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Research article

Nest connectivity and colony structure in unicolonial Argentine ants

N.E. Heller[1], K.K. Ingram[1,2] and D.M. Gordon[1]

[1] Stanford University, Stanford, CA 94305–5020, U.S.A., e-mail: heller.nicole@gmail.com
[2] Current address: Colgate University, Hamilton, NY 13346, U.S.A.

Abstract. Unicolonial ant colonies occupy many nests and individuals rarely show aggression across large geographic distances. These traits make it difficult to detect colony structure. Here we identify colony structure at scales of hundreds of square-meters, within an invasive population of unicolonial Argentine ants. In experiments using labeled food, and in a 3-year census of nests and trails, we found that food was shared and nests were linked by trails at distances up to 50 meters. Food was not distributed to all nearby Argentine ant nests, showing that ants tend to share resources within a spatially bounded group of nests. The spatial extent of food sharing increased from winter to summer. Across different habitats and nest densities, nests were consistently aggregated at spatial scales of 3- 4 meters in radius. This suggests that new nests bud from old nests at short distances regardless of local conditions. We suggest that a 'colony' of Argentine ants could be defined as a group of nests among which ants travel and share food. In our study population, colonies occupy up to $650 \, \text{m}^2$ and contain as many as 5 million ants. In combination with previous work showing that there is genetic differentiation among nests at similar spatial scales, the results suggest that Argentine ant populations do not function ecologically as single, large supercolonies, but instead as mosaics of smaller, distinct colonies consisting of groups of interacting nests.

Keywords: Linepithema humile, supercolonial, foraging, spatial pattern, cooperation.

Introduction

Unicolonial social behavior has generated much recent interest because of the extraordinary success of unicolonial invasive ants (Passera, 1994; Bourke and Franks, 1995; Chapman and Bourke, 2001). In contrast to multi-colonial structure, unicoloniality is characterized by large numbers of spatially distinct nests among which workers mix. Nests typically contain many queens, who also move among nests. Because this structure is spatially, behaviorally and genetically diffuse, it is challenging to identify colonies (Hölldobler and Wilson, 1977; Rosengren and Pamilo, 1983). Nevertheless, correct identification of colony boundaries is essential for empirical studies of social insect behavior and population biology (Pedersen and Boomsma, 1999).

An important trait often associated with unicolonial behavior is reproduction by budding, in which queens and workers walk from parent nests to start new nests, much the way a plant grows vegetatively (Hölldobler and Wilson, 1977). Repeated budding events result in a cluster of nests. Nests within a cluster may remain interconnected through cooperative exchange of food, workers and brood. Alternatively, nests may not exchange workers or food, and relations may be neutral or agonistic (Rosengren and Pamilo, 1983). Recent studies of uni-colonial ants have equated a lack of aggression with nest interconnectivity. For example, the term 'supercolony' is often used interchangeably with 'groups of interconnected nests,' and supercolonies are said to act as 'single cooperative units'. However, the boundaries of super-colonies are defined using aggression only, specifically as the group of nests among which there is no aggression when individual workers are paired in experimental tests (Suarez et al., 1999; Giraud et al., 2002). Here we argue that the group of nests that are interconnected by worker movement and food sharing is a different biological entity from the supercolony as defined by lack of aggression. Colony structure occurs when individuals have cooperative interactions, such as the sharing of food through trophallaxis and joint contributions to the rearing and maintenance of brood and reproductives (Dahbi et al., 1999; Silverman and Liang, 2001). Such colony structure

is ecologically important. Ants from connected nests can join together in recruitment, which determines the number of ants available to obtain and defend resources in a given location (Aron et al., 1990; Human and Gordon, 1996; Holway and Case, 2001) and group size influences the outcome of competitive interactions between unicolonial invasive species and the native ants they displace.

Here we examine colony structure, in the movement of ants between nests and in food sharing, in Argentine ants (*Linepithema humile*). Argentine ants have successfully invaded both urban and protected areas in Mediterranean climates worldwide. They show unicolonial behavior throughout the native and introduced ranges (Heller, 2004; Pedersen et al., 2006). The sizes of supercolonies, with boundaries measured by aggression tests, vary widely. In the introduced range, supercolonies span thousands of square kilometers in California, Europe, New Zealand and Australia (Tsutsui et al., 2000; Giraud et al., 2002; Corin et al., 2007; Björkman et al., 2008) and extend across disjunct areas, islands and continents (Wetterer and Wetterer, 2006); other supercolonies in Southeastern USA and Japan are less than 2500 square meters (Buczkowski et al., 2004; Sunamura et al., 2007) similar in size to those in the native range of Argentina (Heller, 2004; Pedersen et al., 2006). Little is known about patterns of cooperative nest interactions within these supercolonies.

We investigate colony structure within a massive unicolonial population of Argentine ants in the introduced range, in northern California. Previous research in the study population showed local genotypic differentiation among nests separated by more than 100 meters (Ingram and Gordon, 2003). Here we mapped nests and trails in study plots over 3 years to ask: 1) what is the spatial organization of nests? 2) What is the spatial area within which nests are linked by trails? 3) What is the spatial extent of food sharing? And 4) is there evidence of colony boundaries across which ants do not travel or share food?

Methods

Spatial organization of nests

We characterized the abundance and spatial distribution of nests in three different habitats by mapping nests in six 400-m^2 plots and one 500-m^2 plot. Three 400-m^2 plots were at low elevation (65 m) in habitat dominated by annual grasses and native shrubs (referred to as Annual grassland), and 3 were at higher elevation (180 m) in habitat dominated by native perennial grasses and native shrubs (Perennial grassland) at Jasper Ridge Biological Preserve (JRBP). The remaining larger plot was located in a wooded patch with sparse cover of native perennial grasses and annual forbs in a suburban neighborhood near the campus of Stanford University (Wooded). Seven surveys at these 7 plots were conducted at intervals of 3 to 6 months from April 2001 – July 2003.

We examined the spatial structure of nests by calculating omnidirectional correlograms (GAMV, GSLIB software). Correlograms estimate a covariance coefficient, $\rho(h)$, between points in space, taking into account the local mean and local variance, to measure the spatial dependence between variables (Rossi et al., 1992). Plots were gridded at the 1-m^2 and nest data were treated as incidence data, with each 1-m^2 grid square either occupied by a nest or empty. The lag distance at which the covariance coefficient nears zero provides an estimate of nest cluster size or the distance range within which nests are spatially correlated. Covariance coefficients that near 0 at large distances indicate nests are aggregated across large distances; coefficients that near 0 at short distances indicate aggregation at only short distances or nest dispersion. Correlograms were calculated independently for each survey of each plot (7 per plot). The null hypothesis of spatial randomness was tested by 100 simulations of random points on a grid, in which the number of points was equivalent to the mean number of nests for each plot. From these 100 simulations, the highest and lowest value of $\rho(h)$ for each lag distance was used to define the upper and lower bound of a 99% confidence envelope (Manly, 1991). Because the variance between study plots within a habitat type was small, data for each season were averaged across plots within each habitat type.

Spatial extent of links by trails among nests

We mapped nests and trails in the 500-m^2 Stanford Wooded plot monthly for 33 months from March 2000 – February 2003. Each of the surveys lasted approximately 16 hours, conducted over two days at the times when ant activity was greatest, from 7 – 10:30 and 15:30 – 20:00 in March – October, and from 9:00 – 17:00 in November – February. Nests were located using the methods described in Heller (2004) and mapped onto a grid of 1-m^2 cells. All trails were mapped if they were more than 3 m long, and with a rate of at least 1 ant per 5 seconds crossing a pencil point placed perpendicular to the trail. Typically several nests were linked by trails; for example nest 1 linked to nest 2, nest 2 linked to nest 3, and so on. We defined a path as a series of trails linking more than 2 nests, and we measured path distance from the map as the sum of the lengths of all the trails in the path.

Trails often extended outside of the plot boundaries. From February 2002 – February 2003, we increased the size of the study area to approximately 8500 m^2. We surveyed the 500-m^2 plot as before, and to measure path-length we also followed trails that extended outside of the plot boundaries, mapping nests on the trails. Trail data were not collected at JRBP sites because many trails could not be accurately traced through the thick grass.

Spatial extent of food sharing

To investigate the distance over which workers share food in trophallaxis, we fed ants labelled food and measured how far the label spread. We used undiluted food dyes in 3 different colors, FD & C #1 blue, #3 green, and #3 red (Seltzer Chemicals) added to sucrose solutions. We used food dyes to mark ants rather than longer-lasting dyes (i.e. florescent dyes, Vega and Rust, 2001), so that we could vary colors used in nearby sites and change colors across food-sharing trials in the same site. Pilot experiments showed that ants readily feed on sucrose with added food coloring, and that all 3 colors were easily visible when an ant that fed on colored solution was crushed on filter paper. To test how long dyes remained visible, and to compare the color intensity of the mark in crushed ants that had fed directly on baits with the intensity of the mark in crushed ants fed bait only by trophallaxis, we constructed 4 experimental colonies of ~ 150 workers. In one colony, ants were fed dyed sucrose. After the first day, the bait was removed and 3 marked ants were collected. One marked ant was introduced into each of the 3 other colonies. After 6 hours, we offered plain sucrose to all 4 colonies, which was replenished each of the remaining days of the experiment. Each day for 16 – 30 days, 4 ants were sampled from each of the 4 experimental colonies and crushed on filter paper. The tint of the color mark was determined by comparing marks to color standards (Ridgway, 1912). A mark was considered to be bright if the color was similar to the full color standard or no more than 9.5% lighter. A mark was considered light if the mark was similar to the 22.5% tint or lighter. In ants fed dyed sucrose only through trophallaxis, the mark was light from day 1. We found that the dye remained visible for 30 days in 100% of the ants that fed directly on dyed sucrose, and the color intensity of the mark

was bright for 15 days before it began to fade. Dyes were visible for 7 days in 80 %, and for 14 days in 50 % of the ants that received the label only through trophallaxis.

To determine the spatial extent of food-sharing among nests, fifteen food sharing trials were conducted in 9 study sites spread across three habitat types (wooded, annual and perennial grassland). Naturally occurring food sources were not thought to be limited at these sites. At each site, a bait station was established consisting of 50 mL 20 % sucrose solution with 0.05 grams of food coloring. We collected approximately 100 ants, using an aspirator, from each sample nest, 7 and 14 days after baits were placed. Once collected, ants were immediately placed in a cooler with ice and then stored in a freezer at 0° C. Sampled ants were crushed on filter paper to determine the proportion of bright and light marked ants per sample nest. All marks were reviewed by the same person, using color standards as above to determine whether a color was light or bright. In 18 % of nest samples, we crushed an additional 50 ants. There was no difference in the proportion of marked ants found in the first 100 ants and the second 50 ants (Wilcoxon rank test, p = 0.5), indicating that our sampling methods provided a high chance of detecting marked ants. On average 25 nests were sampled at each study site at distances up to 100 meters from baits. We sampled all nests in the 20 m radius around a bait station, and we walked 100-meter transects along 4 cardinal lines searching for nests at 25, 50, 75, and 100 m. Nests within 1 m of each other were treated as a single nest for sampling. At the Wooded plot, where inter-nest trails were mapped, we examined the correspondence between inter-nest trails and food sharing among nests.

To test whether the apparent distance of food-sharing among nests was due to true boundaries of nest affiliations or merely to successive dilutions of the bait through sequential worker exchange we offered bait twice in 3 plots. The first trial was conducted from December 15 – December 31 and the second from March 11 – March 25. In the second trial, we placed the bait at the farthest nest in which marked ants were found in the first trial. A different color of bait was used between trials. We used a 3-month interval to ensure many nests would still be active in the same locations between the first and second trial because Argentine ants move nest sites on average every 3 months (Heller and Gordon, 2006).

To test whether the presence of marked ants in a nest in December increased the likelihood that a nest would contain marked ants in March, we used a logistic regression. The dependent variable was the presence of marked ants in a nest in March, and the independent variables were the presence of marked ants in a nest in December and distance to bait. If the distribution of marked ants in nests was due to successive dilution of the bait and a lack of colony boundaries, then moving the location of the bait between trials would change the spatial distribution of marked ants, and only distance to bait would be a significant factor in the model. If instead, the distribution of marked ants in nests was the result of true boundaries in food sharing, then moving the location of the bait between trials would not change the spatial distribution of marked ants, so that nests with marked ants in December would be likely to have marked ants in March than nests without marked ants in December.

Results

Spatial organization of nests

The abundance of nests was greater in the Annual grassland than Perennial grassland plots (mean no. nests $\pm$ s.e., 67 ± 3.7 compared to 16 ± 3.4 in a 400-m^2 area, t-test $= 10.4$, $P < 0.001$); abundance in the Wooded plot was intermediate, with a mean of 35 ± 2.7 nests in a 500-m^2 area. Over the 3 years of study, nest density grew by an average of 20 % in the Annual grassland and Wooded plots, and 50 % in the Perennial grassland plots.
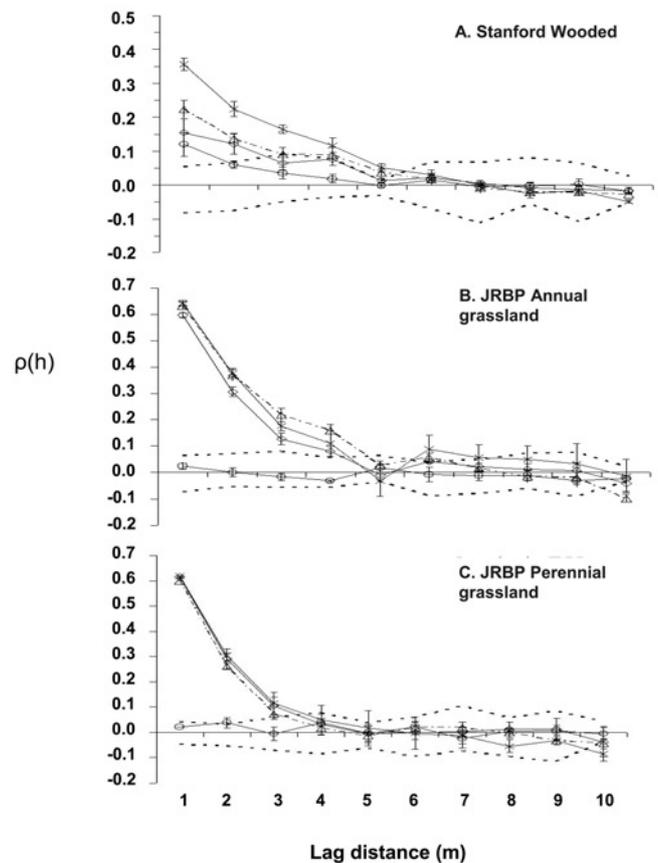
Figure 1. Nests were significantly aggregated in clusters up to 4 meters in radius in winter, spring and fall, and 1 meter in radius in summer. The average covariance coefficient $\rho(h) \pm$ s.e. is plotted against 1 meter interval distances by season: fall (diamond), winter (X), spring (hatched line, triangle), and summer (circle). The dashed lines give the upper and lower bound of a 99 % confidence envelope based on 100 simulations. An aggregated distribution corresponds to a positive value of $\rho(h)$ above the confidence envelope; a regular distribution corresponds to a negative value of $\rho(h)$ below the confidence envelope, and a random distribution corresponds to a $\rho(h)$ within the confidence envelope.

In all plots, nests showed similar patterns of nest aggregation across seasons; nests were aggregated in the winter, spring and fall and dispersed in the summer. At the Wooded plot, nests were significantly aggregated at a range of up to 4 meters in radius in winter, 3 meters in spring, 2 meters in fall, and 1 meter in the summer (Fig. 1A). At Annual grassland plots, nests were aggregated at a range of 4 m in all seasons, except the summer when the distribution was not different from random at any distance (Fig. 1B). At Perennial grassland plots, nests were aggregated at a range of 3 meters in winter, spring and fall, and randomly distributed in summer (Fig. 1C). Thus from October – June, it was likely that any Argentine ant nest had additional nests within every meter up to a distance of 3 – 4 meters from that nest. From July – September, nests were more dispersed; clumped at most at the 1-meter scale. There were no significant differences in mean co-variance coefficients at any lag
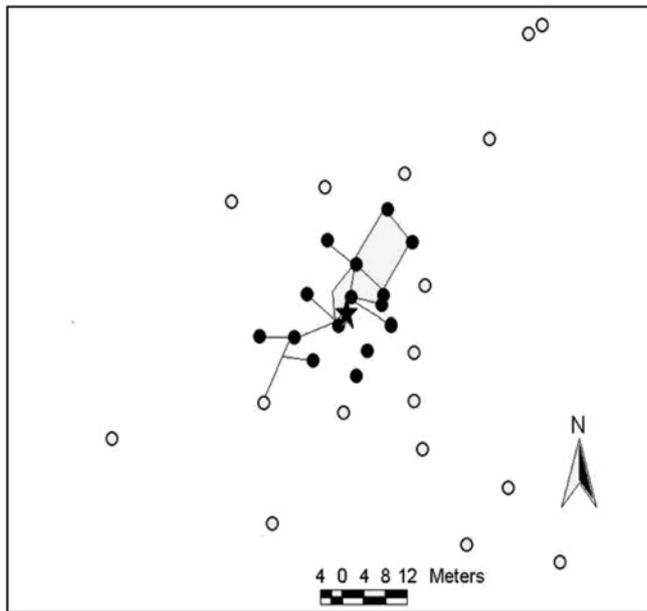
Figure 2. Food sharing occurred between nests that were linked by trails. The figure shows the Stanford Wooded plot. The location of bait is indicated by the star. Lines show well-formed trails between nests; black circles indicate nests with marked ants, open circles nests with no marked ants.

Table 1. Mean maximum distance that food was dispersed from baits and estimates of the spatial area over which food was shared. Some plots were repeatedly sampled (i.e. Plot 1 in December and March).

	December	March	May	July
Max. food-sharing distance (m)	12.5 ± 1	18.7 ± 2	25.7 ± 3	31.8 ± 6
Colony spatial area (m²)	240 ± 10	443 ± 75	397 ± 34	473 ± 154
Annual grassland				
Plot 1	254 m²	379 m²		
Plot 2	240 m²	550 m²		
Plot 3	226 m²	401 m²		628 m²
Plot 4			358 m²	628 m²
Plot 5			408 m²	408 m²
Perennial grassland				
Plot 6			424 m²	
Plot 7				647 m²
Plot 8				302 m²
Wooded		445 m²		

distance in comparisons of seasons across years (i.e. spring 2001 compared to spring 2002; Repeated Measures ANOVA, $P > 0.5$ for all tests).

Spatial extent of links by trails among nests

Path distance was less than 50 meters and varied seasonally. In the winter, there were few trails, which connected only nests within the plot, and the maximum path distance was 13 m. In spring and summer, the number of trails increased, as did the number of nests that were connected by trails, and many trails extended outside of the plot boundaries. The maximum path distance recorded was 43 meters, and trails were lost in cracks in the soil.

Spatial extent of food sharing

Across all sites, food sharing was spatially restricted to nests within 10 – 50 m of baits (mean maximum distance 23.2 ± 2.9 m). The distance across which food was distributed increased from winter to summer (linear trend, $F_{1, 10} = 7.8$, $p < 0.02$, Table 1). After two weeks, we found marked ants in an average of 36% of nests sampled, with an average of 35% ($\pm 6\%$) of ants marked in nests within 2 m of bait, and only 10% ($\pm 6\%$) of ants in samples from nests in the most distant nests in which marked ants were found. Food sharing changed very little from 7 to 14 days after baits were placed. Marked ants were found in 136 nests after 7 days and 142 nests after 14 days. Overall,

60% of marked ants were bright, indicating that they fed directly on bait, and 40% were light, indicating that they were fed by trophallaxis. The proportion of ants in each nest that were light, having received food by trophallaxis, did not increase with distance from the bait (Spearman rank, $r_s = 0.17$, n = 126, p = 0.08).

We estimated the spatial area over which food was shared as the area of an ellipse = ($\prod$* major axis * minor axis) / 4. Spatial area ranged from 226 m² in the winter to 647 m² in the summer (Table 1). At the Stanford site, in which trails were mapped, food-sharing was strongly associated with the presence of trails (Fig. 2). Marked ants were found in 88% of nests linked by trails to the nest nearest the bait, and in none of the nests not linked by trails to the nest nearest the bait.

The restricted range at which food was transferred between nests was due to true boundaries of food sharing, not to successive dilutions of the bait. Marked ants were found in $71 \pm 6\%$ of the same nests after 3 months and after the bait had been moved (Fig. 3). Presence of marked ants the previous December, and proximity to bait, in combination provided the model most likely to explain the presence of marked ants in nests in March, $\beta_0 = 1.25$, $\beta_{1(\text{distance to bait})} = -0.22$ (p = 0.006), $\beta_{2(\text{marked in December})} = 1.84$ (p = 0.03). Nests with marked ants in December were more likely to have marked ants in March than nests that did not have marked ants in December.

Discussion

Interactions among Argentine ant nests were spatially restricted. Workers did not travel on trails or share food with nests more than 50 m away in any direction from a
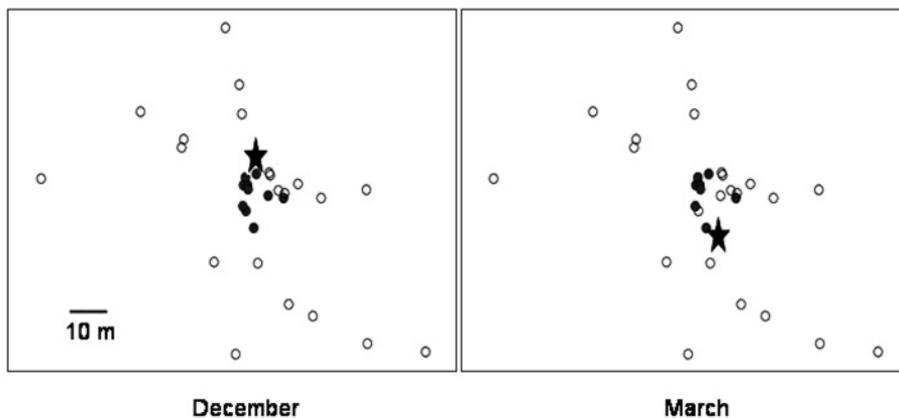
Figure 3. There are stable boundaries in the distribution of food among nests. Results are shown from one site in which repeated trials were conducted in December and March. Stars represent the location of the bait in each trial, black circles show nests with marked ants, open circles show nests with no marked ant.

central bait station. Previous work showed limited dispersal and genetic differentiation between nests about 100 meters apart (Ingram and Gordon, 2003) or between groups of nests connected by trails (Jaquiéry et al., 2005). Our results here, in combination with this previous work, indicate that within unicolonial populations, Argentine ant nests interact in spatially limited regions.

We suggest that the group of nests within which ants travel and share food can be considered to be a colony. Our field observations of nests and trails indicate that colonies show regular patterns of organization and seasonal polydomy (Newell and Barber, 1913; Benois, 1973; Heller and Gordon, 2006). The seasonal spatial organization of nests within colonies was similar across different habitats and nest densities, with nests aggregated in large clusters at the scale of 3–4 m in radius in the winter, spring and fall. This suggests that new nests tend to bud at short distances from parent nests regardless of local conditions, perhaps until a threshold in local ant density is reached. In the summer, nests were more randomly distributed and trails linked nests together over longer distances than in the winter, spring or fall. Dispersion may reflect the population density peak in the summer (Markin, 1970) and greater colony resource needs.

Our food sharing experiment confirms and expands our field observations. As indicated by the pattern of marked ants at nests: worker movements are spatially limited, workers do not mix among all neighboring nests, and the spatial extent of mixing increases from winter to summer. Marked ants were never found more than 50 meters from bait within two weeks of feeding. In repeated food-sharing trials over a 3-month interval at nests in same area using different colored baits and moving the location of the bait between trials, the pattern of marked ants at nests remained similar suggesting stable nest affiliations, at least over 3-month intervals. If ants travel longer distances within two weeks, we should have found marked ants at greater distances than 50 m from baits, but we did not. If the distances detected were the result of

dilution through successive trophallaxis exchange, then the boundaries of food sharing should have changed when baits were moved in repeated trials, but the boundaries did not change (Fig. 3). It is possible, but unlikely, that ants tend to move greater distances, but they do so only after 2 weeks have elapsed since the ants last fed. However, in this case, ants from more distant nests should generally be genetically indistinguishable, but they are not (Ingram and Gordon, 2003). In attempts to eradicate Argentine ants, the application of poison affected only nests within short-distances in both Hawaii and southern California (Vega and Rust, 2003; Krushelnycky et al., 2004). All of these results imply that Argentine ant workers in unicolonial populations tend to travel between nests, and share food at spatial scales of less than 100 meters.

Previous food sharing studies in Argentine ants have been conducted in single sites in orchards and urban areas, sometimes with multiple baiting stations, and food was shared up to maximum distances between 34–61 m (Markin, 1968; Ripa et al., 1999; Vega and Rust, 2003). In these studies, high numbers of marked ants were found in nests at the borders of study areas, leaving open the question whether food sharing may have extended greater distances than those measured. In our study, we sampled 100 meters in 4 directions and did not find labeled ants beyond 50 meters from bait in any trial.

Nest densities were higher in the annual grassland than perennial grassland plots at JRBP, but growth rates were faster in the perennial grassland. The perennial grassland sites were more recently invaded and climatically drier and more wind exposed (Heller, unpubl. data). Ant densities at JRBP are estimated at about 25 – 3,000 ants per m^2 based on previous measures of the relation between nest size and number of individuals (Heller, 2004). Thus colonies are estimated in this population to occupy spatial extents of about 650 m^2, and easily contain anywhere from about 10,000 to as many as 5 million ants. Colony size in unicolonial populations is likely to vary as a function of many different factors, such as resource distribution (Cherix, 1980), vegetation type (Passera,

1994; Way et al., 1997; Jaquiéry et al., 2005), interspecific competition (Ingram, 2002b), nest density (Ingram, 2002a) or time since invasion (Ingram and Gordon, 2003).

Colony size may be more ecologically important for invasion success than supercolony size (Heller, 2004). Supercolonial formation means that in intraspecific encounters, individuals will not waste energy on competitive interactions. However, it is direct interaction and cooperation among conspecifics that determines success in interspecific competition because ecological dominance depends on the competitive displacement of heterospecifics by means of local interactions (Lynch et al., 1980; Andersen, 1992; Morrison, 1996; Sanders and Gordon, 2003), and Argentine ants win competition with native ant colonies through the rapid recruitment of high numbers of workers (Erickson, 1972; Human and Gordon, 1996; Holway, 1999; Holway and Case, 2001; Suarez and Holway, 2004). Very little is known about the factors that determine colony recruitment rates in Argentine ants. In our observations, ants arrived at baits on only one or two trails from nearby nests. These nests were then linked to other nests via trials. In all nests in which marked ants were found, some were dark indicating they had directly fed on baits. In addition, baits were removed faster where ants were at higher local densities. These data suggest that recruitment response is sustained by workers from within the nests near to the encounter and those in the extended path network, or colony.

Distinct colony structure, consisting of groups of interacting nests, may be the rule rather than the exception for unicolonial ant species. In other unicolonial ant species, including the invasive imported red fire ant (*Solenopsis invicta*) and a number of red wood ants (*Formica* spp.), trail connections extend only among limited groups of neighboring nests (Marikovskiy, 1962; Higashi, 1976; Cherix, 1980; Vargo and Porter, 1989), and there is genetic differentiation among nests, indicating limited movement of individuals (Chapuisat and Keller, 1999; Holzer et al., 2006). The patchiness of spatial interactions among Argentine ant nests that we find here suggests that 'supercolonies' may be better described as 'metacolonies'. What was thought to be an enormous phalanx of ants, blanketing huge regions, is instead a mosaic of small, distinct and very effective legions.

Acknowledgments

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