roadsides in North America were 4–7 times higher than fire ant populations in South America. Similar intercontinental differences were found in lawns and on grazing lands. These intercontinental differences in fire ant abundance were not associated with sampling conditions, seasonal variability, habitat differences, or the frequency of polygyny. Although several correlations were found with long-term weather conditions, careful inspection of the data suggests that these correlations were probably more coincidental than causal. Cultural differences in roadside maintenance may explain some of the intercontinental differences in fire ant abundance, but they did not account for equivalent intercontinental differences in grazing land and mowed lawns. Bait tests showed that competition with other ants was much more important in South America; however, we were not able to determine whether this was a major cause of intercontinental differences or largely a consequence of other factors such as the numerous pathogens and parasites that are found in South America. Because this study was correlational, we were unable to determine the cause(s) of the large intercontinental difference in fire ant abundance that we observed. However, we were able to largely exclude a number of possible explanations for the differences, including sampling, season, polygyny, climate, and aspects of habitat. By a process of elimination, escape from natural enemies remains among the most likely explanations for the unusually high densities of fire ants found in North America.

KEY WORDS invasions, exotic species, biological control, populations, mound size, polygyny

WHEN THE RED imported fire ant, *Solenopsis invicta* Buren, was introduced into the United States ≈60 yr ago, almost all of its natural enemies were left behind in South America. Natural enemies of fire ants in South America include at least 18 species of parasitic phorid flies (Williams and Banks 1987, Disney 1994, Porter et al. 1995), 10 or more microorganisms (Jouvenaz 1990, Patterson and Briano 1993), at least 3 species of nematodes (Jouvenaz et al. 1988, Jouvenaz 1990), a parasitic wasp (Heraty et al. 1993, Heraty 1994), a parasitic ant (Silveira-Guido et al. 1973), plus dozens of other symbionts of undetermined importance (Wojcik 1990). By comparison, only 2–3 natural enemies

have been discovered in the United States in spite of extensive surveys (Collins and Markin 1971, Neece and Bartell 1981, Jouvenaz et al. 1977, Jouvenaz and Kimbrough 1991, Kathirithamby and Johnston 1992).

The absence of natural enemies can allow exotic pest populations to reach densities that are much higher than occur in their native habitats (van den Bosch et al. 1973, Huffaker and Messenger 1976). Porter et al. (1992) reported that fire ants were ≈10 times more abundant in the United States than they were in the state of Mato Grosso do Sul, Brazil. These results suggest that the red imported fire ant may have become a pest in the United States because most of their natural enemies were left behind in South America. This possibility offers the hope that importation of these natural en-

[1] Departamento de Ecologia, Instituto de Biociencias, Universidade Estadual Paulista, 13500, Rio Claro, SP, Brazil.

emies could reduce fire ant populations in the United States to levels similar to those found in South America.

Although escape from natural enemies is a likely explanation for the high intercontinental population differences reported by Porter et al. (1992), the actual cause could also result from factors unrelated to biological control agents. The objectives of this study were to measure intercontinental differences in fire ant abundance at selected locations distributed across a large portion of their range and to determine if high populations of fire ants in the United States (Porter et al. 1992) can be better explained by factors such as climate, habitat, geography, seasonal variability, or differences in fire ant population structure.

Materials and Methods

We selected 13 areas in South America and 12 areas in North America (Fig. 1). Areas in both continents were distributed intentionally across a broad a range of climatic conditions. Each area had 5 preselected sample sites situated at least 5 km apart in rural locations around cities with weather stations (areas 15, 19, and 20 had 6 sites). Sites in both continents were along paved highways almost all of which had 2 lanes. Roadsides were used for the primary survey because they were convenient, they provided appropriate fire ant habitat, and they had structurally similar vegetation. Locations of sites were recorded carefully and photographed so that they could be resampled within 10 m or less. In addition to the 5 roadside sites, we also tried, whenever possible, to survey 2 grazing sites and 1 mowed-lawn site in each sample area.

All 25 areas were sampled in the spring (North America, 9 April–7 May 1992; South America, 22 October–13 November 1991). Eight areas in North America and 9 areas in South America were resampled in the fall (Fig. 1, areas 1–6, 7–8, and 17–25). In North America, fall samples were done 3–20 November 1992. Fall samples in South America were done 20–27 April 1991 and 28 April–14 May 1992.

Our sampling protocol was similar to that used by Porter et al. (1992). In the spring, we collected 4 major types of information at each roadside site: (1) habitat and environmental data, (2) measurements of mound densities, (3) foraging activity, and (4) the presence or absence of multiple-queen colonies. We did not measure foraging activity or check for polygyny in the fall.

Habitat and environmental data included soil temperature (5 cm), mean height of grass, soil moisture, amount of bare ground, soil type, width of the right-of-way, and type of habitat adjacent to right-of-ways.

Mound densities at roadside sites were determined from 4 belt transects, 2 on either side of the road. One transect on each side of the road was along the outer border of the right-of-way,
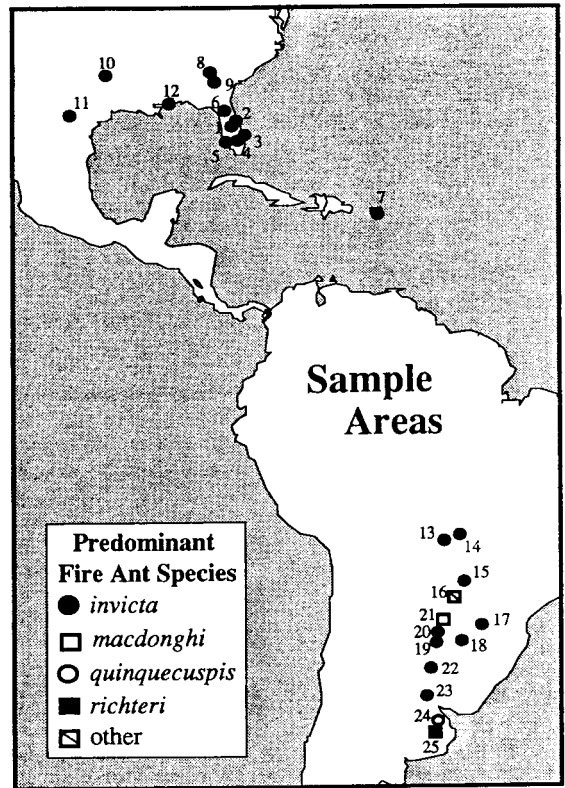

Fig. 1. Locations of sample areas in North and South America. North America: (1) Kissimmee, FL; (2) De Land, FL; (3) West Palm Beach, FL; (4) Belle Glade, FL; (5) Punta Gorda, FL; (6) Gainesville, FL; (7) Guayama, Puerto Rico; (8) Griffin, GA; (9) Byron, GA; (10) Denton, TX; (11) San Antonio, TX; (12) Mobile, AL. South America: (13) Cáceres, Brazil; (14) Cuiaba, Brazil; (15) Campo Grande; Brazil; (16) Ponta Porã, Brazil; (17) Foz do Iguaçu, Brazil; (18) Posadas, Argentina; (19) Resistencia, Argentina; (20) Formosa, Argentina; (21) Asuncion, Paraguay; (22) Reconquista, Argentina; (23) Santa Fe, Argentina; (24) Buenos Aires, Argentina; (25) Las Flores, Argentina. Symbols indicate the predominant fire ant species for each area. Each area was composed of 5 preselected sample sites.

usually along a fence; the other 2 transects were along opposite sides of the road. Transects at lawn sites were generally along a sidewalk or curb. The 4 transects at grazing sites were ≈20 paces apart and aimed into the center of the field. Roadside transects were 70 paces long, whereas transects in lawns and on grazing land were generally 100 paces long. The pace and reach of each investigator were determined and used to calculate the area they sampled. All active mounds within reach of a 1.2-m stick were counted and measured for height, width, and length. The average pace was 0.82 m and the average reach was 2.2 m.

The size of healthy fire ant mounds is proportional to colony population on a log–log scale (Macom and Porter 1996, Tschinkel 1993). Because the average size of fire ant colonies can vary con-

siderably from site to site, we used "total basal area of mounds per hectare" and "total volume of mounds per hectare" as additional estimates of fire ant abundance. The basal areas for fire ant mounds (A) were calculated using the formula for an ellipse $(A = \pi ab$, where a is length/2 and b is width/2). 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). Using mound size to help calculate fire ant abundance assumes that the relationship between mound size and colony population is similar in North and South America. This relationship has yet to be examined in South America, but there is no obvious reason why the general relationship should not hold in both continents. The slope of the relationship could vary, but it did not appear to us that colony populations in South America were unusually high or low for the mounds that they occupied.

Polygyne colonies were detected by the presence of several inseminated queens with histolyzed wing muscles in a single mound (Porter 1992). Queens were collected by removing several shovelfuls of soil from a mound and scattering the soil across a plastic sorting sheet (0.7 by 1.2 m). We inspected up to 5 mounds per site, whenever possible. 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 talcum powder so that workers falling inside could not escape. Voucher samples of these fire ants have been placed in the Museu de Zoologia, Universidade de São Paulo, Brazil, and the Departamento Cientifico de Entomologia, Museo de la Plata, Universidad Nacional de la Plata, Argentina.

Ant community foraging activity was assessed with 16 baits at each site. Eight baits were placed on each side of the road at 10-pace intervals. Baits consisted of a quartered cross section of Vienna sausage placed ≈30 mm inside a disposable culture tube (12 by 75 mm). Each bait tube was shaded with a 15-cm disposable plastic plate held in place by a wire flag. Bait tubes were left out for 20 min, then plugged with cotton and placed in a sealed plastic bag with a small amount of alcohol.

Climatic data for our sample sites were obtained from the National Oceanorgraphic and Atmospheric Administration's (NOAA) Monthly Climatic Data for the World (1990–1992) and NOAA's Climatological Data Annual Summaries for Texas, Alabama, Georgia, and Florida (1990–1992). Additional information was obtained from Schwerdtfeger (1976) and directly from weather stations in Brazil and Argentina. Summer and winter climatic averages were calculated from long-term data for December, January, and February or for June, July, and August.

Mann–Whitney U tests were used to statistically compare intercontinental differences in percentage of site occurrence; this test was used because the data were not continuously distributed. Mound

size and mound density measures along roadsides were statistically analyzed using 3-way analyses of variance (ANOVA) with "continent" and "season" used as fixed factors and "area" as a random factor nested in "continent". The error term for "continent" was "area" and the error term for "season" and "season × continent" was the "season × area" interaction. We analyzed fire ant densities in lawns and on grazing land and fire ant abundance at baits with a similar 2-way ANOVA with "continent" as a fixed factor and "area" as a random factor nested in "continent." Intercontinental comparisons of fire ant densities between monogyne and polygyne sites, between different types of adjacent roadside habitats, and between different types of soil were made with fully crossed 2-way ANOVAs. Square-root transformations were used to equalize the variance and normalize the distributions of all population density comparisons and regressions. Arc-sine-square-root transformations were used with percentile data. Multiple and stepwise regressions were used to examine correlations between mound densities and various independent variables such as precipitation, temperature, and soil moisture. Standard errors of the mean (SEM) were used unless otherwise indicated. All statistical analyses were conducted with SuperANOVA (Abacus Concepts 1989) and StatView (Abacus Concepts 1992).

Results

Intercontinental Differences in Fire Ant Abundance. We found that fire ants were common in both continents, but colony sizes and mound densities were much higher in North America than they were in South America.

Occurrence. In North America, 97% of sample sites had fire ants on the baits compared with 68% in South America (Table 1). Similarly, 93% of North American sites had fire ant mounds in the transects compared with only 77% for South America. 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 98% of North American sites and 93% of South American sites.

Mound Size. Fire ant mounds in North America were generally larger than those in South America. Average mound height was about the same, but basal dimensions were significantly larger in North America (Table 1). The average basal area of mounds measured in North America was ≈100% larger than in South America. The difference for mound volumes was not as great, but the average volume for North America was still 40% larger than the average for South America.

Mound Densities. Not only were fire ant mounds larger in North America, but they were also much more dense (Table 1). The number of mounds per hectare in North America was almost 4 times higher than in South America. Intercontinental comparisons of fire ant densities that took into account

Table 1. Roadside abundance of *Solenopsis* fire ants in South America and North America (means ± SEM)

Measurements of fire ant abundance	South America	North America
Occurrence (all sites)[a,b]		
On baits	68 ± 7%	97 ± 2%**
In transects	77 ± 6%	93 ± 3%*
All methods	93 ± 2%	98 ± 2%
Average mound size (all sites with fire ants)[a,c]		
Height, cm	7.27 ± 0.62	6.62 ± 0.52
Width, cm	23.7 ± 1.5	33.6 ± 1.5***
Length, cm	31.7 ± 2.5	44.1 ± 2.1***
Basal area, cm^2 [d]	681 ± 93	1,402 ± 124***
Vol. liters[d]	5.12 ± 0.86	7.36 ± 0.72***
Ant density measurements (all sites)[a,c]		
Mounds/ha[d]	55 ± 8	209 ± 39***
Total area (m^2) of mounds/ha[d]	3.35 ± 0.55	25.2 ± 3.4***
Total volume (m^3) of mounds/ha[d]	0.25 ± 0.04	1.31 ± 0.18***
Ant density measurements (*S. invicta* sites only)[e,c]		
Mounds/ha[d]	58 ± 10	215 ± 38***
Total area (m^2) of mounds/ha[d]	4.0 ± 0.7	25.9 ± 3.2***
Total volume (m^3) of mounds/ha[d]	0.29 ± 0.06	1.34 ± 0.17***

Statistical significance of intercontinental comparisons: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

[a] Means calculated from 13 areas in South America and 12 areas in North America. Each area contained 5 sites.

[b] Analyzed with Mann–Whitney U tests, spring samples only.

[c] Analyzed with multiway ANOVA, see *Materials and Methods.*

[d] Used square-root transformation to equalize variance and normalize distribution for statistical analysis.

[e] Means calculated from 9 areas in South America and 12 areas in North America. Each area contained 3–5 sites.

differences in mound size were even more disparate. The total basal area of mounds per hectare in North America was >7 times that in South America. Similarly, the total volume of mounds per hectare was >5 times that measured in South America.

Statistical comparisons were done with all 3 measures of fire ant density discussed above, but only volume-based estimates will be reported unless the other 2 estimates of fire ant populations produced different results. We chose "total volume of mounds per hectare" as our primary measure of fire ant density (Table 1) because it adjusted the simple mound count data for differences in mound size. "Total volume" was used in preference to "total area" because it produced more conservative estimates of intercontinental population differences and because field excavations of fire ant colonies in North American pastures indicate that volume-based estimates are generally better than area-based estimates (Macom and Porter 1996). However, the argument can also be made that total mound basal area might provide a better estimate along roadsides where grass cutting activities can artificially truncate mound heights.

In North America, 97% of sites (58/60) contained the imported fire ant *S. invicta*, 8% of sites (5/60) contained both *S. invicta* and *S. geminata*, and 1 site (1/60) contained *S. geminata* but not *S. invicta*. In South America, 72% of our sample sites (49/68) contained *S. invicta*. We found *S. quinquecuspis* and *S. richteri* each at 7% of South American sites (5/68, 5/68). Three sites around Ponta Pora, Brazil (3/68), contained a form of *Solenopsis* fire ants that we were not able to confidently assign

to any one species. One site near Posadas (1/68), Argentina, contained both *S. pythia* and *S. macdonaghi*. Four of the *S. invicta* sites listed above for South America also contained *S. macdonaghi*. The other sites with fire ants appeared to contain only 1 species of fire ant. The remaining 7% of the South American sites (5/68) did not contain *Solenopsis* fire ants. The species of fire ant present at South American sites did not significantly affect the density of fire ants present ($F = 0.28$; df = 4, 62; $P = 0.89$). The average densities of fire ants at sites that contained only *S. invicta* fire ants were almost the same as the averages for all sites (Table 1).

In the remainder of this article, we report data for all sample sites rather than just sites with *S. invicta*. This was done because the utilization of all South American sites includes a range of climatic conditions that is more representative of the range of *S. invicta* in North America. This was also done because it greatly simplified the presentation of the results and because none of the following comparisons were materially altered by the inclusion of all sites or the exclusion of sites with other species of fire ants.

Potential Causes of Intercontinental Differences. Fire ants were clearly much less abundant at sample sites in South America. The absence of natural enemies is a tempting explanation, but a number of other factors including sampling conditions, climatic effects, cultural practices and habitat differences could also explain the observed differences and need to be considered.

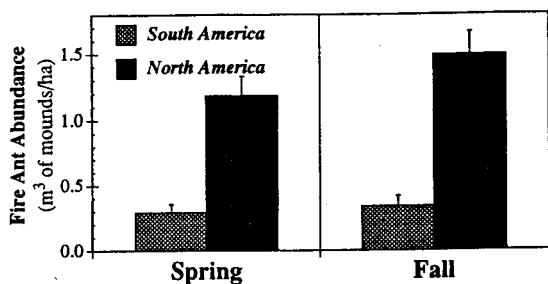*Sampling Conditions.* Sampling conditions were examined because fire ants can abandon their

Fig. 2. Seasonal comparison of roadside fire ant abundance in South and North America. Bars show the mean and standard errors for 9 South American areas (42 sites) and 8 North American areas (40 sites) that were sampled both in the spring and in the fall.

mounds during droughts and extremely hot weather. Consequently, strong intercontinental differences in weather conditions could have affected our population estimates. Sampling conditions in both continents, however, were generally good because recent rains allowed colonies to build obvious mounds and moderate temperatures allowed easy determination of colony activity. Soil temperatures for North American sites sampled in the spring and fall were 25 ± 4 and 24 ± 2°C, respectively. Equivalent temperatures for South America were 28 ± 5 and 22 ± 3°C. Temperatures did not differ significantly between continents ($F = 0.51$; df = 1, 23; $P > 0.05$), although there was a significant interaction between continent and season ($F = 34.1$; df = 1, 15; $P < 0.0001$). Within continents, soil temperatures were not related to the different measures of fire ant populations.

The percentage soil moisture for sites in North America and South America averaged 11.7 ± 1.2 and 11.3 ± 0.6%, respectively in the spring ($F = 0.012$; df = 1, 22; $P = 0.91$) and 14.9 ± 1.6 and 19.2 ± 0.8%, respectively in the fall ($F = 1.69$; df = 1, 10; $P = 0.22$). In the fall, soil moisture was only measured at sites in 4 South American areas, but categorical observations in the remaining 5 areas also indicated moist soil conditions. Soil moisture was not significantly correlated with fire ant density within either continent or across continents (linear regressions; $P > 0.05$)

Seasonal and Temporal Variability. Our sites were sampled in 2 seasons because fire ant populations are known to fluctuate somewhat from season to season (Tschinkel 1993) and we did not want to compare a seasonal low in one continent with a seasonal high from the other. We did not find a significant difference between the total volume of mounds per hectare in the spring and fall (Fig. 2; $F = 2.55$; df = 1, 15; $P = 0.13$) and no significant interaction was observed between continent and season (Fig. 2; $F = 0.65$; df = 1, 15; $P = 0.43$). Results for "total area of mounds per hectare" and "mounds per hectare" were also not significant when compared across season.
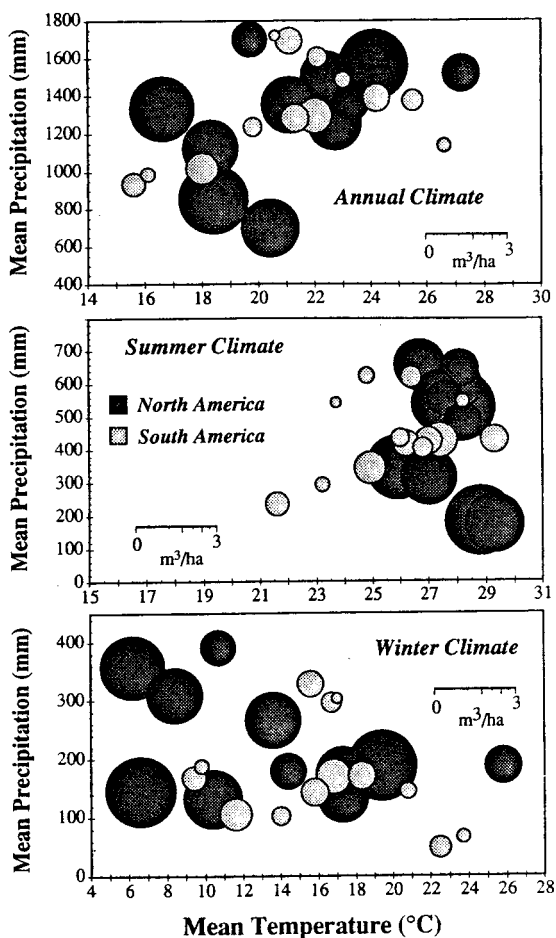

Fig. 3. Fire ant roadside densities in South and North America plotted against long-term averages for total precipitation and mean temperature. Circle area is proportional to mean fire ant density for each sample area (spring and fall estimates were averaged). The top, middle, and bottom graphs use annual, summer, and winter climatic means as indicated.

Climatic and Weather Conditions. Long-term climatic conditions for sample areas in North America and South America overlapped broadly (Fig. 3). This was true regardless of whether we examined annual climate, summer climate, or winter climate. Furthermore, average fire ant densities in each continent generally were not correlated to either precipitation or temperature. Mound volume per hectare was positively correlated with mean summer temperature across continents ($R^2 = 0.24$, $P = 0.013$), but no correlation existed within continents. No correlation was found between fire ant density (mean total volume of mounds per hectare) and the following 7 variables: (1) mean annual temperature, (2) mean winter temperature, (3) mean annual precipitation, (4) mean summer precipitation, (5) mean winter precipitation, (6) mean minimum monthly precipitation, or (7) mean

maximum monthly precipitation. A stepwise regression of fire ant density (y, square root of total volume of mounds per hectare) on the 8 climatic variables mentioned above resulted in a significant positive correlation with mean summer temperature (x_1) and a negative correlation with winter temperature (x_2) with $y = -4.06 + 0.256x_1 - 0.082x_2$ ($R^2 = 0.47$). Summer temperature explained 21% of the variation in fire ant density and winter temperature explained an additional 26%. When we ran a 2nd stepwise regression that included all 8 climatic variables plus a dummy variable for continent, neither summer or winter temperatures made it into the model. Continent (x_1) explained 66% of the variability and summer precipitation (x_2) explained an additional 6% of the variability ($y = 1.56 = 1.30x_1 - 0.0014x_2$.; $R^2 = 0.72$).

We also examined temperature and precipitation at 1-, 3-, and 12-month periods before each area was sampled (4 South American areas were eliminated because weather data were not available). South American sites had almost 100% more rain in the preceding month than the North American sites ($F = 37.1$; df $= 1$, 31; $P < 0.0001$). When we looked at rainfall in the previous 3 mo, we found a significant interaction between season and continent; fall samples in North America received ≈75% more rain than the other 3 categories ($F = 8.6$; df $= 1$, 31, $P = 0.006$). We found no significant intercontinental differences when we examined rainfall during a 12-mo period. No significant intercontinental differences were found in average temperatures over 1-, 3-, or 12-mo periods. Other than precipitation in the preceding month, we found no significant correlations between fire ant density and prior weather conditions either within continents or across continents.

Human Cultural Practices. Intercontinental differences in the care, maintenance, or physical structure of right-of-ways could also affect fire ant densities. One important difference is that roadside sites in Brazil were not mowed frequently; instead the grass was often burned annually or hand cut with scythes. In Argentina, most of the sites apparently were mowed several times a year as they are in the United States except that only the inner half of the right-of-way was regularly mowed. The outer portion of many right-of-ways in Argentina appeared to be plowed about once a year. Another difference is that roads in Brazil were generally more elevated with broader and deeper ditches than in the United States and Argentina. We did not attempt to identify grasses at specific sample sites, but most of the grass along roadsides in Brazil were *Brachiaria* species that had been imported from Africa because of their tolerance to drought and tropical heat. Argentine Bahia grass, *Paspalum notatum*, was planted along roadsides in Florida, Alabama, and northern Argentina. Sites in Georgia probably had bermuda grass and those in
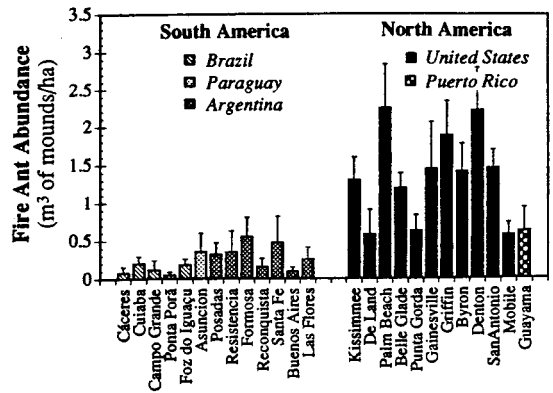

Fig. 4. Fire ant abundance in cubic meters of mound volume per hectare for 13 roadside areas in South America and 12 roadside areas in North America. Each bar indicates the mean and standard error for 1 area; each area contained 5 sample sites.

Texas are usually seeded with a mixture of many species that include buffalo and bermuda grasses.

The average height of the grass along roadsides in North America was 19 ± 1 cm compared with 20 ± 1 cm in South America; neither this difference nor the continent × season interaction were significant ($F = 0.045$; df $= 1$, 23; $P = 0.83$; and $F = 2.03$; df $= 1$, 14; $P = 0.18$). The estimated percentage of bare ground at sites in North and South America was also not significantly different (7.2 ± 0.9% versus 10.4 ± 2.3%; $F = 0.38$; df $= 1$, 23; $P = 0.54$). The average width of right-of-ways in North America was not significantly different from those in South America (12 ± 1 m versus 11 ± 1; $F = 0.029$; df $= 1$, 23; $P = 0.87$). Fire ant mound densities were much higher next to the road then they were along the outer margin of the right-of-way in both continents ($F = 19.0$; df $= 1$, 23; $P = 0.001$, square-root transformed), but the interaction between continent and transect location was not significant ($F = 0.003$; df $= 1$, 23; $P = 0.95$; North America: 254 ± 44 versus 165 ± 41 mounds per hectare; South America: 78 ± 14 versus 32 ± 6 mounds per hectare).

Fire ant population densities in South America were consistently less than those in North America, regardless of the geographic region or the country involved (Fig. 4). Mean fire ant densities (cubic meters of mounds per hectare) for areas in Brazil (0.120 ± 0.026) and Argentina (0.305 ± 0.055) were both significantly less than those in the United States (1.37 ± 0.18, Scheffé S; $P < 0.0001$), but they were not significantly different from each other ($P > 0.05$). (Paraguay was not compared because we only had one area in this country.)

Differences in insecticide use between continents are another possible reason that has been proposed for the observed differences in fire ant abundance (Porter et al. 1992); however, our inquiries indicate that insecticides are used rarely along roadsides in either continent. Furthermore,
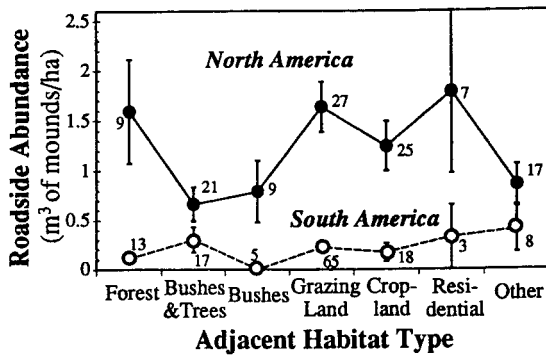
Fig. 5. Fire ant roadside abundance in North and South America plotted above the type of adjacent habitat. Separate mound densities were calculated at each site for each side of the road so that roadside densities could be compared to habitat that was the immediately adjacent. Sample size and standard errors are indicated for each mean.

Fig. 6. Intercontinental comparison of fire ant densities in lawns, grazing lands, and roadsides. Numbers by each habitat pair indicate how many times larger fire ant populations in North America were than those in South America. Means for the 6 bars were calculated from 9 and 7, 12 and 10, and 13 and 12 sample areas, respectively.

sites adjacent to cropland or residential areas, where insecticides are most likely to have been used, did not have unusually low densities of fire ants in either continent (Fig. 5). Reinfestation rebounds from the large-area fire ant eradication campaigns in the United States do not explain high North American densities because only the Griffin, Byron, Denton, and perhaps the Mobile areas were in counties that were treated. Furthermore, >15 yr have elapsed since these treatments and treated areas usually revert to near pretreatment densities within 2–3 yr (Lofgren and Williams 1985).

Habitat. Intercontinental differences in habitat could explain why fire ants are much more abundant in North America. For example, right-of-ways next to grazing land were more common in South America and might have had much lower fire ant densities than right-of-ways next to other types of habitat. In fact, fire ant densities in North America were consistently higher across all adjacent habitat types (Fig. 5). The type of habitat adjacent to the roadside samples was not associated with different levels of fire ant densities ($F = 1.95$; df = 6, 230; $P = 0.074$), although there was a weak continent × habitat interaction ($F = 2.63$; df = 6, 230; $P = 0.03$).

Soil is another important aspect of habitat. At each site, we categorized roadside soils into 6 types: sand, silt , clay, and 3 intermediate categories. Using these soil categories in a 1-way ANOVA, we found no significant differences in average mound volume ($F = 0.48$; df = 5, 89; $P > 0.48$) or average mound basal area ($F = 1.20$; df = 5, 89; $P = 0.31$). Also, no significant interactions occurred between continent and soil categories in either ANOVA above (df = 5, 89; $P > 0.3$). All soil categories in North America had larger mound volume averages than those in South America. To compare fire ant densities with soil coarseness, we
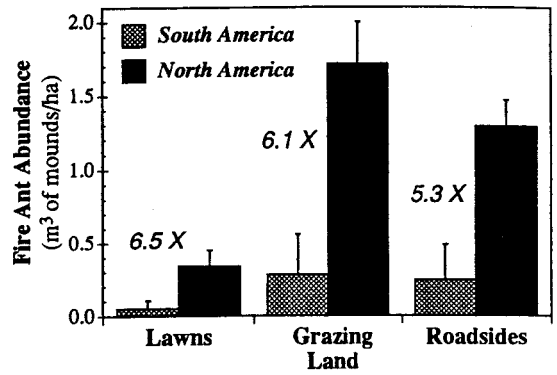
ranked roadside soils from 1 to 5 with 1 for clay, 3 for silt, and 5 for sand. Intermediate soils were scored as 2 or 4 and several clay–sand sites were scored as 3. Fire ant densities at sites in North America were negatively correlated with this index ($R^2 = 0.17$; $P = 0.002$), but sites in South America showed no correlation ($P > 0.10$). Because sites in North America had coarser soils (i.e., more sand) than those in South America (2.6 ± 1.1 versus 1.7 ± 1.0 index units, $t = 5.1$; df = 119; $P < 0.0001$), this index did not explain higher fire ant densities in North America.

Soil chemistry was not measured in this study; however, we did check with highway maintenance departments in the United States concerning their use of fertilizers. We found that fertilizers generally were used only on right-of-ways when the road initially was constructed except in Florida where some management units applied fertilizer once or twice a year along state and federal roads but not county roads. Sites along state and federal roads in Florida did not have significantly higher fire ant populations than sites along county roads ($t = -0.456$; $n = 16$ and 12; df = 26; $P = 0.65$).

It is possible that fire ants are not particularly abundant along roadsides in South America for various reasons, but they are nevertheless very abundant in other types of South American habitats. To test this hypothesis we also measured fire ant densities in mowed lawns and on grazing land, 2 types of habitats that are generally considered excellent for fire ants. Fire ant densities in North American lawns were 6.5 times higher than densities in South American lawns (Fig. 6, $F = 12.3$; df = 1, 14; $P = 0.0035$). Similarly, fire ant densities in North American grazing areas were 6.1 times higher than in South American grazing areas (Fig. 6, $F = 18.2$; df = 1, 20; $P = 0.0004$). Densities in grazing areas were similar to those along roadsides;
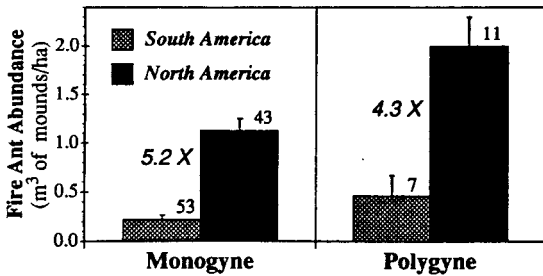
Fig. 7. Roadside abundance of monogyne and polygyne fire ant populations in South and North America. Standard errors and the number of sites involved are indicated above each bar.

Fig. 8. Mean percentage of occupied baits along roadsides that contained fire ants or other ants in South America and North America.

however, densities in lawns were much lower. This difference is partly an artifact of using total volume of mounds to estimate densities in areas where frequent mowing clips mound height and thus total volume. A comparison of the total basal area of fire ant mounds along roadsides and their total basal area in lawns was more similar (3.35 versus 1.14 and 25.2 versus 12.3 square meters of mounds per hectare; South and North American comparisons, respectively), although a 2- to 3-fold difference still remained between roadsides and lawns.

Polygyny. We found polygyny at 20% of the sample sites with fire ants (11/54) in North America, and 12% of sites with fire ants in South America (7/60); this difference was not significant (Fisher exact test, $P = 0.30$) In North America, the number of sites with polygyne colonies were distributed among the areas as follows: Palm Beach, 3; Denton, 4; San Antonio, 3; and Mobile, 1. In South America, they were distributed as follows: Posadas, 1; Resistencia, 1; Formosa, 4; Las Flores, 1. It is likely that we missed several additional polygyne sites in South America because fewer mounds were available for inspection and queens were generally harder to find.

The high density of fire ants at North American sites cannot be attributed to polygyny because frequencies of polygyny were similar in both continents, and the elimination of polygyne sites from density estimates had little impact on relative intercontinental population differences (Fig. 7)—fire ants were still >5 times as abundant in North America. The total volume of fire ant mounds at sites with polygyne colonies was significantly greater in both continents (Fig. 7; $F = 10.6$; df = 1, 110; $P = 0.0015$) and there was no significant interaction between continent and polygyny ($F = 0.86$; df = 1, 10; $P = 0.36$).

Natural Enemies. Competition with other ants was clearly much more important in South America than it was in North America (Fig. 8). Non-*Solenopsis* ants accounted for 77 ± 4% of the occupied baits in South America compared with only 21 ± 5% of occupied baits in North America ($F = 69.7$; df = 1, 23; $P < 0.0001$). However, the foraging intensity as measured by the total percentage
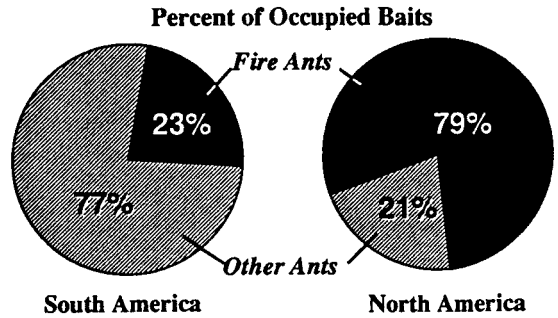
of baits occupied by all species of ants did not differ significantly between North and South America (79 ± 4% versus 78 ± 4%; $F = 0.356$; df = 1, 23; $P = 0.56$).

Multiple and Stepwise Regressions. In addition to the analyses described in the previous sections, we tried a number of multiple and stepwise regressions of fire ant densities on various combinations of the habitat and environmental variables. No combinations of variables were found that helped to further explain intercontinental differences in fire ant abundance except as previously noted.

Discussion

Intercontinental Differences in Fire Ant Abundance. This study confirms the basic conclusion of Porter et al. (1992) that fire ants are considerably more abundant in North America than they are in their South American homeland. Population estimates based on mound counts were ≈4 times higher in the United States than they were in South America (Table 1). Population estimates that accounted for differences in mound sizes were 5–7 times higher. These differences are substantial and clearly indicate why fire ants are considered a major pest in the United States (Lofgren 1986), but not in South America where only a few instances of problems have been reported (Adams 1994, Boock and Lordello 1952, Wojcik and Porter 1995).

The summed volume of mounds that we found per hectare can be converted into estimates of ants per square meter by using an equation that estimates the number of workers per colony from mound volume ($y = 99.4 x^{0.750}$, $R^2 = 0.81$; Macom and Porter 1996). Based on this conversion, the average density of fire ants would be 1,220 ± 120 ants per square meter for North American sites compared with 230 ± 40 ants per square meter for South American sites or slightly more than a 5-fold difference. These density estimates may be somewhat low because the equation is based on mounds in pastures, which were not subject to occasional

truncation by mowing equipment. Macom and Porter's (1996) correlation between worker number and the basal area of the mound ($y = 13.07$ $x^{1.226}$, $R^2 = 0.74$) was not quite as good as the correlation between mound volume and worker number; nevertheless, basal area has the advantage of not being as sensitive to mowing activities or soil characteristics. Estimates of worker densities based on mound basal areas was 1710 ± 160 ants per square meter for North American sites compared with 220 ± 50 ants per square meter for South American sites, or about a 7-fold difference.

The 4- to 7-fold intercontinental differences that we found in this study were less than the almost 10-fold difference reported by Porter et al. (1992); this was primarily because sampling efforts in the previous study were limited to the state of Mato Grosso do Sul in Brazil. In the current study, sampling efforts in South America were much more extensive (Fig. 1). We found that fire ants occurred more frequently in other regions of the South American continent and at somewhat higher densities (Table 1; Fig. 4; compare Porter et al. 1992). Fire ant population densities that we found in North America (Table 1) were similar to previous studies (Porter 1992; Porter et al. 1991, 1992). Average mound volumes found in this study (5–7 liters, Table 1) were considerably less than average volumes reported by Porter et al. (1992) because volumes in the 1992 study were twice what they should have been for both continents because of a calculation error. The average diameter of mounds found in the current study (Table 1), however, were similar to previous reports for North and South America (Porter 1992, Porter et al. 1992).

Causes of Intercontinental Differences. Exotic species can achieve much higher densities in foreign continents than they do in their native homeland (van den Bosch et al. 1973, Huffaker and Messenger 1976). This phenomenon is often the result of escape from natural enemies that were left behind in their homeland; however, a number of other factors can be equally important (Krebs 1978). In an effort to explain the unusually high densities of fire ants in North America, we examined a number of possible factors including differences in sampling conditions, seasonal abundance, climatic conditions, human cultural practices, habitat, population structure, and competition from other ants.

Sampling Conditions. Poor sampling conditions in one continent but not the other is one possible explanation for the intercontinental differences in fire ant populations. However, sampling conditions as measured by soil moisture and soil temperature were generally good to excellent in both continents. Furthermore, we could find no correlation between sampling conditions and fire ant populations within either continent.

Seasonal and Temporal Variability. Strong temporal or seasonal variability in fire ant populations could also have caused or contributed to the ap-

pearance of intercontinental differences in fire ant abundance. However, we found little difference between our spring and fall samples and no evidence of a differential relationship between season and continent (Fig. 2). In other words, the intercontinental difference in fire ant abundance appears to be reasonably stable across both time and season.

Climatic and Weather Conditions. Intercontinental differences in climatic conditions are another likely explanation for differences in fire ant abundance; however, we did not find consistent evidence to support this hypothesis. Climatic conditions at the 13 South American sites and 12 North American sites overlapped broadly (Fig. 3). Furthermore, fire ant densities generally were not correlated to climatic conditions. We did find a correlation with mean summer temperature, but this correlation was probably coincidental rather than causal because no correlation was found within continents and South American fire ant populations were still considerably lower in all areas where summer temperatures overlapped with those in North America (Fig. 5). A multiple regression that included mean summer and mean winter temperatures explained 47% of the variability among our sample areas; however, when continent was added to the model as a dummy variable, it excluded the 2 temperature variables and accounted for 66% of the variability by itself. When we looked at weather conditions in differing periods immediately preceding our sampling efforts, we found that sample areas in South America had received considerably more rainfall in the preceding month than areas in North America. This short-term difference should have had little impact on actual fire ant populations (Porter 1988); however, it might have improved our ability to find fire ant mounds in South America compared with North America because fresh mound construction usually makes mounds easier to see. We also found that North American areas in the fall received more rainfall during a 3-mo period than North American areas in the spring or South American areas in either season. This difference might have affected fire ant populations, but we did not observe a significant seasonal difference in North America (Fig. 7). No correlation was found between fire ant populations and rainfall during the preceding 12 mo. No correlations were found between fire ant populations and mean temperature conditions either during 3- or 12-mo periods before our sample dates. Apparently, variability from site to site usually overwhelms effects of climate or weather, at least within the areas that we sampled. Similarly, Porter et al. (1991) also found only weak correlations ($R^2 \leq 0.06$) between fire ant densities and several aspects of climate in a survey of >400 sites across a wide range of climatic conditions in Texas.

Human Cultural Practices. Cultural differences in the ways roads are built and maintained could

also explain intercontinental differences in fire ant populations. We did not find any significant intercontinental differences in the average height of grass along the roadsides, the width of the right-of-ways, or the percentage of bare ground at our sample sites. Also, our inquiries indicated that insecticides rarely were used along roadsides in either continent. We did, however, observe substantial differences in the way roadsides were maintained in the different countries including differences in the structure of the road bed, the types of grass planted, and the manner of cutting the grass. Overall, cultural practices in Argentina appeared to be more similar to those in the United States than they were to those in Brazil; nevertheless, fire ant densities in Argentina were still considerably less than those in the United States even though they were not significantly different from those in Brazil (Fig. 4). The best indication that cultural differences in road maintenance were not a major cause of large intercontinental differences (Table 1) is that fire ant populations on lawns and grazing land were also much higher in North America than they were in South America (Fig. 6).

Habitat. Intercontinental differences in habitat could also explain intercontinental differences in fire ant abundance. However, as just mentioned, roadsides, grazing land, and lawns all contained considerably more fire ants in North America than they did in South America (Fig. 6). The type of habitat adjacent to our roadside sites was also not useful in explaining intercontinental differences in fire ant populations (Fig. 5). Similarly, intercontinental differences in soil types were not associated with intercontinental differences in fire ant densities or average mound sizes. Other studies have either found no correlation between soil type and fire ant density (Wangberg et al. 1980, Porter et al. 1991) or comparatively small differences associated with soil types (Ali et al. 1986). Similarly, Macom and Porter (1996) reported that the average size of mounds in their study was not effected by soil type. It is possible that chemical analysis of soil nutrients or soil pH could be useful in explaining intercontinental differences; however, no one has yet looked at the relationship between soil chemistry and fire ant abundance in either continent.

Polygyny. The presence of polygyne fire ant colonies generally increases fire ant densities by 2- to 3-fold in the United States (Porter et al. 1991, 1992; Porter 1992; Macom and Porter 1996). Intercontinental differences in the frequency of polygyny could help explain intercontinental differences in fire ant abundance. Our data, however, indicate that polygyny is not important in explaining intercontinental differences (Fig. 7). The frequency of polygyny was similar in both continents and the density of fire ants at monogyne and polygyne sites in South America were both considerably less than the corresponding densities found in North America (Fig. 7).

Natural Enemies. Competition from other ants is another factor that could cause intercontinental differences in fire ant abundance. We found that other types of ants occupied 77% of baits in South America but only 21% in North America (Fig. 8). However, the relative importance of competition with other ants is difficult to determine because the abundance of other ants could either be a cause of low fire ant densities or largely a consequence of some other factor. It is important to note that intercontinental differences in fire ant abundance did not appear to be related to intercontinental differences in total ant foraging intensity because the percentage of baits discovered by ants in 20 min was almost the same for both continents. Imported fire ants in North America are known to displace a large number of native species (Porter and Savignano 1990).

Several dozen species of pathogens and parasites have been found in South America compared with only 2–3 in the United States. The impacts of these natural enemies on fire ant populations in South America are largely unknown, but some evidence suggests their effects are not trivial. For example, various pathogens are reported to infect 10–20% of fire ant colonies in South America (Jouvenaz et al. 1980, Wojcik 1986, Briano et al. 1995). The microsporidian disease *Thelohania solenopsae* is associated with smaller colony size and reduced population densities (Briano 1993). Parasitic phorid flies may also be important natural enemies because fire ant workers have evolved a suite of phorid-specific responses that include "freezing" activity, a characteristic c-shaped defense posture, and rapid termination of foraging for periods of several hours or more (Orr et al. 1995, Porter et al. 1995).

Final Evaluation. We found that fire ant populations were 4–7 times more abundant in North America than they were in their native homeland of South America. We were unable to associate these intercontinental differences in fire ant abundance with differences in collecting conditions, seasonal variability in fire ant abundance, habitat differences, or the frequency of polygyny. We found several correlations with climatic and weather variables; however, careful inspection of the data suggests that they were probably more coincidental than causal. Cultural practices might explain some of the differences in fire ant abundance along roadsides, but they did not appear to account for equivalent intercontinental differences that we found in grazing land and mowed lawns. Competition with other ants is clearly much more important in South America than it is in North America, but it is difficult to determine whether this is a major cause of the difference or largely a consequence of some other factor. Multiple and stepwise regressions using various combinations of the variables previously described did not provide further explanations of intercontinental differences in fire ant abundance. It should be pointed out that although we examined most of the obvious expla-

nations for intercontinental population differences, our efforts were not exhaustive. For example, further information about soil chemistry, cultural practices, and other as yet unidentified factors might prove important.

Overall, the cause or causes of intercontinental differences in fire ant abundance are still not known. However, the relative dearth of natural enemies in North America (Jouvenaz 1990) suggests that the observed population difference may be, at least partly, the result of escape from the numerous natural enemies that were left behind in South America, especially in view of the general lack of correlation with other obvious factors examined above. Based on our current knowledge of potential biological control agents in South America, it seems unlikely that any one organism would be sufficiently virulent to singlehandedly control fire ant populations in North America. However, it does seem likely that parasites and pathogens may work in concert with the effects of competition from other species of ants. If this is true, then the introduction of natural enemies might only need to put a relatively small stress on the productivity of fire ant colonies to tilt the ecological balance in favor of native ant species. Native North American ants, after all, have their own natural enemies to cope with, but they are forced to compete with an imported ant that has largely escaped all of its natural enemies. In short, the introduction of natural biocontrol agents from South America might be able to sufficiently tilt the ecological balance in the United States so that our native ants can compete with this imported pest on an even basis. If the current ecological balance can be tilted in favor of our native ants, it seems possible that fire ant populations in the United States could be reduced to levels similar to those found in South America.

Acknowledgments

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Current Contact Information (Oct. 2004)
Sanford D. Porter

Mailing Address:
USDA-ARS, CMAVE
P.O. Box 14565
Gainesville, FL 32604 USA

Street Address:
USDA-ARS, CMAVE
1600 S.W. 23rd Drive
Gainesville, FL 32608 USA

Office: 352 374-5914
Secretary: 374-5903
FAX: 374-5818
E-mail: sdp@nersp.nerdc.ufl.edu (preferred)
E-mail: sdporter@gainesville.usda.ufl.edu (alternate)
Official Web Site: http://www.ars.usda.gov/pandp/people

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