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Seasonal spatial dynamics and causes of nest movement in colonies of the invasive Argentine ant *(Linepithema humile)*

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Abstract. 1. Colony organisation and movement behaviour of the Argentine ant (*Linepithema humile*) was studied over 3 years in field populations in California and in captive colonies in the laboratory. This invasive species is highly polydomous and unicolonial; colonies consist of expansive and fluid networks of nests and trails. The spatial and temporal organisation of colonies may contribute to ecological dominance.

2. Argentine ant nests and inter-nest trails shift in size, abundance, and location, so that colony networks are spatially contracted in the winter and expanded spring to autumn. Colonies occupy permanent sites; ants migrated to and from the same winter nest locations year after year, and occupied 30% of the same nests repeatedly during seasonal migrations.

3. Nests were moved on average 2–3 m. Forty-two per cent were occupied less than 1 month, 4% the entire study, and the other 54% lasted 3.9 ± 2.3 months (mean ± SD).

4. Nests were located within 2–4 m of woody plants, in warm sites in the winter and cool sites in the summer. Both humidity and food availability influenced nest-site choice in laboratory colonies. However, when faced with a trade-off between factors, the ants chose humid nest boxes over nest boxes near food, and ants moved nests only in response to changes in humidity and not distance to food.

5. The results indicate that *L. humile* colonies are seasonally polydomous, and that nest movements are driven by changes in microclimate. Colony organisation maintains high local density and increases food supply, which may improve the competitive ability of *L. humile* colonies and reduce opportunities for species coexistence.

Key words. Ant, nest budding, networks, seasonal polydomy, space use, supercolonial, unicolonial.

Introduction

Polydomous ant colonies are often organised into networks of nests and trails. Reproduction is by local dispersal through budding, when queens and workers walk from parent nests to found new nests. Trails between old and new nests can remain intact, so colony size grows as colonies bud, much the way a plant grows vegetatively. In this way, polydomous colonies are analogous to a modularly constructed plant or colonial invertebrate; each nest is a subunit of a larger structure (Traniello & Levings, 1986).

Many of the most successful invasive ant species are highly polydomous (Passera, 1994; Chapman & Bourke, 2001; Holway *et al.*, 2002a). The pattern of space use and flexibility that result from multi-nest colony organisation may contribute to the dominance of invasive ants. For example, nests can be dispersed to improve a colony's ability to defend or obtain resources, occupy a large foraging area, and track variable resources in the environment (Hölldobler & Lumsden, 1980; Pamilo & Rosengren, 1984; Traniello & Levings, 1986; McIver, 1991; Pfeiffer & Linsenmair, 1998; Holway & Case, 2000; Cerdá *et al.*, 2002). Experimental studies of invasive ants suggest that polydomy can promote high worker numbers and provide advantages in exploitative and interference competition (Human & Gordon, 1996; Holway *et al.*, 1998; Holway & Case, 2000, 2001). Polydomous colonies are often fluid, with both changes in the

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number of nest units and shifts in the spatial location of nest units, which may enable colonies to maintain advantageous nutritive, reproductive, or micro-environmental conditions (Marikovskiy, 1962; Higashi, 1976; Rosengren *et al.*, 1985; Banschbach & Herbers, 1996a, 1999).

In this study, the colony organisation and movement behaviour in invasive populations of the Argentine ant, *Linepithema humile* (Mayr, 1868), was investigated. Native to the Paraná River drainage in north-eastern Argentina and south-eastern Brazil, *L. humile* has become widespread through dispersal by human activity, particularly in Mediterranean climates (Wild, 2004). It is found in six continents and many oceanic islands (Suarez *et al.*, 2001). Its impact on invaded communities is severe. Usually it decimates local ant communities, and its effects can cascade to multiple trophic levels (Ward, 1987; Cole *et al.*, 1992; Cammell *et al.*, 1996; Human & Gordon, 1996; Suarez *et al.*, 1998; Suarez *et al.*, 2000; Christian, 2001; Sanders *et al.*, 2003). Argentine ants feed on insects and tend aphid and scale insects (Hemiptera) for honeydew excretions, making them an agricultural pest (Newell & Barber, 1913; Way, 1963; Markin, 1970).

Argentine ants are unicolonial; populations are highly polygynous (multiple queens per nest) and polydomous (multiple nests per colony) and intraspecific aggression is infrequent (Hölldobler & Wilson, 1977). Previous research in both the native range in Argentina and introduced range in California, found that nests are locally abundant, spatially aggregated, and interconnected by trails (Heller, 2004). Nests are shallow and are reported to move frequently (Newell & Barber, 1913; Markin, 1970). However, the dynamics of nest movements have never been quantified. Nests may move in response to seasonal shifts in weather (Newell & Barber, 1913; Markin, 1970; Benois, 1973; Gordon *et al.*, 2001), or opportunistically in response to disturbance (Hölldobler & Wilson, 1977), or changes in food availability (Holway & Case, 2000). Soil temperature and humidity are important to the survival of *L. humile* (Holway *et al.*, 2002b; Walters & Mackay, 2003) and may constrain nest location.

Seasonal patterns in the location, size, and persistence of nests and trails was measured over 3 years in field populations in northern California. In laboratory experiments, the effects of food availability and microclimate on nesting patterns was tested. Field data were used to ask: (1) How do the abundance and connectivity of nests and trails change seasonally? (2) How long do nests and trails persist? (3) How do environmental factors affect nest location? (4) When ants move nests, how far do they move? Laboratory experiments were used to ask: (1) How do food proximity and humidity each influence choice of nest site? (2) Do changes in food proximity or humidity cause ants to move nest sites? (3) How is choice of nest site influenced by a trade-off between food proximity and humidity?

Methods

Study areas

Populations of *L. humile* were studied in seven study plots in northern California (37°24′N, 122°13′30″W). The climate is Mediterranean, characterised by a cool, wet (November to April) and a hot, dry (May to October) season. Argentine ants were first recorded in this area in the early 1900s, and have since become dominant in areas below 200 m elevation.

One 500-m^2 study plot was located in a neighbourhood on Stanford University Campus (SC) in an area of native and exotic grasses and trees (*Nassella pulchra*, *Avena* spp., *Eucalyptus* sp., *Quercus berberidifolia*) (20-m elevation). Observations at SC began in March 2000. Six 400-m^2 study plots, three at 65-m and three at 180-m elevation, were located in Jasper Ridge Biological Preserve (JRBP) in mixed annual grassland/shrubland habitat (dominated by *Avena* spp., *Bromus* spp., *Erodium* spp., *Nassella pulchra*, and *Baccharis pilularis*). JRBP is a 481-ha biological preserve in which the distribution and impact of *L. humile* has been monitored since 1993 (Human & Gordon, 1996; Sanders *et al.*, 2003; Heller *et al.*, 2006). Observations at JRBP began in April 2001. Few native ant species were found co-occurring with *L. humile* in any of the seven study plots (Heller, 2004).

Field observations

Nest abundance, persistence, and location. Argentine ant nests are shallow structures of small chambers and passageways spread out horizontally in the top 30–40 cm of soil. There are sometimes small mounds of excavated soil at nest entrances, particularly after rain, but often there is no obvious disturbance to the soil surface. Nests may also occur in trees (Newell & Barber, 1913), but because it was difficult to distinguish whether ants were foraging or nesting in trees, only ground nests were considered in this study.

Direct methods to estimate nest size are destructive (Bestelmeyer *et al.*, 2004) and cannot be used to study how nests change over time. Here, a method was developed that allowed nests to be located and measured without destroying them or causing the ants to emigrate. Study plots were divided into grid squares at 1-m intervals. In each 1-m grid square, the ground was searched systematically by inserting a narrow metal rod into the soil every 10 cm, and around the trunk of all woody plants. All logs, rocks, and pieces of debris were turned over and searched for nests. When a nest chamber was disturbed, workers, typically with brood (eggs, larvae, pupae), flowed out of the ground at a rapid rate ($>$ 20 workers per 5 s). Chambers found in this way were marked with a flag. Flags were placed no closer than 10 cm to each other, so that each flag marked a 20 cm × 20 cm (0.04 m^2) section of a nest. All flags within 35 cm of each other were summed to estimate nest size. Chambers more than 35 cm apart were unlikely to be connected by underground passages, so they were considered separate nests (Heller, 2004). Nest excavations and worker counts from six different nests, which were up to 40 cm deep and ranged in size from 0.04 to 1.6 m^2, indicated that surface area predicted the number of workers in a nest (92% of variation explained) (Heller, 2004). The exact relationship between nest surface area and worker number may vary with local soil and environmental conditions.

The SC plot was searched exhaustively for nests once a month from March 2000 to February 2003; except from November 2001 to January 2001. The six JRBP study plots were searched

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seven times at 3–6-month intervals in autumn (November 2001, 2003), winter (January 2003), spring (April 2001, 2002, 2003), and summer (July 2003). Each survey lasted approximately 16 person-hours, conducted over 2 days when ant activity was highest, from 7.00 to 10.30 hours and 15.30 to 20.00 hours in March to October, and from 9.00 to 16.00 hours in November to February. In each survey, the number of nests and nest size was recorded, and summed to estimate total nest surface area for each plot. In the first 20 surveys at the SC plot, flags were not grouped into nests, so only total nest surface area for the plot was measured.

To study the persistence of nests, at each survey, flags were recorded either as new or persisting from the previous survey. The persistence of a nest was estimated as the total number of months that at least one flag associated with a particular nest persisted.

Trail abundance, length, and traffic. Above-ground trails connect nests to each other and to food resources, such as aphid and scale aggregations in trees (Fig. 1). There are no subterranean tunnels that link nests, but sometimes, during the dry summer months, the ants trail in cracks in the soil. At the SC plot, all inter-nest trails, with a rate of at least 1 ant per 5 s, were marked in each monthly survey. Each trail's path was traced onto a map, and it was determined which trails were new and which persisted from the previous survey. If a trail connected the same nests but its path changed slightly, it was considered it the same trail. Trail data were not collected at JRBP because trails could not be followed accurately in the thick grass. Trails at nests appeared similar in number and pattern to those at the SC plot.

From March to November 2002, the traffic of ants exiting and entering the SC plot on trails was measured. At each trail that extended outside of the plot boundaries, three 1-min counts were made, three times each day (morning, noon, and evening) for 3 days in each month (27 counts per trail per month), for a total of 972 counts. Data were grouped into seasons for comparison: spring (March, April, May), summer (June, July, August), and autumn (September, October, November). Counts were not made in winter months because there were no trails that extended out of the plot (December, January, February).

Environmental factors. The effects on nest location of two potentially important environmental factors were examined: soil temperature and proximity to woody plants. Woody plants modify soil microclimate and host honeydew excreting insects. To evaluate the effect of temperature on nest location, soil temperature was measured near nest chambers at 5 cm belowground. Surface soil temperatures fluctuate rapidly, so it is useful to record temperatures continuously over time to make comparisons across nests. Miniature temperature data loggers (Smartbuttons, ACR Systems, Surrey, BC, Canada) were used to measure temperature hourly for 3 months in the winter, January to March of 2004, and for 3 months in the summer, June to August 2004. In the winter, 18 data loggers were placed near occupied nests, and 18 near unoccupied nests, which had been occupied in the previous summer. In the summer, five data loggers were placed near occupied nests and six near unoccupied nests, which had been occupied in the previous winter. Sample sizes were smaller in the summer than winter because of animal disturbance in many sites.

To evaluate the effect of woody plants on nest location, the distance from the centre of each 1-m grid square to the nearest tree or shrub was measured. All grid squares were within 10 m from a woody plant, so to evaluate the association between woody plants and nests at greater spatial distances, an additional 10 sites were surveyed in May and September 2002. Sites were chosen that contained a small isolated patch of *Baccharis* shrubs. *Baccharis* is a dominant woody plant in California grasslands, on which *L. humile* commonly forages (N. E. Heller,

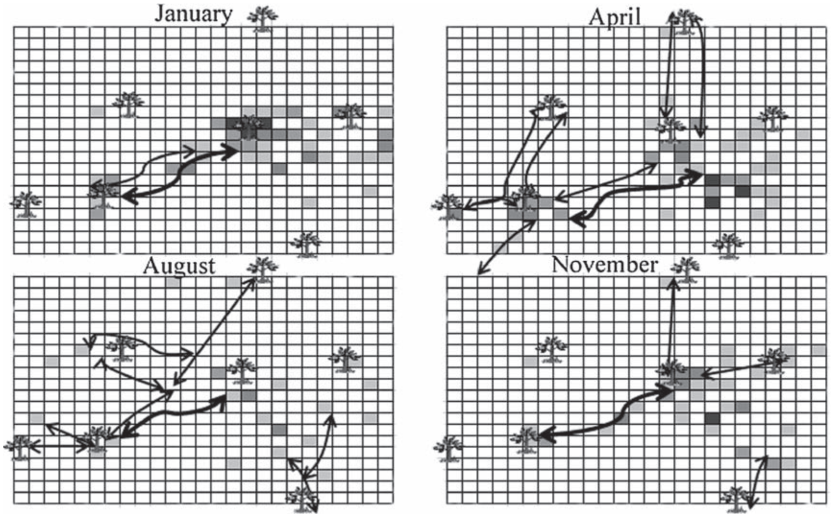

Fig. 1. Nest distribution in four seasons in the SC plot. Each grid square is 1-m^2, and darker colours indicate higher nest density. Lines indicate inter-nest trails with a rate > 1 ant per 5 s; thick lines indicate permanent trails and light lines indicate temporary trails. Trees shown are eucalyptus and oak.

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pers. obs.). Two 1-m wide rings at 2 and 15 m from focal plants were searched for nests and trials.

Distance estimates of budding or nest movement. Argentine ants reproduce by budding, instead of by population-wide mating aggregations. Alate queens mate in the parent nest and disperse by walking with workers to the site of a new nest (Passera, 1994; Keller, 1995). Using data from the SC plot, budding distances were estimated as the distance from a new nest back to the closest nest seen in the previous survey on the same trail. In addition, nest movement was elicited experimentally. From January 2003 to September 2004, 20 nests were located in various habitats, including gardens, paved areas, woodlands, and grasslands. To cause ants to emigrate, nests were flooded with water for 3 min. The distance from the flooded nest to the location where the ants began to dig into the ground, or entered a neighbouring nest, was recorded.

Statistical analysis

Nest abundance, size and density. Mean total nest surface area in plots, nest size, and nest density were compared across seasons using repeated measures ANOVA, with *P*-values corrected using the Greenhouse–Geisser adjustment. To decrease error associated with more sampling in April and November than in July and January at JRBP, only JRBP surveys from 2003 were used and each study plot was treated as a single subject that was sampled repeatedly in the four seasons.

Nest persistence. Time series analysis was used to study seasonal variation in the persistence of nests. Each nest was assigned to one of two seasons, cool, wet (November to April) or hot, dry (May to October) according the month when the nest was first found. A log-rank test was used to examine differences in persistence between the two seasons (Kalbfleish & Prentice, 2002).

Environmental factors and nest location. The effect of season on nest location was examined by calculating the similarity in the number of flags in each 1-m grid square for each of the 33 monthly surveys at the SC plot, using Bray–Curtis similarity coefficients. Each month was categorised into one of the four seasons. The relative similarity of months was plotted using a non-metric multidimensional scaling algorithm (NMDS). The proximity of points in the two-dimensional NMDS plot is proportional to their similarity. To test for seasonal differences in nest location, analysis of similarity (ANOSIM, PRIMER 5.0) based on Bray–Curtis coefficients was performed. This analysis was not carried out for JRBP plots because there were too few surveys in each season.

Laboratory experiments

Three laboratory experiments were conducted to evaluate the effects of humidity and proximity to food on nest site choice and nest emigration behaviour. Humidity influences the survival and colony growth rates of *L. humile* (Holway *et al.*, 2002b; Walters & Mackay, 2003). Temperature also influences survival and growth rates, but in pilot experiments, it was determined that ants were highly sensitive to temperature manipulations and unwilling to nest in nest boxes placed near heat lamps, so temperature was not experimented with further.

In June 2004, a large nest was flooded with water and ants were vacuumed into vials using a handheld vacuum cleaner linked to an aspirator. Ants were housed together in a large plastic container lined with Fluon (Northern Products, Woonsocket, Rhode Island) in a 24 °C laboratory. The relative humidity of the room varied between 40 and 55%. Ants were fed sugar water each day. Live crickets were fed once, 1 day after collection, so that ants would not be protein starved, nor overfed, when experiments began.

After 3 days, the ants were split into experimental colonies of 200–300 workers, ≈ 50 brood (eggs, larvae, pupae), and three queens. Colony sizes were similar to those used in other laboratory studies in which colonies effectively recruited to food resources (Holway *et al.*, 2002b; Roulston & Silverman, 2002). Each experimental colony was introduced to an apparatus that consisted of five circular boxes (9.5 cm (diameter) × 2.4 cm (height) plastic dishes with Fluon-lined edges), two of which were nest boxes (half filled with plaster of Paris with a small tube inserted into the plaster for wetting), one an introduction box, and two food boxes. All five boxes were connected by 16 cm plastic tubing (Fig. 2). Nest boxes were spaced 5 m apart. This distance was based on the distances that ants moved nests in the field (see Results).

To vary humidity in nest boxes, different amounts of water were added to the plaster via inserted tubes. Humidity was varied for two levels high ($> 85\%$ RH) and low (60–68% RH). High humidity boxes replicated Argentine ants preferred humidity levels (Walters & Mackay, 2003) and low humidity boxes were adjusted to slightly higher than room humidity. High humidity nest boxes received approximately 2.5 ml of water every 3 days and low humidity nest boxes received approximately 1.0 ml of water every 4–5 days. The amount of water was determined prior to the start of the experiment by measuring humidity with a thermohygrometer (WD-35612-00, Oakton, Illinois). Humidity levels in nest boxes were monitored periodically throughout the experiments.

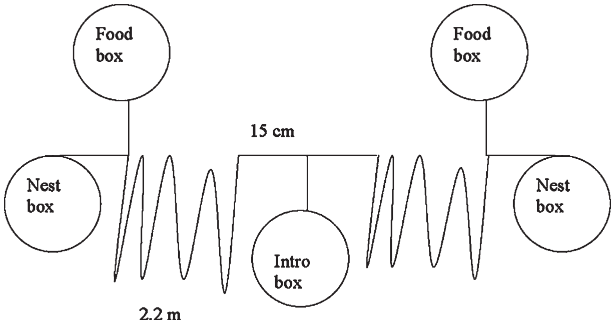

Fig. 2. Diagram of an experimental unit used in the laboratory experiments. Circles indicate boxes and lines indicate tubing. In the trade-offs in nest site experiment, the length of the tubes between the nest box and the introduction box were increased to 5 m in three units.

To control for possible gradients in the microclimate of the room, half of the experimental units were oriented in one direction and half were oriented in the other. In each experiment, ants were introduced at the introduction boxes, and then were allowed to move within the apparatus freely. Ants were fed sugar water and protein (a mixture of frozen crickets and hard-boiled egg) every other day, which was put only in food boxes. Once a day during the course of each experiment, the location of queens and brood was recorded and the number of workers in each box was counted. The box in which queens and brood were located was considered the nest site.

Experiment 1 – nest site preference. The preference of ants to nest near food and in high humidity was tested. (A) Food Test: in six apparatuses, both nest boxes were maintained at high humidity, but food was put near only one of the nest boxes. (B) Humidity Test: in another six apparatuses, food was put in both food boxes, but one nest box was maintained at low humidity and the other at high. Colonies were monitored for 10 days after introduction.

Experiment 2 – causes of nest emigration. The willingness of ants to emigrate in response to changes in humidity or food proximity was tested. After 10 days in A and B described above, the conditions of each nest or food box was switched. In A, food was removed from the food box in which food had been given and switched to the food box that previously was empty. In B, high humidity nest boxes were replaced with low humidity nest boxes and low humidity nest boxes were replaced with high humidity nest boxes. Before switching nest boxes, ants were forced to evacuate nest boxes by putting heat lamps over the nest boxes and shaking them vigorously. Nest boxes in A and B were disturbed in the same way, and new nest boxes were put in all apparatuses to eliminate the possibility of left over chemical signals influencing choice behaviour. Colonies were monitored for another 30 days.

Experiment 3 – trade-offs in nest site choice. To test which factor, humidity or food proximity, was more important to nest site choice, a trade-off in six apparatuses was created. One nest box was maintained at high humidity and the other at low humidity. Food was given only near the low humidity nest box. Colonies were monitored for 21 days. To test whether a greater distance between nest boxes would alter the ant's choice behaviour, in three additional apparatuses, 5 m of tubing was added, so that nest boxes were 10 m apart. These colonies were monitored for 7 days.

Results

Nest abundance, size, and density

The majority of nests were found in soil disturbed by gophers or in areas of sparse vegetation. There was wide variation in nest abundance across study plots. In the SC plot, there was a range of 9–39 nests/plot per search (covering on average 0.7% of soil surface area). In the JRBP low-elevation plots there was a range of 20–103 nests/plot per search (2% of surface area), and in the JRBP high-elevation plots the range was 5–28 nests/plot per search (0.4% of surface area). Individual nests varied in size from 0.04 to 2.8 m^2.

Nest surface area in plots varied with season (repeated measures ANOVA, $F_{3,18} = 6.5$, $P < 0.01$). It was higher in cool, wet months than in the hot, dry months (Fig. 3). The variability was due to seasonal changes in both nest size and nest density (for nest size $F_{3,15} = 14.4$, $P < 0.005$, for density $F_{3,15} = 10.00$, $P < 0.01$; Fig. 4). In late autumn and winter, study plots had a moderate number of nests, many of which were large. In spring, nest density was high, and nest size was moderate. In summer, nest density and nest size were low.

Nest persistence

Ants moved nest sites frequently, but there was wide variation in nest persistence and many nests were repeatedly abandoned and re-colonised. At SC, there were 102 nests observed, of

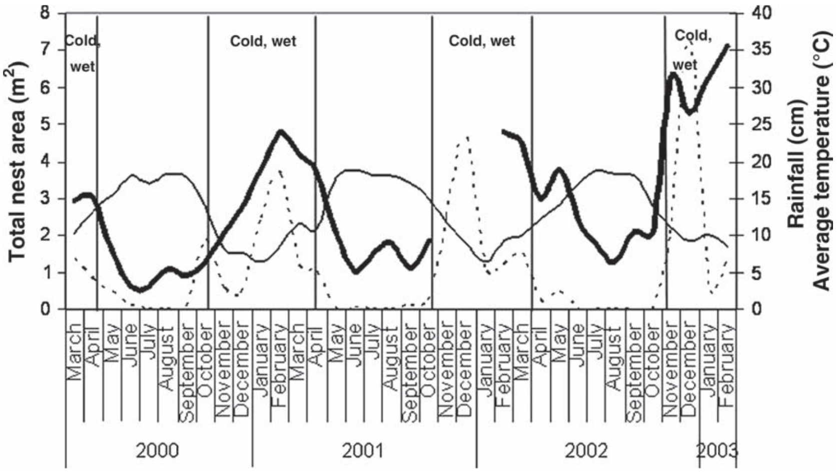

Fig. 3. Seasonal variability in temperature (thin solid line), monthly rainfall (dotted line), and total nest surface area (thick solid line) in the SC plot over 3 years. The SC plot was the site of large winter nest aggregations in the cool, wet season. Ants migrated to nests outside of the plot in the hot, dry months. Climate data were gathered from three nearby weather stations in Palo Alto, Woodside, and JRBP.

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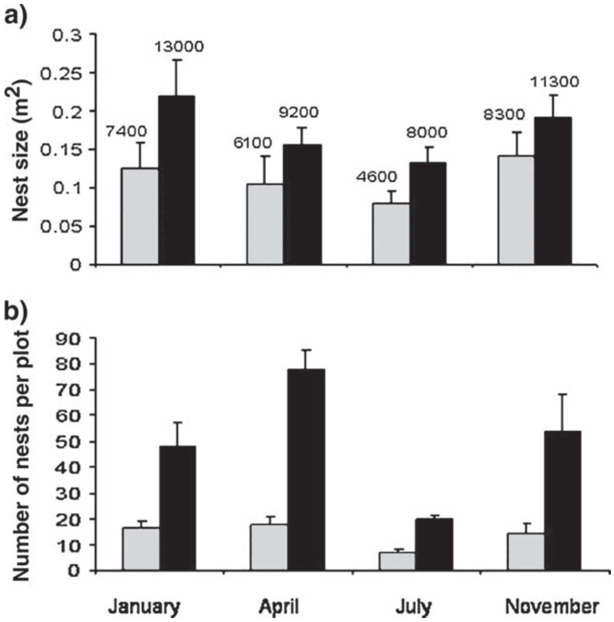

Fig. 4. Mean (± SE) of nest size (a) and nest number (b) from JRBP study plots. Dark bars represent values from low-elevation plots, and grey bars values from high-elevation plots. Numbers above bars in (a) show estimated mean number of ants in a nest = 58868.12 × nest surface area (regression equation in Heller, 2004). The estimated number of ants in a nest ranged from 3000 to 170 000 ants.

which 42% persisted less than 1 month, and 4.5% persisted for the 33 months of study duration. The mean (± SD) continuous persistence of the remaining 54% of nests was 3.9 ± 2.7 months. At JRBP, the 840 nests were classified into three types according to persistence: permanent, present in all searches (> 2.5 years) (4%); intermediate, present for at least 1 year (40%); and temporary, present < 6 months (56%). Thirty per cent of nests were occupied and abandoned repeatedly.

Larger nests persisted longer than smaller nests ($r_s = 0.62$, n = 840, $P < 0.001$). The mean (± SD) size of permanent nests was 0.35 ± 0.40 m^2, for intermediate nests it was 0.16 ± 0.23 m^2, and for temporary nests it was 0.10 ± 0.12 m^2. Permanent nests were found in all study plots, except in a high-elevation JRBP plot with very low nest density (mean of nine nests covering a total of 1 m^2 surface area).

Nests were more stable in the winter than the summer. A nest found at the start of the winter was more likely to persist through the cool, wet season (60%) than a nest found in late spring was to persist through the hot, dry season (35%) (log-rank test, $\chi^2 = 33.08$, d.f. = 1, $P < 0.0001$).

Trail abundance and length and traffic

On average, 57% of nests at the SC plot were linked to another nest by a trail. Trails were more numerous in hot, dry months than in the cool, wet months (Wilcoxon test, $S_{14,19} = 183$, $P = 0.05$). In the winter, there were few trails connecting only the large nest aggregations within the plot (Table 1). During the spring through autumn, the number of trails increased, as did the number of nests that were connected by trails, and the number of trails that extended outside of the plot boundaries, so the spatial area of the interconnected group of nests was greater than the size of the study plot in these months (Fig. 1; Table 1).

Trails, like nests, varied in persistence. Fifty-two per cent persisted less than 1 month, and 5% were present in all searches. The mean (± SD) continuous persistence for the remaining 43% was 3.7 ± 2.6 months. Forty-seven per cent of trails were abandoned and revived repeatedly.

When trail activity increased in the hot, dry months, ants migrated from nests inside the study plots to nests outside the study plots. Ants always travelled in both directions on trails, but in the spring, they exited (24.7 ants min^{-1}) at a significantly higher rate than they entered (20.4 ants min^{-1}) (t-test, $t_{16} = 3.0$, $P = 0.009$). In the autumn, ants entered (34.7 ants min^{-1}) at a higher rate than they exited (30.4 ants min^{-1}), but the difference was not significant ($t_{15} = 1.7$, $P = 0.12$). In the summer, ants entered (29.6 ants min^{-1}) and exited (28.7 ants min^{-1}) at approximately the same rate ($t_{17} = 0.6$, $P = 0.58$). Mostly workers were observed on trails. In 972 observations, only 33 queens, 17 males, and 13 workers carrying brood were counted. Eighty per cent of observations of queens, male, and brood were in the evening. Males and brood were observed only in May and June. Queens were observed in all months (≃1 queen per 1300 workers).

Environmental factors and nest location

Nest location varied in relation to season. Across years, the location of nests in months from within the same season were more similar than months from different seasons (ANOSIM, global $R = 0.28$, $P = 0.001$). Spring ($n = 9$) was different from winter ($n = 7$) ($R = 0.46$, $P < 0.01$), from autumn ($n = 8$) ($R = 0.29$, $P < 0.01$), and from summer ($n = 9$) ($R = 0.22$, $P < 0.01$). Winter was different from autumn ($R = 0.34$, $P < 0.01$) and from summer ($R = 0.45$, $P < 0.01$). Autumn and summer were not different from each other ($R = -0.04$, $P = 0.62$). Nest location in the winter was the most similar from year to year, indicated by the tight clustering of winter months in Fig. 5. Hot, dry months (June to October) were scattered in Fig. 5 indicating greater variability in nest location from year to year. The 'stress' value for the NMDS analysis was 0.20 in two dimensions and 0.14 in three dimensions. Stress is a measure of the goodness of fit of the configuration of points to the numerical similarity between samples.

Soil temperature influenced nest location. Ants nested in warm sites in the winter and moved to cooler sites in the summer. Locations that were always occupied in the winter were significantly warmer (mean ± SD = 13.1 ± 0.4 °C) than those that were abandoned (11.5 ± 0.8 °C) ($t_{1,34} = 67.2$, $P < 0.0001$). In summer months, temperatures were significantly cooler at occupied (27.6 ± 0.5 °C) than at abandoned sites (32.4 ± 0.8 °C) ($t_{1,9} = 34.5$, $P = 0.002$).

In all seasons, woody plants influenced nest location. Nests were most often found within 2–4 m of woody plants ($r_s = 0.95$, $P < 0.0001$; Fig. 6). In surveys of focal plants, ants were

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Table 1. The seasonal patterns of trails in the SC plot based on 33 months of observation. Values indicate mean ± SD.

Season	Number of trails	Per cent nests connected	Distance of trails (m)	Number of trails extending outside plot
Winter	2.5 ± 2.0	35 ± 16	9.0 ± 3.7	0
Spring	7.0 ± 2.4	51 ± 7	6.5 ± 0.8	3.1 ± 1.8
Summer	7.2 ± 2.0	71 ±5	6.9 ± 1.6	3.3 ± 1.6
Autumn	5.1 ± 2.3	74 ± 5	7.4 ± 2.1	2.4 ± 1.9
Total	43			

observed significantly more at 2 m from shrubs compared with 15 m from shrubs ($\chi^2 = 10.2$, d.f. = 1, $P < 0.01$; Fig. 6).

Distance estimates of budding or nest movement

When establishing new nests, ants moved short distances, and often on foraging trails that were observed in the previous surveys. The mean (± SD) budding distance was 2.16 ± 1.74 m ($n = 152$, range 0.5–11 m). The mean distance when nest movement was elicited experimentally was 2.9 ± 2.4 m ($n = 20$, range 0.3–10.0 m). At the SC plot, of all new nests, 44% were found in locations where trails had been recorded in the previous month.

Experiment 1 – nest site choice

Ants chose to nest in nest boxes near food; 100% of the queens and brood and 75% of workers were found in the nest boxes near food 2 days after introduction. Queens and brood were never observed in nest boxes far from food. Ants also chose to nest in high humidity; 100% of the queens and brood and 60% of workers were found in the high humidity nest boxes 3 days after introduction. Queens and brood were never observed in low humidity nest boxes. There were no differences in colony distribution between the Food and Humidity tests with respect to food availability; queens and brood were always found together, and the dispersion of workers from the main colony was not statistically different ($t_{1,20} = 1.5$, $P = 0.23$; Table 2).

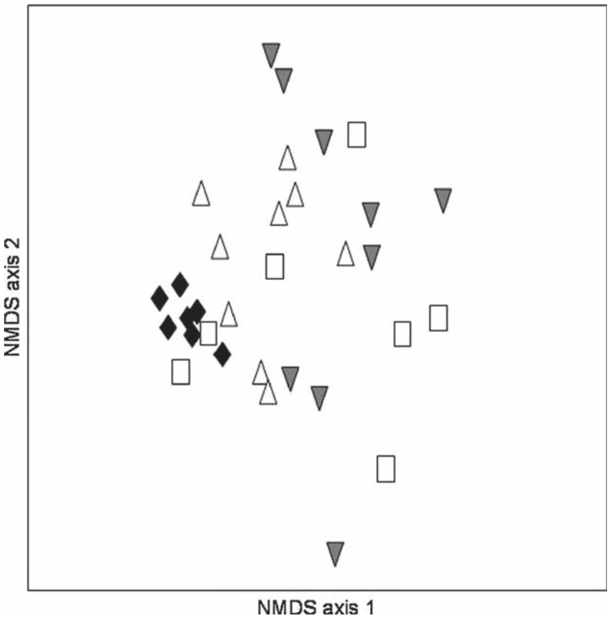

Fig. 5. Similarity in the location of nests at the SC study plot across seasons. Months in which ants nested in similar locations appear close together. Each point represents a single month, with the symbol indicating season: spring (△), summer (▼), autumn (□), and winter (◆).

Experiment 2 – causes of emigration

Ants emigrated when the humidity in nest boxes decreased, but not when food was moved a greater distance. In the Humidity Test, within 1 day after the conditions were switched, 80% of workers and 100% of queen and brood moved to high humidity nest boxes (Fig. 7b). In the Food Test, workers, queens, and brood did not move to the nest boxes closer to food (Fig. 7a).

Experiment 3 – trade-offs in nest site choice

When faced with a trade-off, ants preferred to nest in the high humidity rather than near food. On average 90% of workers and 100% of queens and brood were found in the high-humidity nest boxes (Table 2). The results when the distance between nest boxes was 10 m were not different from those in which the distance between nest boxes was 5 m; 75% of workers and 100% of queens and brood choose to nest in the high humidity nest boxes.

Discussion

Argentine ant nest and trail networks show a distinct seasonal fission–fusion cycle (Fig. 1). Nest size, abundance, and location, and inter-nest trail length and number varied in similar ways across sites and years. In the winter, colony networks were contracted; nests were large and linked only within 15 m. In each colony, a few nests and trails were maintained year-round, and winter nests were clustered in the same sites year after year. In the spring through summer, colony networks expanded because more trails were established from winter nests, and ants budded into many new nests. New nest buds maintained social exchange with parent nests by inter-nest trails. Workers always moved in both directions on all trails indicating extensive

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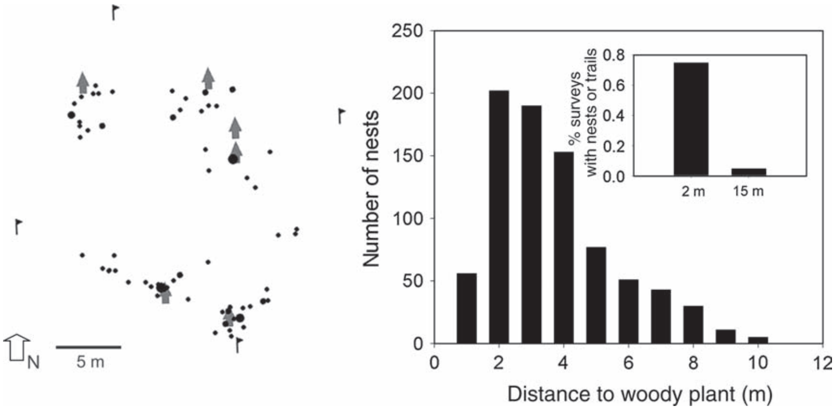

Fig. 6. Nests were associated with the location of woody plants, illustrated by a JRBP 400-m^2 high-density plot in winter. Nests are shown as black circles; larger circles indicate larger nests. *Baccharis* shrubs are shown as grey arrows. The large graph shows the frequency distribution of nests at different distances to shrubs. The small graph shows the proportion of surveys at 2 and 15 m from *Baccharis* shrubs in which nests or trails were found.

communication among linked nests. The number of nests per unit area approximately doubled in the spring compared with winter. In the spring, the ants begin reproduction of sexuals (Markin, 1970; Benois, 1973).

The seasonal changes in nest size and location observed here in northern California are similar to descriptions of colony dynamics in *L. humile* populations in southern France and New Orleans (Newell & Barber, 1913; Benois, 1973). Markin (1970) described nest migrations from a sunny hillside in winter to shady orchard in the summer in southern California. Here, it was shown for the first time the way in which trails change in association with nests, and that colony networks occupy permanent, distinct sites. Permanent site occupation results because colonies coalesced around the same nest sites each winter, and formed nests and trails in about 30% of the same sites during seasonal migrations year after year.

In other work, it was found that the interconnected group of nests can cover 650 m^2 in the summer, and that food-sharing among *L. humile* nests is spatially limited, but extends over a greater spatial area in the summer than in the winter (N. E. Heller, K. K. Ingram & D. M. Gordon, unpublished). Ingram and Gordon (2003) found genetic structuring in the study population at a spatial scale of less than 100 m, similar to the distances at which nests are connected by trails.

The colony cycle of *L. humile* is analogous to the 'seasonal polydomy' found in unicolonial populations of mound building *Formica* ants (Marikovskiy, 1962; Ito, 1973; Rosengren *et al.*, 1985; Elias *et al.*, 2005), as well as in some small polydomous, monogynous ant colonies (Alloway *et al.*, 1982; Herbers & Tucker, 1986; Traniello & Levings, 1986; Banschbach & Herbers, 1999; Cerdá *et al.*, 2002; Dillier & Wehner, 2004). Little is understood about the adaptive significance of seasonal polydomy (Banschbach *et al.*, 1997).

Both our field and laboratory studies indicate that the proximate cause of Argentine ant nest movements is changes in microclimate. In the laboratory, workers and queens rapidly abandoned nests when humidity became unfavourable, but not when food conditions changed. Colonies also always chose to locate nests in high humidity over close proximity to food. In the field, *L. humile* shifted from large nests in warm sites in the winter to smaller nests in cooler sites in the summer. Shallow nests are not well buffered from changes in external climate. Argentine ants may condense into larger groups in the winter to increase nest temperature. Larger group size in social insect colonies can generate greater metabolic heat (Seeley & Heinrich, 1981) and higher queen survival (Bourke & Franks, 1995). Nest location and turnover was more variable from year to year in the hot, dry months compared with cool, wet months. This may be because sites with high sun exposure are more reliable, so that ants consistently use the same sites in the winter. In contrast, sites with high humidity fluctuate more in time and space because of strong competition for soil moisture in the Mediterranean summer (Chiariello, 1989).

In seasonal polydomous *Formica* ants, the available evidence suggests that nest movements also function as a climate regulation strategy (Ito, 1973; Higashi, 1976; Rosengren *et al.*, 1985). The dome-shaped mounds and large group size of nests in *Formica* ants (red wood ants) are highly efficient at thermoregulation through the generation of metabolic heat (Rosengren *et al.*, 1987). However, in some unicolonial *Formica* populations (i.e. *F. truncorum*, *F. yessensis*) nests are messy and lack the mounds characteristic of the species. Instead, location and construction appears to maximise external heating through sun insolation and ants move nests sites with changes in season (Rosengren *et al.*, 1985). Banschbach *et al.* (1997) tested directly how temperature affected nest site choice and movement in *Myrica punctiventris*, and found no support for the hypothesis that seasonal polydomy is a thermoregulatory mechanism. Instead, seasonal polydomy may be a strategy to diminish worker–queen conflicts in reproductive allocation (Banschbach & Herbers, 1996b; Cerdá *et al.*, 2002). Queen–worker conflict may also play a role in the seasonal cycle of *L. humile*. Queens can inhibit the maturation of sexual pupae (Passera *et al.*, 1995). Nest dispersion in the spring may be a worker strategy to move brood away from mature queens. However, in traffic counts of ants on trails, *L. humile* workers were rarely observed moving

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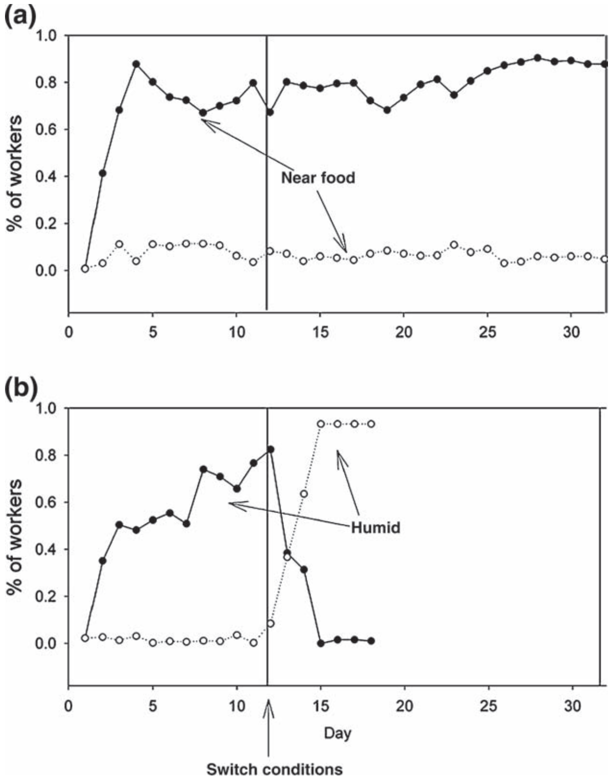

Fig. 7. Ants choose to nest near food and in high humidity. However, the ants emigrated only when humidity decreased, but not when distance to food increased. In (a), the per cent of workers in nest boxes near food (●) and in nest boxes far from food (○) in the Food Test are shown. In (b), the per cent of workers in high humidity (●) and low humidity (○) in the Humidity Test are shown. On day 12 (horizontal line), the conditions of nest boxes were switched, so that nest boxes near food were made far from food, and high humidity nest boxes were made low.

brood between nests. It may be that workers move brood at night when observations were not made. Alternatively, workers may reduce queen control by executing the majority of mature queens in early spring (Keller *et al.*, 1989).

Holway and Case (2000) suggested that *L. humile* moves nests opportunistically in response to food. They found that in the field *L. humile* constructed nests near sites with supplemented food. Nests may often be located near food because ants use foraging trails to emigrate and establish new nests (Aron *et al.*, 1990). In this study, 44% of new nests appeared on foraging trails that had been established at least 1 month before. However, the likelihood of ants establishing nests near food depends on microclimate conditions. In laboratory experiments here, ants only nested near food if humidity was optimal. Holway and Case (2000) found that in the laboratory, *L. humile* moved nests to be closer to food, but only when food was placed at 20 m from nest boxes. Changes in the distance to food beyond 10 m were not considered in this study because in the field, *L. humile* moved nests only 2–3 m (maximum 11 m). Food sharing across nests linked by trails produces nutritional stability for the colony as a whole (Rosengren & Pamilo, 1983) and may eliminate the need for nest emigration in response to food.

Woody plants strongly affect the location and fragmentation of *L. humile* colonies (Cammell *et al.*, 1996; Way *et al.*, 1997). Nests were most abundant within 2–4 m of woody plants, and rarely observed in open grasslands. In study sites where there were more woody plants, colonies were fractionated into a greater number of nests. Woody plant canopies increase and stabilise soil moisture and temperature compared with grass canopies (Breshears *et al.*, 1998; McLaren *et al.*, 2004) and provide access to tree-living Hemiptera populations, contributing to the ability of *L. humile* to monopolise these important food resources (Way, 1963; Lach, 2005). The close association of nests and woody plants, in combination with the ants' tendency to move only short distances when emigrating, suggests that population expansion at invasion edges may be limited when the distances between woody plants are great.

The rate at which an invading population spreads depends on the distance and frequency of dispersal. Argentine ant colonies tend to bud monthly and disperse up to 11 m during the hot, dry season, resulting in expected rates of spread as fast as 66 m per year. Nest location at two invasion fronts was monitored at JRBP, and the front advanced at a rate of 0–10 m per month from May to September (N. E. Heller, unpublished data). In northern California, the distribution of Argentine ants expands in the summer and contracts in the winter (Sanders *et al.*, 2001; Heller *et al.*, 2006), and rates of spread of 0–50 m per year are typical, with occasional spread up to 200 m per year (Ward, 1987; Human & Gordon, 1996; Holway, 1998; DiGirolamo & Fox, 2006). At JRBP, rapid spread occurs in years of high rainfall (Heller, 2005). In this study, we measured budding in an established colony. Budding dynamics at the invasion front may differ from those of established colonies.

In the study plots examined in this study, nest abundance was low in the summer, although other studies find annual peaks in worker abundance in the summer (Markin, 1970; Benois, 1973).

Table 2. The mean proportion (± SD) of worker ants in different boxes in laboratory colonies

Test	Nest box		Food box	
Food	Near food 0.75 ± 0.07	Far from food 0.07 ± 0.04	With food 0.02 ± 0.01	No food 0.06 ± 0.03
Humidity	High humidity 0.6 ± 0.11	Low humidity 0.04 ± 0.01	Near high humidity nest 0.10 ± 0.02	Near low humidity nest 0.06 ± 0.02
Humidity vs. food	High humidity far from food 0.90 ± 0.06	Low humidity near food 0.05 ± 0.03	With food 0.02 ± 0.01	No food 0.03 ± 0.01

Low nest abundance occurs because ants migrated out of the study plots and increased the spatial dispersion of the colony in the summer compared with winter, so nest abundance in the summer does not encompass the worker abundance of the colony. However, the relative differences in nest abundance in the summer compared with the other seasons should be interpreted with caution (Fig. 4). First, ants were not measured in woody plants. Observations of queens and brood indicate that if ants are nesting in woody plants in the study population, it is most likely in the summer. Second, nests may be deeper in the summer than in other months (Markin, 1970), so nest surface area may underestimate the number of workers in a nest.

Traits associated with unicoloniality, such as flexibility in queen number and nest density (Ingram, 2002a, b) and reproduction by budding (Passera, 1994; Keller, 1995; Holway & Case, 2001) help explain why *L. humile* excels at invading new environments. The organisation of colonies into spatially expanded networks that shift seasonally provides another mode of social flexibility that may contribute to their ecological dominance. Argentine ants have been most successful when invading in Mediterranean climates, which are characterised by strong seasonality in resource availability (Fig. 3) and various studies have shown that the competitive ability of *L. humile* depends on high worker numbers (Erickson, 1972; Holway & Case, 2001; Suarez & Holway, 2004). Shifts in colony organisation in response to the dry and wet season may facilitate more effective foraging. In the summer, when worker numbers are high and worker and queen production is at a peak, colony dispersion may increase access to food resources. In the winter, when ants are less active and worker numbers are low, colony contraction maintains high local worker densities (Markin, 1970). By contrast, native ant species that are displaced by *L. humile* typically inhabit single, sessile nests and become inactive during parts of the year when climate conditions are unfavourable.

Argentine ants are often aggressive in interactions with native ants and can drive native ants from resources (Human & Gordon, 1999). The spatial fluidity and network structure of *L. humile* colonies may promote high interaction rates with native ants (Aron *et al.*, 1990) and increase the ability of *L. humile* to cover space and dominate in exploitative competition (Human & Gordon, 1996; Holway, 1999). Frequent nest movement may increase nest site competition with native ants. For example, at the SC plot, only 17% of the 1-m^2 grid squares had *L. humile* nests in any one search, but when summed across the 3 years, *L. humile* had nested in 60% of the plot.

Seasonal polydomy has not been previously reported in *L. humile*. In various *Formica* species there is a link between flimsy nest construction, seasonal polydomy, and unicoloniality (Rosengren *et al.*, 1985). Elias *et al.* (2005) speculated that the mixing of workers from different nests during seasonal nest migrations may result in the breakdown of colony-specific recognition cues and contribute to the formation of unicolonial societies. Similarly, it has been suggested that nest movements and mixing in response to seasonal flooding may have promoted unicoloniality in the native range of *L. humile* (Bourke & Franks, 1995; Ingram, 2002b). Our results show that *L. humile* colonies are seasonally polydomous and move nests in response to changes in microclimate. This lends support to the hypothesis that seasonal nest movements coupled with extensive worker exchange may be an important influence in the evolution and maintenance of unicolonial social systems. Studies of the spatial colony dynamics of other invasive, unicolonial ants (i.e. *Anoplolepis gracilipes*, *Pheidole megacephala*, *Wasmannia auropunctata*, and *Lasius neglectus*) would be useful to increase our understanding of the link between seasonal polydomy and unicolonial behaviour.

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