A Grassland Ant Community in Argentina: The Case of *Solenopsis richteri* and *Camponotus punctulatus* (Hymenoptera: Formicidae) Attaining High Densities in Their Native Ranges

PATRICIA J. FOLGARAIT,[1] PAOLA D'ADAMO,[2] AND LAWRENCE E. GILBERT[3]

Centro de Estudios e Investigaciones, Universidad Nacional de Quilmes, Roque Saenz Peña 180, Bernal B1876BXD, Buenos Aires, Argentina

ABSTRACT   We studied the structure of an ant community along a 900-m transect of grassland in Argentina. Two ant species, *Solenopsis richteri* Forel and *Camponotus punctulatus* Mayr, monopolized space and food. These two species were distributed as a mosaic with most of the transect always controlled by either one or both. Within monospecific areas, each species reached mound densities comparable to those seen where each is an invasive species. Sampling with tuna and sugar water revealed that these two species together monopolized 95% of all baits. Where they co-occurred, *S. richteri* recruited more effectively and controlled more baits than *C. punctulatus.* In each area where *S. richteri* or *C. punctulatus* was most abundant, each dominant species arrived first at baits but did not differ from the other species in their persistence at these baits. Both species seemed to prefer to forage in the mornings in areas where each was most abundant; however, only *C. punctulatus* retained this pattern in the areas at which both species had similar densities. The rare occurrence of *Pseudacteon* parasitoids, and the susceptibility to flooding in the area, may explain the abundance of *S. richteri* and *C. punctulatus*, respectively, in this grassland.

KEY WORDS   ant foraging, diversity, flooding, nest density, *Pseudacteon*

ANT COMMUNITIES ARE IN GENERAL, diverse (Folgarait 1998). However, some exceptions occur in unusually harsh environments where good-tolerator species become dominant (Hölldobler and Wilson 1990) or in natural systems altered by humans, which favor the sudden dominance of one species (Andersen and Mc-Kaige 1987, Suarez et al. 1998, Folgarait and Gorosito 2001). Other causes involve the presence of exotic species that are able to become established in foreign habitats, displacing other ant species and drastically reducing diversity in an area (Williams 1994). What seems to occur in these instances is a change in the competitive hierarchy within the ant community in favor of the invasive species (Hollway 1999, Morrison et al. 2000).

Ant communities are organized according to competitive hierarchies (Hölldobler and Wilson 1990). Such hierarchies arise from differences in social organization and worker densities and foraging strategies (Savolainen and Vepsäläinen 1988). A species position in the hierarchy depends on a trade-off based on its ability to dominate resources after they are discovered versus its ability to discover those resources rapidly (Hollway 1999). Poor competitors tend to find food resources first but are later replaced by more aggressive species with well-developed systems of recruitment that allow them to dominate at contested resources (Vepsalainen and Pisarski 1982, Andersen 1986). Submissive ants that are neither good competitors nor fast at finding resources are either restricted to foraging during times with harsh environmental conditions, or are eliminated from the community (Savolainen and Vepsäläinen 1988, Bestelmeyer 1997). Therefore, aggressive ants with well-developed systems of recruitment have a greater chance of becoming dominant in the hierarchy, and therefore being abundant. Furthermore, if circumstances allow (i.e., introduced into less competitive communities), these ants could be removed from the constraint imposed by the mentioned trade-off (Hollway 1999). An additional factor determining competitive outcomes in ants is parasitoid flies of the family Phoridae (e.g., Feener 1981). Much recent attention has been given to the possibility that freedom from phorid attack in the introduced range of fire ants (*Solenopsis richteri* Forel and *S. invicta* Buren) helps account for their higher densities in the United States (e.g., Porter et al. 1997).

Depauperate ant communities, assemblages dominated by one or two species, offer unique opportuni-

[1] E-mail: pfolgarait@unq.edu.ar.
[2] Laboratorio Entomología Forestal. EEA INTA Bariloche, CC 277 (8400) Rio Negro, Argentina.
[3] Brackenridge Field Laboratory and Section of Integrative Biology, University of Texas, Austin, TX 78712.

ties to study community organization (Hölldobler and Wilson 1990). Here we focused on two ant species native from Argentina, where for different reasons and in different places, have exploded demographically and become dominant in the invaded ant community. One is the case of the fire ants *S. invicta* and *S. richteri*, which are native to Argentina and Brazil and were accidentally introduced in the United States around the 1930s. Porter et al. (1997) have concluded that these ants were four times more abundant (mound densities) in Texas (North America) than in their native habitats in northeast Argentina and Brazil (South America), and that this difference is not explained by sampling conditions, seasonal variability, habitat differences, or the frequency of polygyny. However, in certain areas of Brazil some fire ant populations can be as high as in the United States, often exceeding 494 colonies per hectare (Banks et al. 1985, Adams 1994). The high density of fire ants in the United States has reduced ant and arthropod abundance and diversity locally (Porter and Savignano 1990, Wojcik et al. 2001) and is a nuisance or worse for vertebrates (Allen et al. 1995, Wojcik et al. 2001).

The other case is that of *Camponotus punctulatus* Mayr, also native to Argentina (Kusnezov 1951), and which becomes numerically important only under specific circumstance. Although this ant has a typical hypogeous life history, under certain circumstances, it becomes epigeic and builds mounds. Mound density is generally low in the majority of natural grasslands where it occurs (25–50 nests/ha; Folgarait et al. 2002) but becomes extremely high when flooding (500 mounds/ha; Lewis et al. 1991) and agricultural activities, especially intensive ones, favors its demographic explosion and epigeic mode of life (Folgarait et al. 2002, 300–2,500 mounds/ha). Studies in sown pastures, where this ant becomes numerically abundant, have shown that *C. punctulatus* does not eliminate other ants or other arthropods but does depress the abundance of other ant species (Folgarait and Gorosito 2001).

At the Otamendi Natural Reserve in Buenos Aires, Argentina, *S. richteri* and *C. punctulatus* are common in a grassland habitat that is susceptible to flooding. To understand the coexistence of *C. punctulatus* and *S. richteri*, we asked specific questions, such as the following: (1) Do they partition their nest area as truly territorial ants do (Savolainen and Vepsäläinen 1988)? (2) Do they have different efficiencies at finding and keeping food resources? (3) Do they differ in their periods of foraging activity? (4) Do they affect other arthropods? To answer these questions, we characterized the position of *C. punctulatus* and *S. richteri* in the ant community by analyzing nest densities and distribution, establishing their competitive rank, estimated by bait discovery, bait dominance, and monopolization, determining their periods of foraging activity, and analyzing the relative effect each species has on arthropod diversity.

Materials and Methods

The study took place at the Otamendi Natural Reserve, located in Río Luján (34° 10′ S, 58° 45′ W), Buenos Aires Province, Argentina. Established as a Reserve in 1990, the area was used previously for cattle ranching, hunting and fishing activities. Most of the protected area has a flat to concave relief. It suffers periodic pluvial flooding due to poor drainage and the presence of superficial water tables (Chichizola 1993). We established a 855 m transect oriented at 70° NW, encompassing different degrees of flooding intensity, and extending from the railway (at the Río Luján train station) towards the river. The transect consisted of 29 stations, each 30 m apart. At each station, a pitfall trap (30 ml volume and 3 cm diameter) filled with 70% ethylene glycol was buried on the ground, and left opened for four consecutive days, to determine arthropod diversity (Nazzi et al. 1989, Paoletti et al. 1995). Pitfalls can be simultaneously used to determine ant activity and diversity (Romero and Jaffe 1989, Jusino-Atresino and Phillips 1994, Bestelmeyer and Wiens 1996). To measure mound density, we counted mounds in a rectangular strip (30 by 5.15 m) extending perpendicularly from both sides at each station. From October to December, all ant mounds in the 8,961-m^2 sampling area were counted and identified. Mound-building ant species included *Acromyrmex* sp. Mayr, *Pheidole* sp. Westwood, *Linepithema* sp. Mayr, *S. richteri*, and *C. punctulatus*. Some incipient mounds, built at the base of grasses or tussocks, were also considered (e.g., *Pheidole* sp.). *Linephitema* sp. is not known to build mounds but we found them in mounds; we do not know if these mounds originally belonged to other species and were secondarily occupied by *Linephitema* or if they had built them.

To explore feeding strategies, we offered sugar water and tuna baits on four different days (24 October 1996, 4 November 1996, 9 December 1996, 12 December 1996) throughout the daytime. Tuna and sugar represented protein and carbohydrate sources respectively, similar to those collected by ants (dead insects, honeydew, nectar) with the advantage of being more practical (Fellers 1987). These baits are commonly used in studies of ant community structure (Savolainen and Vepsäläinen 1988, Bestelmeyer 1997, Hollway 1999) and assure the presence of ants feeding different diets. Baits were offered throughout the day. Sugar water was placed in 2-cm-diameter tubes plugged with cotton, and tuna was placed 1 m away in petri dishes of 3.5 cm diameter. Both baits were offered *ad libitum*, being replaced during each sampling period if necessary. We identified ant species and the number of individuals present at each bait every 60 min (the time needed to walk the entire transect). We always started the measurements from the railway side and continued to the riverside. The number of observations per station varied from 3 to 5 counts depending on the census date. The maximum number of ants that could be precisely counted was 20; if more ants were observed, we registered the observation as >20 ants. For 2 d (4 November and 9 December), data on air
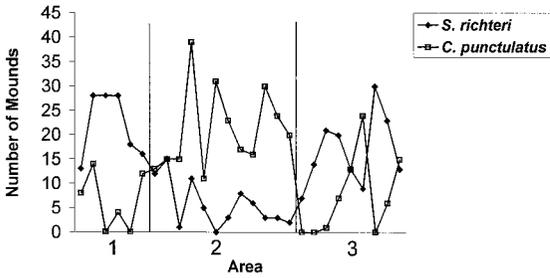
Fig. 1. Number of mounds found along strips of 309 m^2 at each of 29 stations separated by 30 m. Area classification was based on a change in the dominance between *S. richteri* and *C. punctulatus*; at area 1 *S. richteri* had a significantly greater mound density than *C. punctulatus*, whereas the opposite occurred at area 2, whereas densities did not differ between species at area 3 (see text for details).

temperature (°C) were taken in the field site at each station and sampling time.

Foraging strategy was studied by counting the number of individuals recruiting to the baits and, later calculating the proportion of sugar and tuna baits visited by different numbers of individuals of each species. A species was considered to monopolize a bait if it was the only species present (Cerdá et al. 1997). Discovery time was determined by counting the proportion of first arrivals to the bait (over the total number of baits along the transect). This number represented an indirect way of measuring the time needed to find the bait for the first time by each species. Bait dominance was measured as the persistence of ants at baits at consecutive sampling times. If ants abandoned the bait before the second observation, the species scored a low level of persistence; otherwise it scored a high level of persistence. Species other than *S. richteri* and *C. punctulatus* occurred at few baits; therefore, this type of analyses was not applied to them.

Data were analyzed using nonparametric statistics (Siegel 1974). Only *C. punctulatus* and *S. richteri* were abundant enough to be analyzed statistically.

To compare the distribution of nests in the transect between species we used Kolmogorov-Smirnov (shown as *KS*). To compare the number of mounds for each ant species across areas, or number of morphospecies or ants found in pitfalls across areas we used Kruskall-Wallis (shown as *H*). To compare num-

ber of mounds of *C. punctulatus* and *S. richteri* within areas we used Wilcoxon matched test for two paired variables (shown as *Z*). Finally chi-square comparisons were used for analyzing frequency tables to compare total number of mounds across species and areas, total cases of occupied and monopolized baits between species within areas and across areas, and across hour ranges, as well as to compare frequency of baits with high and low persistence, discovered first or later, between species within areas, or among areas by species.

Results

Nest Densities and Distribution. The study site was basically shared by two species, *C. punctulatus* and *S. richteri*, representing >90% of the nests located. Although the total number of mounds in the sampling area did not differ between *S. richteri* ($n = 350$) and *C. punctulatus* ($n = 358$), ($\chi^2 = 0.09$, df $= 1$, $P > 0.76$), the distribution of the mounds of each species was not homogenous ($KS = 0.27$, $P < 0.0001$; Fig. 1). To account for this spatial partitioning in the bait-related analyses, we defined areas by using the criterion of finding a simultaneous change in the ranking of the two species at any single station and comparing the mound density between both species. In this way, three areas from the railway toward the river were found (Fig. 1; Table 1). Number of mounds differed significantly across the three areas; *S. richteri* ($H = 15.7$, $P < 0.0014$) and *C. punctulatus* ($H = 13.2$, $P < 0.0013$). Area 1 was dominated by *S. richteri* ($Z = 2.2$, $P < 0.028$), area 2 was dominated by *C. punctulatus* ($Z = 2.93$, $P < 0.003$), and area 3 was not completely dominated by either ant species ($Z = 1.68$, $P < 0.93$). Mounds from other ant species comprised 7% of the total sampled in all three areas (Table 1).

Recruitment. Frequencies with which tuna (*S. richteri:* 53%, *C. punctulatus:* 47%) and sugar water (*S. richteri* 45%, *C. punctulatus* 55%) baits were occupied by *S. richteri* and *C. punctulatus* did not differ throughout the transect (2 × 2 contingency table $\chi^2 = 0.27$, df $= 1$, $P > 0.1$). Therefore, data for sugar and tuna baits were combined for all analyses.

Foraging strategies were different for *S. richteri* and *C. punctulatus*. Many *S. richteri* workers were recruited to the baits, while *C. punctulatus* recruited relatively fewer individuals (Fig. 2). *Camponotus*

Table 1. Mound density (mounds/ha) of ant species for the three areas of the transect (for details, see footnote and Fig. 1)

Area	# S	AS (cm^2)	# TM	D	*S. richteri*	*C. punctulatus*	*Acromyrmex*	*Linephitema*	*Pheidole*
A1	6	1,854	185	999	707 (70.81%)a,a	205 (20.54%)ac,b	76 (7.57%)	0 (0%)	11 (1.08%)
A2	12	3,708	348	938	186 (19.83%)b,a	685 (72.99%)b,b	3 (0.29%)	5 (0.57%)	59 (6.32%)
A3	9	3,399	230	682	441 (65.22%)a,a	200 (28.69%)c,a	0 (0%)	41 (6.09%)	0 (0%)
Combined	27	8,961	763	852	391 (46%)	399 (47%)	17 (2%)	18 (2%)	27 (3%)

Percentage of mound density per species and area is specified in brackets. # S = number of stations, AS = area, # TM = total number of mounds, D = density of mounds from mounds from all species. Comparisons across areas for each species denoted by the first letter, comparisons between species for each area denoted by the second letter. If letters are the same, comparisons are not significantly different ($P > 0.05$), if letters are different, comparisons are significantly different ($P < 0.05$). Statistical comparisons (Kruskall-Wallis and Mann-Whitney) were possible only between *S. richteri* and *C. punctulatus*. Two stations were under water at the time of sampling, therefore were not censused.
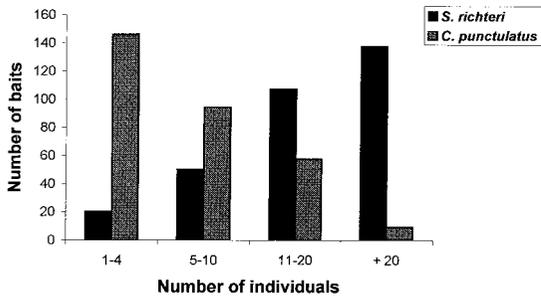
Fig. 2. Frequency of baits occupied by *S. richteri* and *C. punctulatus* throughout the study. Maximum number of ants that could be accurately counted was 20. From 928 observations (across stations, types of baits, sampling days, and times sampled per day) *S. richteri* occupied 314 baits, *C. punctulatus* 306, whereas other ant species occupied 34 baits.

punctulatus workers are, on average, larger than *S. richteri* workers (P.J.F., unpublished data).

The number of baits monopolized by *S. richteri* and *C. punctulatus* did not differ (2×2 contingency table; $\chi^2 = 1.12$, df $= 1$, $P > 0.29$). Together, these two species monopolized 95% of discovered baits (46% by *C. punctulatus* and 49% by *S. richteri*).

Foraging Strategy. *Bait Discovery.* Combining all observations across the 4 d of sampling, 68% of the baits were discovered either *S. richteri* or by *C. punctulatus.* We found differences in the frequency of baits among areas discovered first by *C. punctulatus* (2×3 contingency tables; $\chi^2 = 60.03$, df $= 2$, $P < 0.0001$), and by *S. richteri* ($\chi^2 = 59.85$, df $= 2$, $P < 0.0001$) (Fig. 3a). Baits placed in an area were discovered first by the ant species most abundant in that area. *S. richteri* had a greater frequency of cases in which it arrived first than second to the baits in comparison to *C. punctulatus* at areas 1 (2×2 contingency table; $\chi^2 = 26.33$, df $= 1$, $P < 0.0001$) and 3 ($\chi^2 = 15.48$, df $= 1$, $P < 0.0001$), whereas *C. punctulatus* arrived first more often than *S. richteri* at area 2 ($\chi^2 = 78.0$, df $= 1$, $P < 0.0001$).

Bait Dominance. There were no differences in the frequency of cases of low and high persistence for *S. richteri* at baits among areas (2×3 contingency table; $\chi^2 = 4.52$, df $= 2$, $P > 0.104$), but significant differences did exist for *C. punctulatus* ($\chi^2 = 7.53$, df $= 2$, $P < 0.023$) (Fig. 3 b and c). Analyzing each area separately, we found that *S. richteri* had more cases of high persistence at baits than did *C. punctulatus* at area 3 (2×2 contingency table; $\chi^2 = 10.54$, df $= 1$, $P < 0.001$). However, persistence at areas 1 and 2 did not differ between species ($\chi^2 = 2.53$, df $= 1$, $P > 0.11$, $\chi^2 = 3.17$, df $= 1$, $P > 0.075$, respectively for each area).

Foraging Time. During the sampling period, temperature in the field varied from 21 to 35°C (Fig. 4). We did not find any correlation between temperature and foraging activity (P.J.F., unpublished data), however, *C. punctulatus* seemed to forage more in the mornings, whereas *S. richteri* appeared to forage more in the afternoons (Fig. 4). Temporal activity patterns were studied by analyzing the number of occupied baits along three ranges of hours for which we had a

similar number of observations and temperatures ranges differed most (from 0800 to 1300 hours, $n = 224$, from 1301 to 1500 hours, $n = 108$, and from 1501 to 1900 hours, $n = 178$). The proportion of occupied versus nonoccupied baits varied along the 3-h ranges, both for *S. richteri* (3×2 contingency tables; for S1: $\chi^2 = 40.89$, df $= 2$, $P < 0.0001$, $n = 126$; for S2: $\chi^2 = 11.22$, df $= 2$, $P < 0.0036$, $n = 208$; for S3: $\chi^2 = 53.82$, df $= 2$, $P < 0.0001$, $n = 176$) and *C. punctulatus* ($\chi^2 = 21.71$, df $= 2$, $P < 0.0001$, $n = 208$; $\chi^2 = 14.84$, df $= 2$, $P < 0.0006$, $n = 176$; for S2, and S3, respectively). No differences existed for *C. punctulatus* at area 1 ($\chi^2 = 3.49$ df $= 2$, $P > 0.17$, $n = 126$). *Solenopsis richteri* foraged preferentially in the morning at area 1, where it was most abundant, and in the afternoon in areas 2 and 3, where it was less (area 2) or equally (area 3) abundant compared with *C. punctulatus*, respectively. *Camponotus punctulatus* appeared at a higher propor-
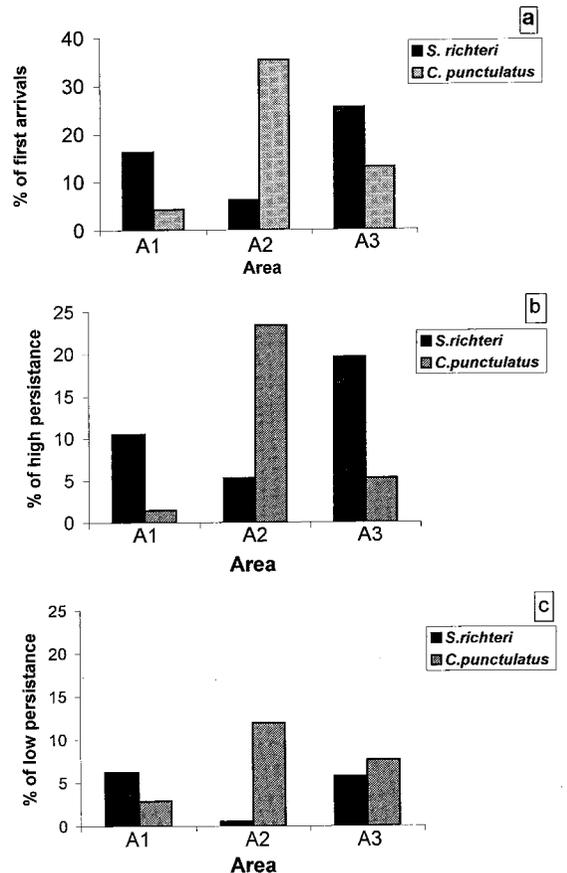

Fig. 3. (a) Percentage of first arrivals for *S. richteri* and *C. punctulatus*, at each area from a total of 232 observations (across stations, types of baits, sampling days) on baits. There were eight cases in which no ants arrived at the baits and 14 cases at which other ant species arrived first. (b and c) Percentage of cases from a total of 210 observations in which *S. richteri* and *C. punctulatus* had a high (b) or low (c) persistence at baits across all observations for each area (see text for details).
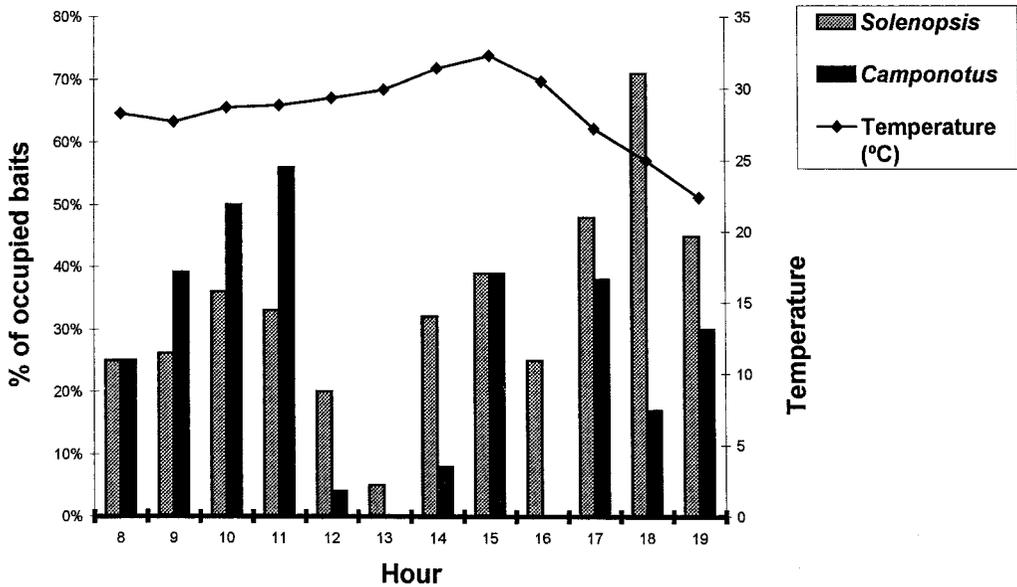
Fig. 4.   Daily distribution of temperatures along the transect at the field site and percentage of baits occupied by *S. richteri* and *C. punctulatus*. Percentages were calculated for each hour separately, considering the total number of baits offered at each hour, and calculating the proportion occupied by each of the two species at each hour. Only baits for the 2 d at which temperatures were registered in the field were considered.

tion of baits in the morning in areas 2 and 3, and did not show preferences at area 1.

Diversity. The number of morphospecies of walking arthropods per pitfall trap did not differ across the three areas ($H = 0.827$, df $= 2$, $n = 26$, $P > 0.66$) (number of morphospecies/pitfall ranged from 5–20). Furthermore, no differences in the number of individuals per pitfall ($H = 1.79$, df $= 2$, $n = 26$, $P > 0.408$) existed among the areas (number of individuals/pitfall varied from 8–134). We found no significant differences among areas, either, in the number of individuals fallen in the pitfalls but discriminated by species, for *S. richteri* ($H = 0.78$, df $= 2$, $n = 26$, $P > 0.68$), for *C. punctulatus* ($H = 5.28$, df $= 2$, $n = 26$, $P > 0.07$), as well as for "other" ant species ($H = 1.84$, df $= 2$, $n = 26$, $P > 0.4$). However, we were able to find differences between the frequency of pitfalls with and without *S. richteri*, *C. punctulatus* and 'other' ants across the whole transect (2×3 contingency table, $\chi^2 = 17.46$, df $= 2$, $P < 0.0002$), as well as within area 1 (2×2 contingency table, $\chi^2 = 9.33$, df $= 1$, $P < 0.009$) and 3 ($\chi^2 = 6.1$, df $= 1$, $P < 0.04$) in favor of *S. richteri* and "other" ants but not at area 2 ($\chi^2 = 3.6$, df $= 1$, $P < 0.165$).

Discussion

The results on mound densities and bait samples showed that the community of ants in the study area was dominated by two species: *S. richteri* and *C. punctulatus*, which occurred in equally high nest densities. Other species (i.e., *Acromyrmex* sp., *Pheidole* sp., *Linepithema* sp.) occurred at much lower densities. Baits are commonly used for studies of soil ant com-

munity organization (Levings and Traniello 1981, Hollway 1999), and simultaneous mapping of the nests improves the possibility of evaluating relations among the species on the baits (Vepsalainen and Pisarski 1982). Moreover, the use of pitfalls increases the efficiency of ant species richness estimations (Andersen 1997), especially when baits are monopolized by one or a few species (Andersen and McKaige 1987, Suarez et al. 1998). Our results showed that mound density (e.g., such as the big ones found at our field area), which is evidence of "long-term" success of a species, positioned both species as similarly dominant (sensu Savolainen and Vepsäläinen 1988), although mediated by spatial partitioning. Baiting results demonstrated that the speed of bait discovery was related to mound abundance of a species, whereas persistence of a species at a bait was not. Each species arrived faster where it was most abundant but did not differ in its dominance over the bait at these areas. This suggests that competitive encounters at baits occurred and changed the persistence of a species at a bait (this could have happened because every bait was checked once per hour). Finally, pitfall sample size may have been insufficient to quantify ant activity when great spatial heterogeneity occurs. In fact, the frequency of pitfalls with and without *S. richteri*, *C. punctulatus*, and other ants mirrored mound data except for *C. punctulatus* at area 2, where it was underestimated by pitfalls.

Spatial partitioning has been proposed as a possible way of limiting competitive interactions in ants (Levings and Traniello 1981) and permitting the coexistence of dominant ant species in a mosaic type of distribution (Leston 1978, Majer et al. 1994). *S. richteri* and *C. punctulatus* had similar overall abundance and

our data suggest habitat partitioning between these species. Although we cannot reject the hypothesis that these species were dividing space according to preferences or constraints, such as flooding, type of food present, soil texture, or presence of natural enemies, observations both in the field and in the laboratory suggest that *C. punctulatus* and *S. richteri* tend to avoid each other, as they were rarely found together at baits, and encounters had to be forced to study their interactions. On an individual level confrontation, *C. punctulatus* seemed to win, but if encounters occurred at the colony level, the greater recruitment of *S. richteri* helped them to succeed. Manipulative experiments (e.g., transplants, short-term introductions or removals) in the field will be needed to clarify the reasons for the observed habitat partitioning.

Were *S. richteri* and *C. punctulatus* behaving as dominant argentine ants do in exotic habitats (Hollway 1999), where the numerical dominance allowed argentine ants to escape from the constrains imposed by the trade-off between finding the resource versus keeping it? Our data showed that both species were fast at finding baits and successful at controlling them. We hypothesize that spatial heterogeneity may allow these species to achieve the mentioned numerical abundance and position them similarly at the top of the hierarchy of this ant community. Alternatively, the dominance of *C. punctulatus* and *S. richteri* could be a consequence of the abiotic conditions of the area, which gave rise to an ant community with low diversity and high dominance by the few species present, as it is often the case with species that tolerate harsh environments (Hölldobler and Wilson 1990).

Solenopsis richteri and *C. punctulatus* did not seem to partition the food resource, at least, at this time of year. We did not find a different proportion of tuna and sugar water baits occupied and monopolized by each species during the study. However, food preferences might depend upon the growth stage of the colony (Stradling 1987). Our preliminary data suggest that *S. richteri* and *C. punctulatus* temporally partition visits to baits. Each species foraged in the mornings at the area where each was most abundant. However, at area 3, where *S. richteri* and *C. punctulatus* did not differ statistically in mound abundance, *C. punctulatus* foraged predominantly in the mornings, whereas *S. richteri* foraged in the afternoons, which suggests dominance by *C. punctulatus.* At this area, however, *S. richteri* had a greater proportion of baits discovered and controlled than *C. punctulatus* (probably due to *S. richteri* style of massive recruitment).

We have shown that in its native habitat, *S. richteri* attain densities as high as those reported for fire ants in the United States (608 m/ha; Porter et al. 1992, 1997), where it is an exotic species. There are few other reports of *Solenopsis* attaining such high densities at disturbed and flooding-susceptible areas (Adams 1994); however, these events are rare in their native habitats. *S. richteri* at other areas of Buenos Aires, Argentina, normally exhibits a lower density (J. Briano, personal communication). Then, how did *S. richteri* attain such unusually high densities in this study? It has been suggested (Porter et al. 1997) that the absence of species-specific parasitoids in the United States could account for the high abundance of fire ants there. We hypothesize that something similar might have happened at Otamendi.

Observations at different times of the year at this locality showed that *Pseudacteon* phorid parasitoids of fire ants were extremely rare compared with our other sites (only *P. borgmeieri* Smith was collected once). Indeed, during this study, we never observed phorids attacking worker ants at the baits (P.J.F., unpublished data). Why are phorids absent? Frequent floods could represent a source of mortality for larval or pupal *Pseudacteon* which occur inside the heads of dead ants and, probably, in the mound or middens (P.J.F., unpublished data). Therefore, the system we studied provides additional circumstantial support for the idea that phorid parasitoids play a role in altering the level of dominance of their specific hosts in the ant community, and as possible regulators of ant abundance. Although our Otamendi study constitutes a single data point, had we found abundant phorids and a *Solenopsis richteri* population of this abundance and dominance, the potential of phorids as biocontrol would have had a serious counter example; as it is, fire ant density at Otamendi Reserve may be "an exception" that proves the rule. Further evidence that suggest an effect of natural enemies on *S. richteri* densities exists. *S. richteri* infection with *Thelohania solenopsae* Knell, Allen & Hazard (Microsporida) also varies geographically in Buenos Aires, and those places free of infection (Las Flores) show larger mounds and greater density (104–285 mounds/ha; J. Briano, personal communication) in comparison to those infected (Saladillo, 28–162 mounds/ha; J. Briano, personal communication) by this microsporidian disease (Briano et al. 1995), although in both cases mound sizes were much smaller than those found at our field site (P.J.F., unpublished data). It will be interesting to determine whether other cases of high fire ant density in their native habitats will be found to be associated with temporary freedom from natural enemies due to natural or human disturbance.

Why did *C. punctulatus* also attain such high densities? In lowland areas with great probability of flooding of the Chaquenian Region, *C. punctulatus* mound densities are also high (Lewis et al. 1991). The transect used in this study was located in a lowland area, susceptible to flooding (Chichizola 1993), which may have promoted the epigeic nesting habit of *C. punctulatus.* (Kusnezov 1951). We observed a record flooding event that occurred during our ant-sampling period. A preliminary analysis of the effect of flooding showed that the first arrivals of *C. punctulatus* to the baits increased significantly ($\chi^2 = 7.98$, df = 1, $P < 0.0047$) after flooding. We suggest that normal floods, which are common in the study area, allows *C. punctulatus* to obtain a dominant position in the frequently flooded low lying parts (i.e., area 2) of the landscape.

According to our pitfall data it would appear that the high densities of *S. richteri* and *C. punctulatus* did not affect arthropod diversity. However, we interpret

these results with caution since a control area, without *S. richteri* or *C. punctulatus,* was not available in our transect for comparison. The lack of effect on athropod diversity by high-ant densities is in agreement with the pattern found for *C. punctulatus* in agricultural systems in Corrientes, Argentina (Folgarait and Gorosito 2001).

In conclusion, we investigated a depauperate ant community that was numerically dominated by two native species of similar competitive rank. These two species appear to minimize competition with one another and thereby coexist in the same local site by spatial partitioning of foraging activity and nesting areas, and by temporal displacement of foraging activity. Because mounds represent long-lasting evidence that reflects the relative importance of different ant species in a community, the patterns of mounds observed in this study are likely to represent the results of interactions on a longer time frame than our short study. Nevertheless, data gathered at other times of the year will be necessary to reveal whether foraging patterns observed in this study persist over different seasons and through varied precipitation regimes. Likewise, revealing a relationship between *S. richteri* density and the incidence of pathogens and/or parasitoids, such as phorid flies, will require the study of additional sites sampled through time.

References Cited

Adams, S. 1994. Fighting the fire ant. Agric. Res. (January): 4–9.

Allen, C. R., R. S. Lutz, and S. Demarais. 1995. Red imported fire ant impacts on Northern Bobwhite populations. Ecol. Appl. 3: 632–638.

Andersen, A. N. 1986. Diversity, seasonality and community organisation of ants at adjacent heath and woodland sites in south eastern Australia. Aust. J. Zool. 34: 53–64.

Andersen, A. N. 1997. Measuring invertebrate biodiversity surrogates of ant species richness in the Australian seasonal tropics. Mem. Mus. Vict. 56: 355–359.

Andersen, A. N., and M. E. McKaige. 1987. Ant communities at Rotamah Island, Victoria, with particular reference to disturbance and *Rhytidoponera tasmaniensis.* Proc. R. Soc. Victoria 99: 141–146.

Banks, W. A., D. P. Jouvenaz, D. P. Wojcik, and C. S. Lofgren. 1985. Observation on fire ants *Solenopsis* spp., in Mato Grosso, Brazil. Sociobiology 11: 143–152.

Bestelmeyer, B. T. 1997. Stress-tolerance in some Chacoan dolichoderine ants: implications for community organization and distribution. J. Arid Environ. 35: 297–310.

Bestelmeyer, B. T., and J. A. Wiens. 1996. The effects of land use structure of ground-foraging ant communities in the Argentine Chaco. Ecol. Appl. 6: 1225–1240.

Briano, J., R. Patterson, and H. Cordo. 1995. Relationship between colony size of *Solenopsis richteri* (Hymenoptera: Formicidae) and infection with *Thelohania solenopsae* (Microsporida: Thelohaniidae) in Argentina. J. Econ. Entomol. 88.

Cerdá, X., J. Retana, and S. Cros. 1997. Thermal disruption of transitive hierarchies in Mediterranean ant communities. J. Anim. Ecol. 66: 363–374.

Chichizola, S. E. 1993. Las comunidades vegetales de la Reserva Natural Estricta Otamendi y sus relaciones con el ambiente. Parodiana 8: 227–263.

Fellers, J. H. 1987. Interference and exploitation in a guild of woodland ants. Ecology 68: 1466–78.

Feener, D. H. 1981. Competition between ant species: outcome controlled by parasitic flies. Science 214: 815–817.

Folgarait, P. J. 1998. Ant biodiversity and its relationship to ecosystem functioning: a review. Biodiver. Conserv. 7: 1221–1244.

Folgarait, P. J., S. Perelman, N. Gorosito, R. Pizzio, and J. Fernández. 2002. Effects of *Camponotus punctulatus* ants on plant community composition and soil properties across land use histories. Plant Ecol. 163: 1–13.

Folgarait, P. J., and N. Gorosito. 2001. Invasion of *Camponotus punctulatus* ants mediated by agricultural disturbance: consequences on biodiversity and ant community foraging. Ecol. Aust. 11: 49–57.

Hölldobler, B., and E. O. Wilson. 1990. The ants. The Belknap Press of Harvard University Press, Cambridge, MA.

Hollway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive argentine ant. Ecology 80: 238–251.

Jusino-Atresino, R., and S. A Phillips. 1994. Impact of red imported fire ants on the ant fauna of Central Texas, pp. 259–268. *In* D. F. Williams (ed.), Exotic ants biology, impact, and control of introduced species. Westview, Boulder, CO.

Kusnezov, N. 1951. El género *Camponotus punctulatus* en la Argentina (Hymenoptera, Formicidae). Acta Zool. Lill. 12: 183–252.

Leston, D. 1978. A neotropical ant mosaic. Ann. Entomol. Soc. Am. 71: 649–653.

Levings, S. C., and J.F.A. Traniello. 1981. Territoriality, nest dispersion, and community structure in ants. Psyche 88: 265–319.

Lewis, J. P., E. A. Franceschi, and S. L. Stofella. 1991. Effect of anthills on the floristic richness of plant communities of a large depression in the Great Chaco. Rev. Biol. Trop. 39: 31–39.

Majer, J. D., J.H.C. Delabie, and M.R.B. Smith. 1994. Arboreal ant community patterns in Brazilian cocoa farms. Biotropica 26: 73–83.

Morrison, L. W., E. A. Kawazoe, R. Guerra, and L. E. Gilbert. 2000. Ecological interactions of *Pseudacteon* parasitoids and *Solenopsis* hosts: environmental correlates of activity and effects on competitive hierarchies. Ecol. Entomol. 25: 433–444.

Nazzi, F., M. G. Paoletti, and G. G. Lorenzoni. 1989. Soil invertebrate dynamics of soybean agroecosystems encircled by hedgerows or not in Fiuli, Italy. Agric. Ecos. Environ. 27: 163–176.

Paoletti, M. G., U. Schweigl, and M. R. Favretto. 1995. Soil macroinvertebrates, heavy metals and organochlorines in low and high input apple orchads and a coppiced woodland. Pedobiologia 39: 20–33.

Porter, S. D., and D. A. Savignano. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. Ecology 71: 2095–2106.

Porter, S. D., H. G. Fowler, and W. P. Mackay. 1992. Fire ant mound densities in the United States and Brazil (Hymenoptera: Formicidae). J. Econ. Entom. 85: 1154–1161.

Porter, S. D., D. F. Williams, R. S. Patterson, and H. G. Fowler. 1997. Intercontinental differences in the abundance of *Solenopsis* fire ants (Hymenoptera: Formicidae): an escape from natural enemies? Environ. Entomol. 26: 373–384.

Romero, H., and K. Jaffe. 1989. A comparison of methods for sampling ants (Hymenoptera: Formicidae) in savannas. Biotropica 21: 348–352.

Savolainen, R., and K. Vepsäläinen. 1988. A competition hierarchy among boreal ants: impact on resource partitioning and community structure. Oikos 51: 135–154.

Siegel, S. 1974. Estadística no paramétrica. Trillas, Mexico DF.

Stradling, D. J. 1987. Nutritional Ecology of Ants, pp. 927–969. *In* F. Slansky and G. J. Rodriguez (eds.), Nutritional ecology of insects, mites, spiders and related invertebrates. Wiley, New York.

Suarez, A. V., D. T. Bolger, and T. J. Case. 1998. Effects of fragmentation and invasion on native ant communities in coastal southern California. Ecology 79: 2041–2056.

Vepsäläinen, K., and B. Pisarski. 1982. Assembly of island ant communities. Ann. Zool. Fenn. 19: 327–335.

Williams, D. F. 1994. Exotic ants biology, impact, and control of introduced species. Westview, Boulder, CO.

Wojcik, D. P., C. R. Allen, R. J. Brenner, E. A. Forys, D. P. Jouvenaz, and R. S. Lutz. 2001. Red imported fire ants: impact on biodiversity. Am. Entomol. (spring): 16–23.