

## BIOLOGICAL CONTROL

Field Studies of the Parasitic Ant *Solenopsis daguerrei* (Hymenoptera: Formicidae) on Fire Ants in ArgentinaL. A. CALCATERRA,<sup>1</sup> J. A. BRIANO,<sup>1</sup> AND D. F. WILLIAMS<sup>2</sup>

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**ABSTRACT** The workerless parasitic ant *Solenopsis daguerrei* (Santschi) has been considered a potential candidate for biological control of imported fire ants in the United States since the 1970s. We estimated the detrimental effects of *S. daguerrei* in fire ant colonies from Argentina by comparing the composition of parasitized and nonparasitized field colonies of the black imported fire ant *S. richteri* Forel. We recorded mound density and volume, incidence of polygyny, number of queens per colony, queen weight, and presence and abundance of brood and sexuals. Also, we studied aspects of the parasite's biology such as parasitization rates, presence of sexuals, abundance and weight of queens, and sex ratio. *S. daguerrei* occurred in 1.2-23.7% of the colonies at 21 collecting sites. The mound density at parasitized sites was significantly lower than in parasite-free sites (161 versus 239 mounds per hectare). Parasitized colonies had significantly fewer host queens than nonparasitized ones (2.9 versus 5.5 queens per colony). The percentage of colonies with worker brood was significantly lower (in fall) in parasitized than in nonparasitized colonies. Also, worker brood was significantly less abundant (in fall and spring) in parasitized colonies. A short delay in the production of sexual brood by the host was observed in parasitized colonies. These detrimental effects look promising but should be evaluated in the long-term and confirmed in other areas. A better understanding of the host and parasite is required to introduce *S. daguerrei* into the United States to control imported fire ants.

**KEY WORDS** *Solenopsis richteri*, *Solenopsis daguerrei*, fire ants, parasitic ants, colony composition, biological control

THE IMPORTED FIRE ants *Solenopsis invicta* Buren and *S. richteri* Forel are major pests in the southeastern United States (Lofgren 1986). According to Porter et al. (1997), their higher densities in the United States might be, at least partially, the result of biological release from natural enemies present in their native South America, where fire ant populations are 4-7 times less abundant than in North America. This suggests that the importation of successful biological control agents of fire ants should reduce the pest to levels similar to those found in South America.

The workerless parasitic ant *Solenopsis daguerrei* (Santschi) (formerly *Labouchena daguerrei*) has been considered a potential candidate for biological control of imported fire ants in the United States since the 1970s. Jouvenaz (1990) and Wojcik (1990) reported that this parasitic ant could be one of the most promising candidates among the arthropods for introduction into the United States. *S. daguerrei*, like the parasitic ant *Teleutomyrmex schneideri* Kutter and other species, is a permanent parasite because it spends its entire life cycle in the nest of the host species (Hölldobler and Wilson 1990). *S. daguerrei* queens attach to the host queens and fire ant workers tend them in a

similar manner to their own mother queen, whereas the parasite brood are reared by the host workers simultaneously with the host brood (Bruch 1930).

The presence of the parasite was surveyed in South America (Silveira-Guido et al. 1962-1969, Briano et al. 1997) and it appears that *S. daguerrei* has no specific habitat preferences. It can be found in dry and wet environments, in different soil types and topography, and in different plant communities. However, the parasite has been found only in nests of *Solenopsis saevissima* F. Smith complex species such as *S. richteri*, *S. invicta*, *S. saevissima*, and *S. macdonaghi* Santschi (Silveira-Guido et al. 1973, Briano et al. 1997).

Observations on the biology and behavior of *S. daguerrei* were reported by Bruch (1930), Silveira-Guido et al. (1962-1969, 1973) and Briano et al. (1997). According to Bruch (1930), under laboratory conditions the parasite can kill the host queens by decapitation. Silveira-Guido et al. (1965, 1973), however, found no evidence of decapitation, but reported that the parasite inhibits egg production, especially the production of host sexuals. In extreme cases this causes the collapse of the host ant colony. Yet, little is known about the actual impact of this and other natural enemies on native South American fire ant populations (Porter et al. 1997). The objectives of this study were to estimate detrimental effects of *S. daguerrei* in native Argentine fire ant colonies and to study some aspects of the parasite's biology.

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## Materials and Methods

**Study Area.** The study was conducted from May 1996 (fall) to June 1997 (fall) at San Eladio, Buenos Aires Province (59° 10' W, 34° 45' S). This area was selected because it had the highest abundance (7.0%) of *S. daguerrei* in South America (Briano et al. 1997). The area has a mean annual temperature of 18.7°C with extremes of 41°C (December) and -8°C (June), an average of 57.5 d with frost per year (range, 30–81 d), and an annual rainfall of 1,009 mm (10-yr records, Ministerio de Asuntos Agrarios 1987–1996). Topographically, the area is flat and the formation of temporary puddles is common. The vegetation is composed mainly of gramineae and is used for livestock grazing. These natural pastures have not been cultivated for the last few years. Annual crops have been introduced recently in the area.

**Percentage of Parasitism and Mound Density.** A total of 2,580 colonies of fire ants (mainly *S. richteri*) was examined by excavating and scattering them on the ground to detect the presence of adults or queens of the parasitic ant. The collecting sites were located in natural pastures on 5 ranches (San Mariano, Cheroga, Pylmaiquén, Santa Cándida, and Santa Lucia) where the parasite was found. The area of the pastures ranged from 1/3 to 30 ha. The density of fire ant colonies in each pasture was estimated in 3 transects randomly located. Each transect was ~300 m long by 3 m wide (except in a couple of small pastures, where they were shortened to ~100 m). All active mounds found within the transects were counted. For the purpose of this study, we considered each mound as a colony because mounds are fully functional units (Macom and Porter 1996). Mound density in the sites where the parasite was present was compared with the mound density of 53 parasite-free pastures surveyed in 20 localities from November 1995 to April 1996 (L.A.C., unpublished data). The localities were 40–150 km apart from San Eladio and were similar in habitat, land use, and climate. In each pasture the density of fire ants was estimated in 3 transects randomly located as above.

**Mound Volume.** We measured the height, length, and width of the mounds of 62 parasitized and 84 nonparasitized colonies of *S. richteri*. All parasitized colonies found within the pastures were measured. Nonparasitized colonies were selected within the transects mentioned above using a random number table. Mound volume ( $V$ ) was calculated using the formula for half a spheroid,  $V = \frac{2}{3} \pi abc$ , where  $a$  is the length/2,  $b$  is the width/2, and  $c$  is the height (Porter 1992).

**Host Colony Composition.** The *S. richteri* colony composition was compared between 149 nonparasitized and 140 parasitized colonies. After excavation, the colonies were put in 10-liter buckets dusted with talc and brought to the laboratory. The colonies were separated from the soil by flotation (Banks et al. 1981), put in plastic rearing trays (40 by 30 by 15 cm), and examined for polygyny, number of queens per colony, worker brood, sexual brood, and winged females and

males. Those colonies with no host queen were not included in the data for polygyny and number of queens. The abundance of each caste or stage was rated by using 3 categories: 0, none; 1, few; and 2, many.

Host queens were dissected and their spermatheca examined to confirm insemination. Colonies with only 1 inseminated queen were considered as *probable monogyne* and colonies with >1 inseminated queen as *polygyne*. The live weight of 278 queens from 52 nonparasitized and 138 queens from 34 parasitized colonies was recorded. For comparison studies, the weights of queens in polygyne colonies were averaged.

**Parasite Colony Composition.** The presence and abundance of *S. daguerrei* multiple queens were recorded from 96 parasitized colonies excavated in the field. Every queen ( $n = 114$ ) from 33 of these colonies was weighed. For comparison studies, the weights of parasite queens per host colony were also averaged. We considered queens as those physogastric wingless females or those found yoked to the host queens. The presence of sexuals was monitored in the field seasonally.

In addition, 30 colonies of *S. daguerrei* collected from December 1995 to January 1997 in several localities of Buenos Aires Province were sampled for sex ratio. In small colonies, all sexuals of the parasite were counted; and in large colonies, a sample of ~150 sexuals was used. A total of 3,566 sexuals was counted.

After examination in the laboratory, some of the parasitized colonies were shipped to the quarantine facilities of the USDA-ARS, Center for Medical, Agricultural, and Veterinary Entomology, Gainesville, FL, for further research. Voucher specimens were kept at the USDA-ARS, South American Biological Control Laboratory and some were sent to the Museo de La Plata, Paseo del Bosque, 1900 La Plata, Buenos Aires Province, Argentina.

**Statistical Analysis.** Statistical analysis to compare the parasitized and nonparasitized colonies was done with Minitab Statistical Software (1991). A 2-sample *t*-test was used to compare mound density, volumes of mounds, and weight of host and parasite queens. Chi-square tests were used to analyze the proportion of polygyny, plus presence of sexuals and brood. Mann-Whitney *U* tests were used to compare the number of queens per colony and the abundance of sexuals and brood. We used linear regression to relate the number of queens per colony with queen weight. The means  $\pm$  1 SE are reported.

## Results and Discussion

**Percentage of Parasitism and Mound Density.** Of the 2,580 colonies of *S. richteri* examined within the 21 collecting sites from the area of San Eladio, we found *S. daguerrei* in 131 colonies (5.1%). The percentage of parasitism in the different pastures ranged from 1.2 to 23.7% of the colonies (average 4.6%) (Table 1). Because of the low parasitism rates in most of the pastures, a large number of host colonies were exam-

Table 1. Abundance of *S. daguerrei* in San Eladio, Argentina

| Collecting site no. | No. of mounds/ha | No. of colonies examined | Colonies parasitized |      |
|---------------------|------------------|--------------------------|----------------------|------|
|                     |                  |                          | No.                  | %    |
| 1                   | 44               | 35                       | 1                    | 2.9  |
| 2                   | 70               | 58                       | 1                    | 1.7  |
| 3                   | 89               | 60                       | 1                    | 1.7  |
| 4                   | 111              | 50                       | 1                    | 2.0  |
| 5                   | 122              | 277                      | 39                   | 14.1 |
| 6                   | 122              | 50                       | 1                    | 2.0  |
| 7                   | 122              | 53                       | 1                    | 1.9  |
| 8                   | 122              | 38                       | 9                    | 23.7 |
| 9                   | 144              | 109                      | 3                    | 2.7  |
| 10                  | 161              | 125                      | 9                    | 7.2  |
| 11                  | 161              | 75                       | 2                    | 2.7  |
| 12                  | 167              | 240                      | 3                    | 1.2  |
| 13                  | 167              | 140                      | 3                    | 1.8  |
| 14                  | 170              | 107                      | 3                    | 2.8  |
| 15                  | 189              | 130                      | 5                    | 3.8  |
| 16                  | 200              | 105                      | 2                    | 1.9  |
| 17                  | 200              | 205                      | 12                   | 5.8  |
| 18                  | 222              | 275                      | 22                   | 8.0  |
| 19                  | 233              | 102                      | 5                    | 4.9  |
| 20                  | 237              | 74                       | 1                    | 1.3  |
| 21                  | 333              | 272                      | 9                    | 3.3  |
| Total or range      | 44-333           | 2,580                    | 131                  | 5.1  |
| Avg                 | 161              | 122.9                    | 6.2                  | 4.6  |

ined to obtain the required number of parasitized colonies for comparison studies.

The high variation observed in the parasitism rate among the pastures surveyed (1.2–23.7%) might be the result of the population dynamics of the parasite, which showed a contagious distribution. We speculate that this might be explained by the fact that a single polygyne colony occupies several interconnected nests, through which the parasite could disperse easily as brood or adult. Further field work is needed to test this assumption. Differences in land use (history of the pastures) could also increase variation in the density of the host and parasite.

The highest parasitization rate (23.7%) in San Eladio is smaller than one reported by Silveira-Guido et al. (1973) in the area of Las Flores (38.4%) Buenos Aires Province, type locality of *S. daguerrei*. However, in a recent study, Briano et al. (1997) did not detect the presence of the parasite in that area. The reason for this remains uncertain.

Although the low presence of *S. daguerrei* in San Eladio is discouraging, it might not be a good indicator of its ecological impact on its host. Feener (1981) found that the competitive ability of the ant *Pheidole dentata* Mayr dramatically decreased against its enemy *Solenopsis texana* Emery because of the effect of phorid flies, whose parasitism rate was <5%. If this is also the case for *S. daguerrei* remains unclear and should be confirmed. Once in a new habitat (e.g., the United States), the establishment and dispersal of *S. daguerrei* will be difficult to predict, as has been the case for most natural enemies artificially introduced for biological control. Eventually, the prevalence of this parasite could be increased as soon as its dispersal mechanism is understood.

The mound density at parasitized sites was  $161 \pm 14$  mounds per hectare (range, 44–333; Table 1). This

density is significantly lower than the one observed in nonparasitized sites,  $239 \pm 15$  mounds per hectare (range, 78–600) ( $t = 3.74$ ,  $df = 61$ ,  $P < 0.001$ ). However, other potential sources of variation in the density of fire ants colonies such as topography, soil type, and presence of other natural enemies were not included in this study.

Briano et al. (1995) reported densities of 120–162 colonies per hectare at Saladillo, Buenos Aires Province, where *S. richteri* colonies were highly infected with the microsporidium, *Thelohania solenopsae* Knell, Allen & Hazard, (Microsporida: Thelohaniidae). The presence of *S. daguerrei*, however, was very low (1.4%).

The mound densities recorded in Argentina are much lower than the ones reported by Porter et al. (1991, 1992) for polygyne populations of *S. invicta* in the United States (544–680 mounds per hectare); and higher than the densities reported by Porter et al. (1992) for probable monogyne populations of *S. invicta* in Brazil (27 mounds per hectare). However, comparisons of fire ant densities are of relative value because the studies were conducted under different habitats (roadside versus pasture), land use, and sampling methods.

The mean percentage of parasitism was 3.5% in sites with high mound density (above the mean), whereas in sites with low mound density (below the mean) it was 5.7%. This suggests an inverse relationship between mound density and parasitization levels, but it was not significant ( $r^2 = 0.04$ ;  $F = 0.08$ ;  $df = 1, 19$ ;  $P = 0.777$ ). The effect of *S. daguerrei* on the density of the host colonies should be evaluated over the long-term. Even small reductions in the host population levels could be biologically important.

**Mound Volume.** The volume of parasitized colonies was  $6.0 \pm 0.5$  liters (range, 0.3–21.3), which is similar to the mound volume of nonparasitized colonies,  $5.9 \pm 0.5$  liters (range, 0.5–34.6) ( $t = 0.08$ ,  $df = 144$ ,  $P = 0.94$ ). In previous surveys in different areas of Argentina and Uruguay (L.A.C., unpublished data), we found similar volumes for parasitized colonies ( $5.2 \pm 0.9$  liters; range, 0.9–18.8) ( $t = 0.78$ ,  $df = 85$ ,  $P = 0.439$ ). These volumes are smaller than those reported by Briano et al. (1995) for *S. richteri* in Saladillo and Las Flores ( $10.3 \pm 1.2$  and  $18.7 \pm 1.7$  liters), but similar to the volumes reported by Porter et al. (1997) for *Solenopsis* spp. in South America (5.1 liters), and for *S. invicta* in North America (7.4 liters). However, because the mound size varies greatly with different soil types, soil moisture, vegetation, and sampling habitat (Lofgren et al. 1975), comparisons are also of relative value.

The size distribution of mounds in nonparasitized and parasitized colonies was similar. Around 30% of the mounds had a volume up to 3.5 liters, 40% of the mounds were between 3.6 and 7.0 liters, and the remaining 30% were >7.0 liters (Fig. 1).

When all colonies (parasitized and nonparasitized) were considered, the mound volumes of monogyne and polygyne colonies were similar ( $5.2 \pm 0.5$  liters; range, 0.3–16.5 versus  $5.3 \pm 0.6$  liters; range, 0.5–21.3,

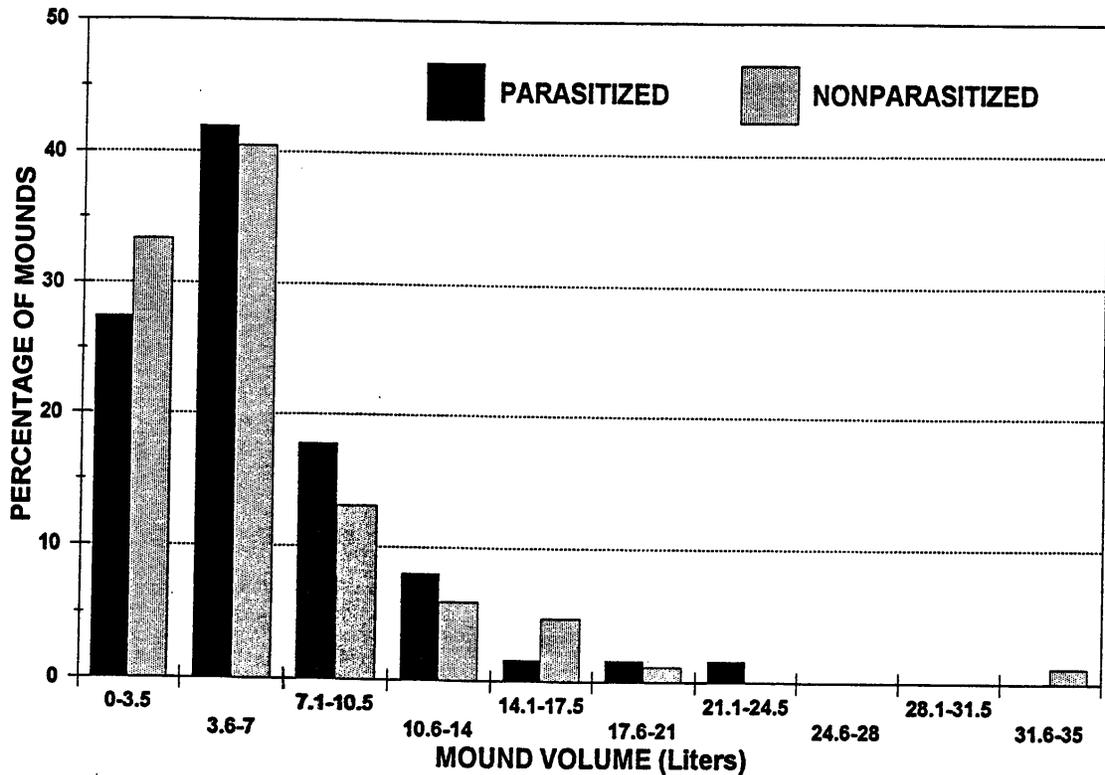


Fig. 1. Mound size distribution of parasitized and nonparasitized colonies of *S. richteri* ( $n = 146$ ) in San Eladio, Argentina.

respectively;  $t = -0.1$ ,  $df = 115$ ,  $P = 0.92$ ). Briano et al. (1995) reported similar volumes in Saladillo, 6.2 and 5.8 liters, in monogyne and polygyne colonies respectively.

**Host Colony Composition.** *Polygyny* Approximately half of the *S. richteri* colonies examined in San Eladio was polygyne. The presence of multiple queens in nonparasitized colonies was 57.6%, which was not significantly different from the 43.7% found in parasitized colonies ( $\chi^2 = 3.610$ ,  $df = 1$ ,  $P > 0.05$ ,  $n = 188$ ). These percentages are consistent with the high incidence of polygyny reported by Briano et al. (1995) in fire ant populations in Argentina. They found polygyny in 25.7–41.5% of the *S. richteri* colonies in Saladillo and in 46% of the colonies in Las Flores. According to Porter (1992) and Porter et al. (1991, 1992), polygyny is also common in the southern United States (15–54% of the sampled sites for *S. invicta*). Porter et al. (1992) reported 67% of the colonies of *S. invicta* at polygyne sites were confirmed as polygyne. *S. invicta* has not been reported in the polygyne form in Brazil (Jouvenaz et al. 1989; Porter et al. 1992, 1997).

Monogyne and polygyne colonies of *S. richteri* coexisted in the sites surveyed in San Eladio. We did not find any exclusively monogyne sites, which contrast with Jouvenaz et al. (1989) who reported that 25 of 33 sites (76%) had only monogyne colonies of *S. richteri* in Argentina.

According to Macom and Porter (1996), an important reason for the high incidence of polygyny is the

lack of aggression toward polygyne conspecifics. Because polygyne colonies are less territorial, they use available resources better, resulting in larger fire ant populations. This lower aggressiveness of polygyne populations permits the integration of fertilized young queens into colonies of their own species and would also allow the parasite to establish more easily than in monogyne populations (Buschinger 1986).

Porter et al. (1992) suggested that the occurrence of polygyny might be linked to the absence of biological control agents. Moreover, Keller (1995) mentioned that 1 potential advantage of polygyny is an increased genetic variability and lower susceptibility to parasites. Our data contrast with Porter's and Keller's hypotheses because we found a high incidence of polygyny (56.7%) in parasitized populations. Why polygyny is so common in San Eladio and other areas of Argentina is unknown. However, according to Hölldobler and Wilson (1977), ant populations may change from the monogyne to the polygyne form (and vice versa) depending on environmental conditions. Moreover, according to Buschinger (1986) and Hölldobler and Wilson (1990), host polygyny is a sufficiently frequent phenomenon in ants to represent a condition from which a permanent parasite such as *S. daguerrei* may have evolved.

**Number of Queens per Colony.** The mean number of fire ant queens per colony was significantly lower in parasitized colonies ( $2.9 \pm 0.5$ ; range, 1–40) than in nonparasitized colonies ( $5.5 \pm 2.0$ ; range, 1–180) ( $U =$

Table 2. Percentage of parasitized and nonparasitized *S. richteri* colonies with brood and sexuals from 1 May 1996 to 28 May 1997 in the area of San Eladio, Argentina

| Presence of                       | Late fall 1996 <sup>a</sup> | Winter 1996 <sup>b</sup> | Spring 1996 <sup>c</sup> | Summer 1996-1997 <sup>d</sup> | Early fall 1997 <sup>e</sup> |
|-----------------------------------|-----------------------------|--------------------------|--------------------------|-------------------------------|------------------------------|
| Parasitized colonies (n = 140)    |                             |                          |                          |                               |                              |
| Worker brood                      | 5.7%                        | 11.1%                    | 93.9%                    | 100.0%                        | 68.0%                        |
| Sexual brood                      | 0%                          | 0%                       | 36.4%                    | 15.0%                         | 0%                           |
| Winged females                    | 7.5%                        | 22.2%                    | 6.1%                     | 20.0%                         | 24.0%                        |
| Winged males                      | 1.9%                        | 11.1%                    | 3.0%                     | 10.0%                         | 20.0%                        |
| No. of colonies examined          | 53                          | 9                        | 33                       | 20                            | 25                           |
| Nonparasitized colonies (n = 149) |                             |                          |                          |                               |                              |
| Worker brood                      | 25.0%                       | 17.4%                    | 100.0%                   | 100.0%                        | 72.7%                        |
| Sexual brood                      | 0%                          | 0%                       | 21.7%                    | 10.0%                         | 0%                           |
| Winged females                    | 8.3%                        | 4.3%                     | 8.7%                     | 20.0%                         | 18.2%                        |
| Winged males                      | 6.2%                        | 4.3%                     | 8.7%                     | 10.0%                         | 13.6%                        |
| No. of colonies examined          | 48                          | 46                       | 23                       | 10                            | 22                           |

<sup>a</sup> Late fall, 1 May-20 June.

<sup>b</sup> Winter, 21 June-20 September.

<sup>c</sup> Spring, 21 September-20 December.

<sup>d</sup> Summer, 21 December-20 March.

<sup>e</sup> Early fall, 21 March-28 May.

8,272.5;  $n_1 = 96$ ,  $n_2 = 92$ ;  $P < 0.05$ ). This reduction of queen number (47%) in parasitized colonies could be an important detrimental effect of *S. daguerrei* on fire ant populations. The magnitude of this effect could be of enormous value in biological control of the fire ant. Additional laboratory tests are needed to confirm Bruch's hypothesis (1930) of decapitation. We speculate that the parasite might increase the number of monogyne colonies in *S. richteri* populations because of the detrimental effect on the number of host queens. This might be associated with the lower densities at parasitized sites and must be investigated.

**Worker Brood.** The percentage of colonies with worker brood during the study ranged between 5.7% (late fall 1996) and 100% (summer) for parasitized colonies and 17.4% (winter) and 100% (spring and summer) for nonparasitized colonies (Table 2). We observed seasonal differences in the worker brood production between parasitized and nonparasitized colonies only in late fall and spring of 1996. In late fall of 1996, the percentage of colonies with worker brood was 5.7% for parasitized colonies and 25.0% for nonparasitized colonies ( $\chi^2 = 7.45$ ,  $df = 1$ ,  $P < 0.01$ ). Worker brood were less abundant in parasitized than in nonparasitized colonies ( $U = 2,452.5$ ;  $n_1 = 53$ ,  $n_2 = 48$ ;  $P < 0.01$ ). In spring, the percentage of parasitized and nonparasitized colonies with worker brood were similar, 93.9 versus 100%, respectively ( $\chi^2 = 1.45$ ,  $df = 1$ ,  $P > 0.1$ ); however, worker brood were less abundant in parasitized than in nonparasitized colonies ( $U = 795.0$ ;  $n_1 = 33$ ,  $n_2 = 23$ ;  $P < 0.005$ ).

In parasitized colonies, we found worker brood in May, August, October, November, and December of 1996, and in January, February, March, April, and May of 1997. In nonparasitized colonies, we found worker brood in every month from May 1996 to May 1997. The lower production of worker brood in parasitized colonies in late fall and spring of 1996 suggests a detrimental effect of the parasite on the seasonal growth of the host colonies. This would be consistent with Wilson (1971), who reported that an inquiline species

inhibits the growth of its host by maximizing the production of parasite queens and males.

**Sexual Brood.** The presence of *S. daguerrei* did not significantly affect fire ant sexual brood production. The percentage of colonies with sexual brood was 36.4% (spring) and 15.0% (summer) for parasitized colonies, which is similar to the 21.7% (spring) and 10.0% (summer) for nonparasitized colonies (Table 2). We found no differences in sexual brood abundance.

We did not find sexual brood in the fall and winter, presumably because of the low temperatures. We observed a short delay in the production of sexual brood in parasitized colonies (October to mid February) compared with nonparasitized colonies (September to mid February).

The unexpected larger percentage of parasitized colonies with sexual brood, although not significant, may be explained by the fact that more queens were found in nonparasitized colonies, which, according to Vargo and Fletcher (1987), could inhibit the production of sexuals.

**Winged Females and Males.** Winged forms were observed throughout the study period in parasitized and nonparasitized *S. richteri* nests in similar frequencies and abundances. The presence of winged females ranged between 6.1% (spring) and 24.0% (early fall 1997) for parasitized colonies, and between 4.3% (winter) and 20.0% (summer) for nonparasitized colonies (Table 2).

In parasitized colonies, we found females in May, June, July, and October of 1996, and in January, February, April, and May of 1997 (in September of 1996, we did not find parasitized colonies). In nonparasitized colonies, we found females from May 1996 to January 1997, and from April to May 1997.

Adult males were less common than females in both parasitized and nonparasitized colonies. The percentage of colonies with adult males ranged between 1.9% (late fall 1996) and 20.0% (early fall 1997) for para-

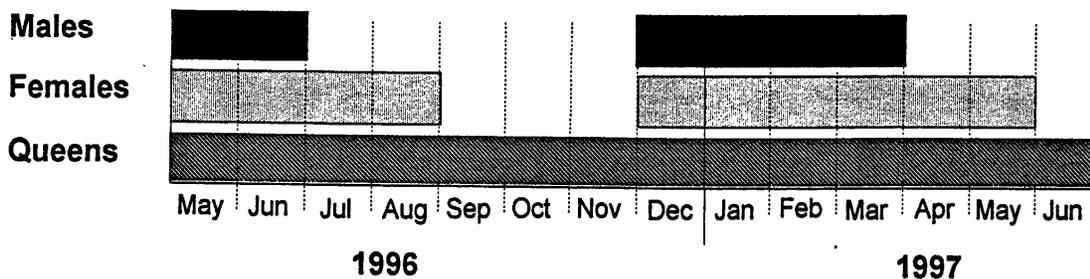


Fig. 2. Seasonal presence of males, females, and queens of *S. daguerrei* in fire ant colonies of San Eladio, Argentina.

sitized colonies, and between 4.3% (winter) and 13.6% (early fall 1997) for nonparasitized colonies (Table 2).

In parasitized colonies, we found males in June, July, and October of 1996, and in January and April of 1997; whereas in nonparasitized colonies, we found them in May, June, July, and October of 1996, and in January, April, and May of 1997.

The presence of sexuals of the host in parasitized colonies is in contrast with the findings of Silveira-Guido et al. (1973), who did not observe them in parasitized colonies. They assumed that the presence of the parasite inhibited the production of fire ant sexuals, but this was not confirmed in our study.

**Weight of Host Queens.** Fire ant queen weights were similar in parasitized and nonparasitized colonies, both in polygyne (14.9 versus 14.8 mg;  $t = 0.1$ ,  $df = 44$ ,  $P = 0.88$ ) and monogyne colonies (18.5 versus 19.0 mg;  $t = 0.4$ ,  $df = 44$ ,  $P = 0.70$ ). Queens from parasitized monogyne colonies were heavier than queens from parasitized polygyne colonies (18.5 versus 14.9 mg;  $t = 3.4$ ,  $df = 32$ ,  $P < 0.005$ ). As expected, queens from nonparasitized monogyne colonies were heavier than queens from nonparasitized polygyne colonies (19.0 versus 14.8 mg;  $t = 4.1$ ,  $df = 49$ ,  $P < 0.001$ ).

The weights of nonparasitized polygyne queens of *S. richteri* were similar to those reported by Porter (1992) for *S. invicta* (14.4 mg). However, the average weight of nonparasitized monogyne queens was  $\approx 5$  mg lower. We found physogastric queens ( $>17$  mg) from August to early December (late winter-spring).

Although we did not find evidence to show that *S. daguerrei* reduces the weight of individual host queens, any detrimental effect could be masked by the fact that fewer queens (and consequently heavier queens) are associated with the presence of the parasite. As expected according to Vargo and Fletcher (1989) for *S. invicta*, queen weight was inversely related to the number of queens per colony both in nonparasitized ( $r = -0.53$ ;  $F = 8.77$ ;  $df = 1, 23$ ;  $P < 0.01$ ) and parasitized colonies ( $r = -0.67$ ;  $F = 13.91$ ;  $df = 1, 17$ ;  $P < 0.005$ ).

**Parasite Colony Composition. Polygyny and Number of Queens.** Based on our study, polygyny seems to be the most common form of *S. daguerrei* in San Eladio. We found multiple queens in 64.9% of the colonies examined. This agrees with Buschinger (1986), who stated that most interspecific inquilines, and their hosts, are polygyne. The mean number of

queens per colony was  $3.8 \pm 0.7$  (range, 1–64). However, the mean number of parasite queens was higher in polygyne fire ant colonies than in monogyne ones ( $6.2 \pm 1.7$ ; range, 1–64 versus  $2.1 \pm 0.2$ ; range, 1–10, respectively;  $U = 1,744.5$ ;  $n_1 = 49$ ,  $n_2 = 39$ ;  $P < 0.001$ ).

In parasitized colonies maintained in the laboratory under standard rearing procedures (Banks et al. 1981), we observed the emergence of new parasite queens (L.A.C., unpublished data). This agrees with Silveira-Guido et al. (1973), who reported that sexuals of *S. daguerrei* mate inside the mound, at the exit-holes, or on top of mounds, and with Wilson (1971), who stated that in rare ant species such as *S. daguerrei*, there is no evidence of mating with members of other colonies (exogamy). According to Wilson (1971) endogamy (or inbreeding) in rare and isolated species would ensure that many queens will be inseminated in each colony and that the loss of virgin reproductive females will be reduced. We believe that, probably because of their small size, *S. daguerrei* sexuals are not good flyers. We have never observed them flying out of their host colony in the field. However, in parasitized colonies maintained in the laboratory, we have observed very short and erratic flights of female parasites, never males. The dispersal mechanisms of this parasite are currently under study.

**Presence of Sexuals.** The presence of males and females of *S. daguerrei* was seasonal during the study period (Fig. 2). We found males in May–June of 1996 (fall) and from December 1996 to March 1997 (summer); females from May to August 1996 (fall–winter) and from December 1996 to May 1997 (summer–fall). Females were observed in the colonies for 2 mo more than males during both 1996 and 1997, but females and males disappeared 3 mo earlier in 1997 than in 1996. This was probably due to a severe drought during the warm season of 1996–1997. We did not find sexuals of *S. daguerrei* from September to November 1996 (spring) and in June of 1997 (fall) we found only queens.

According to Silveira-Guido et al. (1973), *S. daguerrei* has 2 well-defined oviposition periods in this latitude, the 1st from July to October (winter-spring) and the 2nd from December to March (summer). Our observations contrast with this, and indicate that *S. daguerrei* starts an oviposition cycle only at the beginning of the warm season (probably in October) around 2 mo before the appearance of the 1st sexuals

(December). The end of the oviposition cycle remains uncertain but it is probably at the end of the warm season (May). The period in which the sexuals stay in the colony after emergence has not been determined.

We observed that sexuals of the host and the parasite emerged simultaneously within the colony. This is in contrast with Bourke (1991) who speculated that female larvae of parasitic species mask their sexuality by being small and by acting as worker larvae. They would emerge with the workers and before the host sexuals to avoid gyne suppression. Clearly, further research on this and other parasitic ant species is required to determine if a reproductive isolation mechanism, such as temporal or spatial separation of mating episodes, gave origin to inquiline species such as *S. daguerrei*.

**Weight of Queens.** The parasite queens were 10 times lighter than the average host queen. The mean weight of queens of *S. daguerrei* was  $1.9 \pm 0.1$  mg (range, 0.6–3.2) and no differences were observed between monogyne and polygyne host colonies ( $2.2 \pm 0.1$  versus  $1.9 \pm 0.1$  mg, respectively;  $t = 1.66$ ,  $df = 31$ ,  $P = 0.11$ ). We found, as in the host, physogastric parasite queens ( $>1.7$  mg) from September to early December (spring).

**Sex Ratio.** In the majority of colonies sampled, females were more numerous than males. The ratio of males to females was  $\approx 1:3$  (23.2–76.8%), however, high variation was observed among the colonies. Percentages of males within a colony ranged from 0 to 95.3%, and percentages of females ranged from 4.6 to 100%. The sex ratio reported here agrees with Silveira-Guido et al. (1963–1964), who stated that the males constitute 25% of the population of *S. daguerrei*.

We conclude that the reduction in the host queen number observed in parasitized colonies is a major factor in favor of *S. daguerrei* as a potential biological control organism for fire ants. The biological impact of this detrimental effect should be evaluated over a longer period in large fire ant populations. The finding of lower densities of fire ants in parasitized pastures compared with nonparasitized ones looks very promising but needs to be studied in other areas to confirm if the sole presence of the parasite was responsible for this reduction. In addition, the lower production of *S. richteri* worker brood found in fall and spring and the delay in the presence of sexual brood in parasitized colonies might provide additional evidence of detrimental effects of *S. daguerrei* against fire ants; the magnitude of these effects needs to be determined.

The search for other sites in South America with high densities of this parasite should be intensified to replicate findings, to conduct additional field studies, and to monitor the host-parasite relationship over a long period. A better understanding of the population dynamics of the host and parasite is required to introduce *S. daguerrei* into the United States to control imported fire ants.

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