Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant

DAVID A. HOLWAY & TED J. CASE

Department of Biology, University of California, San Diego

Many species of ants occupy multiple nests, a condition known as polydomy. Because of their decentralized structure, polydomous colonies may be removed from some of the constraints associated with classic central-place foraging. We used laboratory and field experiments to assess the mechanisms involved in dispersed central-place foraging in polydomous colonies of the Argentine ant *Linepithema humile*, a widespread invasive species. Both in the laboratory and in the field, Argentine ants established new nests at sites located near food. Laboratory colonies of *L. humile* redistributed workers, brood and resources among nests in response to the spatial heterogeneity of food resources. In addition, laboratory colonies formed recruitment trails between nests in the context of foraging, providing a mechanism for the transport of material between nests. This highly flexible system of allocating nests, workers and brood throughout a colony's foraging area potentially increases foraging efficiency and competitive ability. The importance of polydomy as a determinant of competitive ability is underscored by its prevalence among ecologically dominant ants, including most, if not all, highly invasive species.

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Social insects have long served as model systems for the study of foraging behaviour. Their usefulness in this regard stems from their modularity and complex social organization (Oster & Wilson 1978; Traniello 1989; Hölldobler & Wilson 1990). Modularity allows for great flexibility to apportion the labour demands of the colony among castes (Wilson 1985; Gordon 1996) and, in addition, makes possible the simultaneous defence of all portions of a territory (Hölldobler & Lumsden 1980). Despite this flexibility, most social insect colonies occupy a single nest and are thus highly centralized. A single, well-protected nest site provides safety from predators and serves as a buffer from environmental fluctuations but commits a colony to a single location. If food resources are located far away, occupation of a single, immobile nest may limit colony growth, as foragers will have to make long, round trips to procure food. Many ants behave consistently with the predictions of central-place foraging theory (Traniello 1989; Hölldobler & Wilson 1990), providing evidence of the potential costs associated with occupying a single nest.

Although central-place foraging is a prominent theme in the literature on social insect foraging (Hölldobler & Wilson 1990; Ydenberg & Schmid-Hempel 1994), many

ant colonies (and those of some termites) occupy multiple nests, a condition referred to as polydomy. The foraging behaviour of polydomous colonies can deviate from simple central-place foraging. By dispersing nests in space, polydomous colonies may avoid transporting food to a centrally located nest (Hölldobler & Lumsden 1980). At least in theory, polydomy could permit dispersed central-place foraging (McIver 1991): the establishment of new nests and the redistribution of workers, brood and food among nests in response to spatiotemporal variation in resource availability. Such flexibility would allow colonies to circumvent some of the costs associated with simple central-place foraging, improving foraging efficiency and competitive ability (Hölldobler & Lumsden 1980; McIver 1991; Davidson 1997). Despite these advantages, few experimental studies have tested how variation in food availability influences the distribution of nests, workers and brood within polydomous colonies.

Here, we examine the mechanisms of dispersed central-place foraging in the Argentine ant *Linepithema humile*. This invasive species has spread via human commerce from its native South America to subtropical and mild temperate regions throughout the world (Hölldobler & Wilson 1990; Passera 1994). In its introduced range, the Argentine ant outcompetes native ants through a combination of superior exploitative and interference abilities (Human & Gordon 1996; Holway 1999). Like many

Correspondence: D. Holway, Department of Biology 0116, University of California, San Diego, 9500 Gilman Drive, La Jolla, CA 92093-0116, U.S.A. (email: dholway@biomail.ucsd.edu).

invasive ants (Hölldobler & Wilson 1977; Passera 1994), Argentine ants (at least in their introduced range) are unicolonial, occupying expansive and highly polygynous supercolonies composed of many physically separate nests. The distribution of nests, workers and queens within supercolonies is dynamic (Newell & Barber 1913; Markin 1968, 1970a). Argentine ants invest little in their nests (which are often in shallow soil) and move them frequently due to changes in abiotic conditions and possibly in response to food availability (Newell & Barber 1913; Markin 1970a). Workers often move between nests as well. For example, by following ^{32}P-labelled workers through a citrus orchard for 1 week, Markin (1968) found that worker turnover at a centrally located nest exceeded 50% and that radioactive tracer spread from this central location throughout the approximately 3600-m^2 orchard. In spite of the Argentine ant's remarkably fluid colony structure, little is known about how their polydomous colonies respond to variation in resource availability.

To obtain a clearer understanding of the importance of polydomy in the Argentine ant, we used a combination of field and laboratory experiments to answer four questions. (1) Do colonies establish new nests in response to the location of food? (2) Do colonies engage in internest recruitment? (3) Do colonies redistribute workers among nests in response to the distribution of food? (4) Do colonies redistribute brood and resources among nests in response to resource heterogeneity? Such capabilities, if present, would provide polydomous colonies with competitive advantages lacking in species with simpler colony structures.

METHODS

Laboratory Colonies

We collected source material for laboratory colonies from a supercolony of Argentine ants occupying riparian woodlands along San Clemente Creek, San Diego County, California (32°50′N, 117°12′W). After removal from the field, supercolony fragments were divided into experimental nests and housed in plastic containers (30 × 14 cm and 8 cm high) lined with Fluon™ and Tanglefoot™ to prevent ants from escaping. Each nest container held three nest chambers (glass test tubes measuring 16 mm × 150 mm), half full of water and stopped with cotton. The outside of each test tube was covered with aluminium foil to keep the chamber dark. Experimental nests were kept under standard laboratory conditions (12:12 h light:dark cycle at 24°C) and fed scrambled eggs, crickets, vitamins and 25% sugar water, roughly approximating the nutrient content of the diet of colonies in the field (Newell & Barber 1913; Markin 1970b; Human et al. 1998). Before the onset of each experiment, we left experimental nests in an unmanipulated state for at least 2 weeks. Argentine ants thrive under laboratory conditions such as those described here and are commonly used in behavioural studies for this reason (Keller 1988; Deneubourg et al. 1990; Vargo & Passera 1991; Gordon 1995; Nonacs & Soriano 1998).

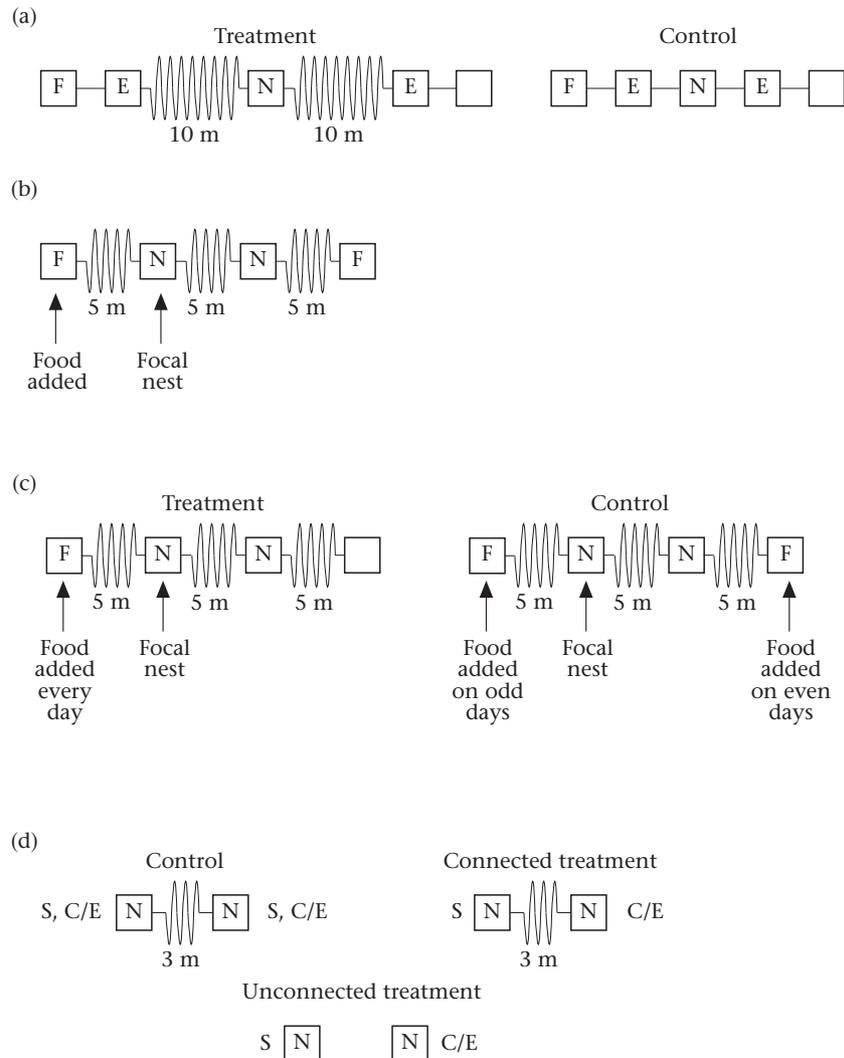## Nest Establishment Experiments

Laboratory experiment

We tested whether experimental nests establish new nests at sites near food. We set up 20 experimental nests, each consisting of five queens and approximately 1000 workers. At the start of the experiment, we divided nests randomly into treatment (N=10) and control (N=10) groups and connected each established nest to one of two configurations of empty nest containers, foraging containers and empty containers (Fig. 1a). In the treatment group, workers had to travel over 10 m from their nests to reach food, whereas workers in the control had to travel only about 30 cm (Fig. 1a). Empty nest containers held three nest chambers but contained no ants at the start of the experiment. Foraging containers and empty containers were identical to nest containers but lacked nest chambers. After the start of the experiment, we placed food only in the foraging containers. Empty containers never held food. We counted workers, queens and brood in all containers every 5 days, on average, over a period of 80 days.

Field experiment

To complement the above experiment, we tested whether colonies of Argentine ants in the field establish new nests at sites near food. We conducted this experiment in June 1998 in *Eucalyptus* woodland on the campus of the University of California, San Diego. We located 40 points (more than 50 m away from one another) where Argentine ants were observed foraging on bare ground and designated 20 as treatment points and 20 as control points. Treatment and control points were interspersed evenly throughout the study site. By placing baits at all 40 points, we then determined the distance between each point and the nearest Argentine ant nest. Once these distances were measured, we provided daily supplements of food (tuna fish, scrambled eggs and Pecan Sandies™) at each treatment point; no food was provided at control points. During these daily visits, we also noted whether ants were present at each point. To reduce disturbance from other animals, we placed food inside 5-cm^3 wire cages staked to the ground; cages were also placed at control points (to control for any possible cage effect). After 20 days, we again baited all 40 points and measured the distance between each point and the nearest Argentine ant nest to determine whether colonies had established new nests near experimental points. We consider cases where workers repeatedly carried food into a hole in the ground to be indicative of nesting. At the end of the study, newly established nests at treatment points were excavated to determine the presence of queens or brood.

Internest Recruitment Experiment

We investigated whether recruitment takes place between nests in the context of a food discovery. We set up 20 experimental nests, each consisting of approximately 500 workers and five queens, and joined nests into

Figure 1. Schematic diagrams of laboratory experiments. (a) Treatment and control designs for the laboratory nest establishment experiment. Squares depict plastic containers. N: Containers with established nests; F: foraging containers; E: empty nest containers (i.e. unoccupied at the start of the experiment). Squares without letters depict empty containers (i.e. lacking both nest chambers and food). Solid lines are plastic tubes connecting containers; tubes allow transit between containers. In the treatment group, 10 m of plastic tubing separated the original nest container (centre) from each empty nest container; all other connections (in both groups) were 10 cm in length. (b) Design for the internest recruitment experiment; codes and symbols as in (a). (c) Design for the worker redistribution experiment; codes and symbols as in (a). (d) Design for the brood and resource redistribution experiment; codes and symbols as in (a). For nest pairs in the control group, sugar water (S) and crickets and scrambled eggs (C/E) were placed in both nest containers. In the two treatment groups, sugar water was placed in one nest container and crickets and scrambled eggs were placed in the other.

pairs (N=10) with 5 m of plastic tubing. Each nest within each pair was then connected to its own foraging container (also via 5 m of plastic tubing; Fig. 1b). For 30 days prior to the start of this experiment, we alternated which foraging container within each pair of nests received food at each feeding. This prevented ants from developing an expectation about the location of food (Nonacs & Soriano 1998). At the onset of this experiment, we starved all nest pairs for 72 h and randomly selected one of the nests within each pair as the focal nest. We then placed food (one dead cricket and 5 ml 25% sugar water) in the foraging container adjacent to the focal nest and counted the number of workers entering the focal nest from the nonfocal nest (travelling one way passed a fixed point) for

1-min periods at 30-min intervals extending from 60 min before food was presented to until 180 min after food was presented.

Worker Redistribution Experiment

We determined whether workers redistribute themselves among established nests in response to resource availability. To test this hypothesis, we randomly assigned nest pairs from the internest recruitment experiment into control (N=5) and treatment (N=5) groups. At the start of the experiment, we counted workers in each nest within each pair of nests. For each pair of nests in the treatment group, we randomly selected one of the two

nests as the focal nest and placed food exclusively in its foraging container for 30 days; we never placed food in the foraging container of the nonfocal nest (Fig. 1c). For each nest pair in the control group, we also randomly selected one of the two nests as the focal nest but alternated which foraging container received food at each feeding (Fig. 1c). All pairs were fed daily. After 30 days, we again censused the number of workers in each nest. For each pair of nests, we calculated the difference between the number of workers in the focal nest and the number of workers in the nonfocal nest at the beginning of the experiment and again at the end of the experiment. Again for each pair of nests, we calculated the difference of these differences (i.e. difference at the end − difference at the beginning) and used this value in the analysis. Although this dependent variable measures how many workers moved into the focal nest during the course of the experiment, it is also influenced by brood that may have been relocated to the focal nest and that eclosed as workers during the course of the experiment. However, because the complete development time of workers (i.e. from egg to adult) for Argentine ants at 24°C is over 50 days (Newell & Barber 1913), the dependent variable used here (i.e. the difference of the difference) will not be influenced by disparities in colony growth between nest pairs in the treatment and control groups. One of the pairs in the treatment group was excluded from analysis due to unusually large numbers of workers drowning in the sugar water during the course of the experiment.

Brood and Resource Redistribution Experiment

We tested whether colonies redistribute brood or resources among nests in response to the spatial heterogeneity of carbohydrates and proteins; these resources are consumed in different amounts by different members of the colony. For example, Markin (1970c) found that Argentine ant workers distributed radiolabelled sugar primarily to other workers and radiolabelled protein primarily to queens and larvae. These findings reflect the nutritional needs of social insects more generally: queens require protein to remain fecund, brood need protein to develop properly, and workers often subsist largely on carbohydrates. Polydomy could therefore allow colonies to redistribute brood or resources among nests depending on the spatial distribution of these essential resources. We tested this idea in the following manner. We established 36 experimental nests, each consisting of three queens, 500 workers, and fewer than 50 pieces of brood. Using these 36 nests, we formed 18 pairs and randomly divided pairs into three experimental groups of six pairs each. These experimental categories included a connected treatment group, an unconnected treatment group and a control group (Fig. 1d). For the connected treatment and the control groups, we joined nests within each pair together via 3 m of plastic tubing. Nests within each pair in the unconnected treatment group were unjoined. We fed the ants crickets, scrambled eggs and 25% sugar water but placed food in different arrangements in each experimental group (Fig. 1d). For nest pairs in the control group, we placed all three food types in both nest con-

tainers. For both the connected and the unconnected treatment groups, we placed sugar water in one of the nest containers and crickets and scrambled eggs in the other nest container; the food type for each of the nest containers remained fixed throughout the experiment for these two treatments. Although the placement of the food differed across the three groups, the absolute amount of food delivered to each pair of nests at each daily feeding remained equal. For the pairs in both the control and connected treatment groups, we placed a foil barrier at the exit tube of each nest container; each barrier had a small hole that allowed the passage of workers (and workers carrying brood) but not the larger queens.

There are two main predictions of this experiment. First, if colonies redistribute resources among nests, then the productivity of nest pairs in the connected treatment group should be similar to that of nest pairs in the control group but higher than that of nest pairs in the unconnected treatment group. Second, if colonies redistribute brood among nests, then pairs of nests in the connected treatment group should have more brood in nest containers supplied with crickets and scrambled eggs than they do in nest containers supplied with sugar water. We tested these hypotheses in the following manner. After 90 days, we calculated overall worker mortality (the number of dead workers in each nest pair), number of living workers, and number of brood (eggs, larvae and pupae summed) for each pair of nests. We also measured the extent to which workers travelled between nests in the connected treatment and in the control. Just before the end of the experiment, we counted the number of workers travelling past a fixed point in the plastic tubing halfway between the two nests within each pair 1 h after feeding.

RESULTS

Nest Establishment Experiments

Laboratory experiment

Argentine ants relocated brood (and sometimes entire nests) to new nest sites in response to the location of food. Figure 2 shows the number of workers present over the course of the experiment in the nest container adjacent to the foraging container, in the foraging container, in the nest container adjacent to the empty container, and in the empty container. Twenty days after the start of the experiment, two of the colonies in the treatment group completely relocated to the nest container adjacent to the foraging container; these nest relocations account for the high variance in measures of worker abundance in this container for colonies in the treatment group (Fig. 2a). Also in the first 20 days, one of the nests in the treatment group moved into the coil of plastic tubing separating the original nest container from the empty nest container. No additional nest relocations occurred after 40 additional days, so we doubled the length of the tubing in the treatment so that workers had to travel more than 20 m to reach food. At this time, we also closed the connection between the original nest container and the empty nest container adjacent to the empty container
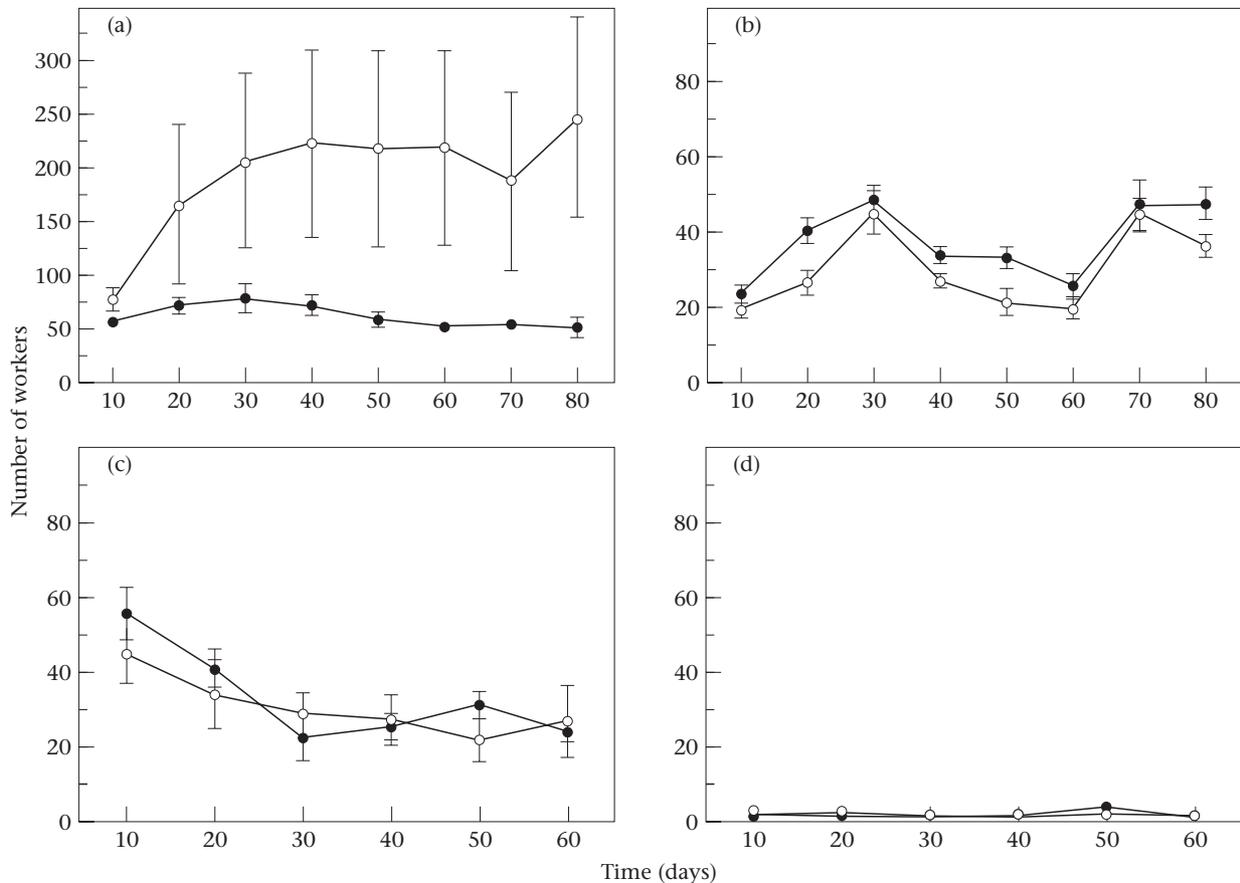
Figure 2. Results of the laboratory nest establishment experiment. The mean±SE number of workers (a) in the nest container adjacent to the foraging container, (b) in the foraging container, (c) in the nest container adjacent to the empty container, (d) in the empty container, at 10-day intervals. ○: Treatment; ●: control.

in both the treatment and the control groups because the empty containers were largely unused by ants (Fig. 2c, d). The increased distance over which workers in the treatment group now had to travel to reach food stimulated brood relocation. Twenty days after the length of tubing in the treatment was doubled, eight of the 10 nests in the treatment group had moved brood to the nest container adjacent to the foraging container, whereas only three of the 10 nests in the control group had moved brood to the nest container adjacent to the foraging container (G test: $G_1=5.30$, $P<0.05$). By the end of the experiment, three nests in the treatment group had completely relocated to the nest container adjacent to the foraging container, whereas none of the nests in the control group had moved (or ever did move in the course of the experiment).

Field experiment

The results of the field experiment also suggest that Argentine ants establish new nests near food. At the start of the field experiment, Argentine ant nests were as far from treatment points (mean ± SE=2.56 ± 0.25 m) as from control points (1.96 ± 0.26 m) (two-sample t test: $t_{36}=1.65$, NS). Food supplements regularly attracted ants to treatment points. Argentine ants were present, on average, during 95% of the visits to treatment points

compared with 10% of the visits to control points (two sample t test: $t_{36}=18.66$, $P<0.0001$, data arcsine transformed). After 20 days, there was evidence of nest establishment at 55% (10/18) of treatment points compared with only 5% (1/20) of control points (G test: $G_1=13.06$, $P<0.001$). At treatment points, the 10 new nests each had more than 50 workers below ground. Six of these nests contained either queens or brood, indicating that the criterion used here to identify nests (i.e. the presence of workers carrying food into holes in the ground) often indicated the presence of additional nesting activity. Two of the treatment points were excluded from these analyses due to repeated disturbance from mammals.

Internest Recruitment Experiment

The results of this experiment indicate that recruitment can occur between physically separate nests in the context of foraging. The number of workers travelling into the focal nest container from the nonfocal nest container increased more than 150% after food was placed in the foraging container adjacent to the focal nest (Fig. 3). This is a significant increase (repeated measures ANOVA: $F_{8,72}=4.39$, $P<0.0002$). Because workers were unmarked, it is uncertain whether workers from the focal nest recruited workers from the nonfocal nest to the food, or if workers
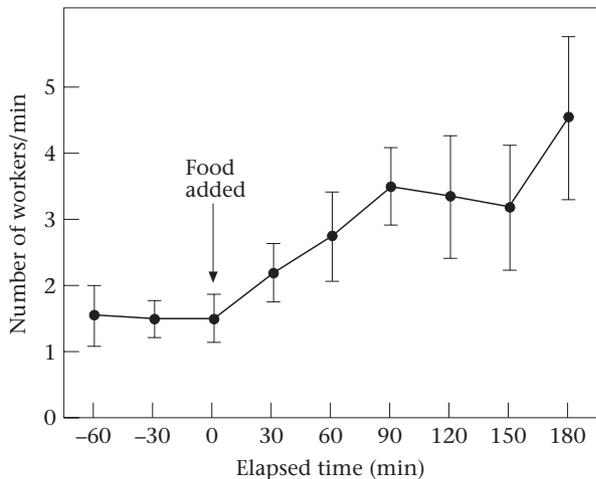
Figure 3. Results of the internest recruitment experiment. The graph shows the mean±SE number of workers travelling from the nonfocal nest to the focal nest at 30-min intervals before and after food was placed in the foraging container adjacent to the focal nest.
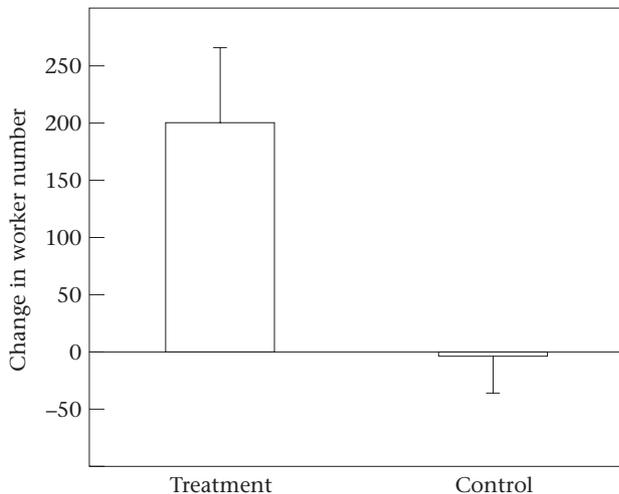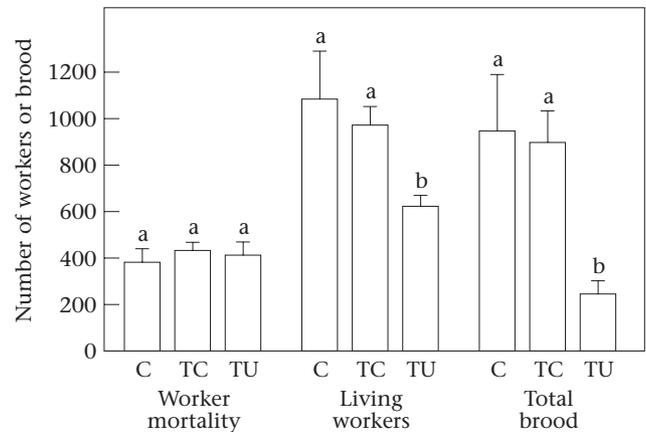

Figure 4. Results of the worker redistribution experiment. The graph shows the mean±SE number of workers that moved into the focal nest from the nonfocal nest over the 30-day duration of this experiment. Some of the workers present in the focal nest in the treatment group at the end of the experiment may have been relocated brood that eclosed as workers during the 30-day experiment.

from the nonfocal nest found the food on their own and recruited workers from the nonfocal nest to the food.

Worker Redistribution Experiment

After 30 days, the number of workers in treatment focal nests increased, on average, by approximately 45%, whereas the number of workers in control focal nests remained unchanged (Fig. 4; two sample t test: t_7=2.88, P<0.05). This suggests that workers redistributed themselves among nests in response to the location of food, but the relocation of brood (to the focal nest) that eclosed into workers during the course of the experiment

Figure 5. Results of the brood/resource redistribution experiment. The three sets of three bars illustrate worker mortality during the experiment, number of workers alive at the end of the experiment, and total brood at the end of the experiment for the control group (C), the connected treatment group (TC), and the unconnected treatment group (TU). Within each of the three comparisons, different letters show statistically significant differences from Dunnett's tests after one-way ANOVA.

also may have contributed to the disparity shown in Fig. 4.

Brood and Resource Redistribution Experiment

Colonies relocated both resources and brood among spatially separated nests. Two lines of evidence suggest resource redistribution. First, as predicted, pairs of nests in the control and in the connected treatment groups maintained similar numbers of surviving workers and brood, but, on average, supported 65% more living workers and produced 270% more brood than did pairs of nests in the unconnected treatment group (Fig. 5). In the unconnected treatment group, queens in nest containers provided with only sugar water were producing few eggs by the end of the experiment, probably due to their deficient diet. By the end of the experiment, for example, nest containers in the unconnected treatment group that were supplied with crickets and scrambled eggs had more eggs (mean ± SE=128 ± 28) than did nest containers with just sugar water (13 ± 11 eggs) (two-sample t test: t_{10}=4.36, P<0.01, data log transformed). Second, rates of worker-interchange between nests within nest pairs in the connected treatment group were higher than they were for nest pairs in the control group: mean ± SE 7.2 ± 2.4 versus 0.5 ± 0.2 workers/min (Mann–Whitney U test: U=34.50, N_1=N_2=6, P<0.01). This implies that workers in the connected treatment group were foraging between nests in response to the spatial heterogeneity of essential resources. The results of this experiment also demonstrate the occurrence of brood redistribution. In the connected treatment group, nest containers provided with crickets and eggs had a mean ± SE of 691 ± 144 pieces of brood compared with 208 ± 51 pieces of brood for nest containers provided with just sugar water (paired t test: t_5=3.85, P<0.05, data log transformed). Because total brood production in the

connected treatment did not differ from that of the control (Fig. 5), this disparity more likely resulted from brood relocation rather than differences in productivity between nest containers.

DISCUSSION

The results of this study provide unique experimental data on key mechanisms involved in dispersed central-place foraging. Argentine ants moved brood to new nest sites located near food and redistributed workers, brood and food among established nests in response to resource heterogeneity. In addition, Argentine ants engaged in internest recruitment in the context of foraging, providing a mechanism for the transfer of workers, brood and resources among nests.

Dispersed central-place foraging probably improves both the foraging efficiency and the competitive ability of polydomous colonies. Allocating nests, workers and brood throughout a colony's foraging area in response to the distribution of resources probably reduces foraging costs through reductions in travel distances, travel times and exposure to natural enemies (Hölldobler & Lumsden 1980; McIver 1991; Davidson 1997). Polydomy also might allow colonies to defend resources more effectively. Because the outcome of interference contests between competing ant colonies often hinges on numerical advantages (Hölldobler & Lumsden 1980; Adams 1990), distributing nests and workers near food could allow the rapid mobilization of workers for defensive purposes. These advantages would be especially important if food sources were clumped and stable through time (e.g. aggregations of honeydew-excreting Homoptera). However, polydomy may also be advantageous given uniformly distributed resources. For example, both Traniello & Levings (1986) and Pfeiffer & Linsenmair (1998) suggest that the dispersed nests within a polydomous colony may serve to station workers widely, permitting the efficient discovery and retrieval of resources that appear more or less uniformly in space. As emphasized by Traniello & Levings (1986) and Pfeiffer & Linsenmair (1998), the distribution of nests within a polydomous colony will be influenced by many factors, including the patchiness of the resource base, distance between patches, foraging costs, nest site availability, and the competitive environment.

In the above discussion, we emphasized the benefits of polydomy and dispersed central-place foraging, but these behaviours also incur costs (Tsuji 1988; Brown 1999). Nest relocation, in particular, is risky because it exposes queens and brood to predators and the vagaries of the abiotic environment. The perceived costs of nest relocation might explain why, in the laboratory experiment on nest establishment, most of the nests in the treatment group failed to move when foraging for food that was 10 m away. The advantages of establishing new nests near food will also be influenced by the availability of suitable nest sites. Although not a factor in the laboratory experiment on nest establishment, in the field, lack of appropriate nest sites may partly explain why only 55% of nests near treatment points established new nests near food.

Clearly, not all polydomous ants relocate nests or respond to patchy resources in the ways implied here. The extreme unicoloniality of introduced populations of Argentine ants sets them apart from other polydomous species in several respects. For example, the poor nestmate discriminatory ability typical of introduced populations of Argentine ants makes possible the highly flexible and dynamic behaviour of their supercolonies. The exchange of queens, workers and brood among nests is probably less common in other polydomous species. In addition, Argentine ants relocate nests frequently in part because they invest so little in nest construction. This is in contrast to some polydomous species, such as wood ants (in the *Formica rufa* group), that construct large, long-lived and elaborate nests (Bourke & Franks 1995). Even for species that do not invest heavily in nest construction, the establishment of new nests is probably more often influenced by physical factors and nest site availability than by proximity to food (Smallwood 1982; Herbers 1986, 1989; Hölldobler & Wilson 1990).

Similarities between Polydomous Ants and Clonal Plants

The colony-level foraging behaviour of polydomous Argentine ant colonies shows striking similarities to the resource acquisition behaviour of clonal plants. Although numerous ecologists have drawn comparisons between ants and plants (Wilson 1971; Traniello & Levings 1986; Andersen 1991, 1995; Lopez et al. 1994), the similarity in foraging behaviour of polydomous ants and multiramous clonal plants has received little attention. These taxa are similar in three main respects. First, the ability to establish new nests near food is directly analogous to the ability of some clonal plants to establish ramets in nutrient rich patches of soil (Cook 1983; Slade & Hutchings 1987a; but see DeKroon & Hutchings 1995). Second, polydomous ant colonies redistribute workers, brood and resources among nests in response to patchy resources. Such transport resembles that found between ramets of clonal plants. For example, interconnected ramets of some clonal plants are physiologically integrated with one another permitting the redistribution of photosynthates, water and limiting nutrients among ramets in response to resource heterogeneity (Alpert & Mooney 1986; Slade & Hutchings 1987b; Freidman & Alpert 1991). Lastly, ramets may differentiate morphologically in response to the local abundance of certain resources, altering their root:shoot ratios depending on whether they are primarily removing nutrients from the soil or capturing light from the sky (Stuefer et al. 1996; Hutchings & Wijesinghe 1997). Such ramet-level division of labour is akin to ant nests specializing on capturing protein for brood rearing or carbohydrates for sustaining workers. Although division of labour among workers is well known in social insects (Wilson 1985; Gordon 1996), these results suggest it may occur among nests as well (see also Hölldobler & Lumsden 1980; Cherix 1980; Hölldobler 1983; Pfeiffer & Linsenmair 1998). The surprising similarities between polydomous ants and clonal plants suggest that these distantly related taxa have

evolved qualitatively convergent strategies for the procurement of resources. Although this resemblance may be due to coincidence or to entirely different selective forces, it will be interesting to determine whether other modular animals (e.g. cnidarians, bryozoans) display similar behaviour.

Conclusions

The findings of this study argue for more quantitative analyses of (1) how spatiotemporal heterogeneity of food resources affects the number, dispersion and demographic composition of nests within polydomous colonies, and (2) how the putative advantages of dispersed central-place foraging influence efficiency and competitive ability. Ecologically dominant ants are often polydomous, and the foraging behaviour of these species suggests that nest relocation and the maintenance of multiple nests play a role in their competitive prowess (Hölldobler & Lumsden 1980; Hölldobler 1983; McIver 1991; Bourke & Franks 1995; Davidson 1997, 1998). Examples of other polydomous, dominant ants come from invasive species, such as *Pheidole megacephala*, *Wasmannia auropunctata*, and the polygyne form of *Solenopsis invicta* (Hölldobler & Wilson 1977; Clark et al. 1980; Porter & Savignano 1990; Passera 1994).

References

Adams, E. S. 1990. Boundary disputes in the territorial ant *Azteca trigona*: effects of asymmetries in colony size. *Animal Behaviour*, **39**, 321–328.

Alpert, P. & Mooney, H. A. 1986. Resource sharing among ramets in a clonal herb, *Fragaria chiloensis*. *Oecologia*, **70**, 227–233.

Andersen, A. N. 1991. Parallels between ants and plants: implications for community ecology. In: *Ant–Plant Interactions* (Ed. by C. R. Huxley & D. F. Cutler), pp. 539–558. Oxford: Oxford University Press.

Andersen, A. N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *Journal of Biogeography*, **20**, 15–29.

Bourke, A. F. G. & Franks, N. R. 1995. *Social Evolution in Ants*. Princeton, New Jersey: Princeton University Press.

Brown, M. J. F. 1999. Nest relocation and encounters between colonies of the seed-harvesting ant *Messor andrei*. *Insectes Sociaux*, **46**, 66–70.

Cherix, D. 1980. Note preliminaire sur la structure, la phenologie et le regime alimentaire d'une super-colonie de *Formica lugubris* Zett. *Insectes Sociaux*, **27**, 226–236.

Clark, D. B., Guayasamin, C., Pazmino, O., Donoso, C. & de Villacis, Y. P. 1982. The tramp ant *Wasmannia auropunctata*: autecology and effects on ant diversity and distribution on Santa Cruz Island, Galapagos. *Biotropica*, **14**, 196–207.

Cook, R. E. 1983. Clonal plant populations. *American Scientist*, **71**, 244–253.

Davidson, D. W. 1997. The role of resource imbalances in the evolutionary ecology of tropical arboreal ants. *Biological Journal of the Linnean Society*, **61**, 153–181.

Davidson, D. W. 1998. Resource discovery versus resource domination in ants: a functional mechanism for breaking the trade-off. *Ecological Entomology*, **23**, 484–490.

DeKroon, H. & Hutchings, M. J. 1995. Morphological plasticity in clonal plants: the foraging concept reconsidered. *Journal of Ecology*, **83**, 143–152.

Deneubourg, J. L., Aaron, S., Goss, S. & Pasteels, J. M. 1990. The self-organizing exploratory pattern of the Argentine ant. *Journal of Insect Behavior*, **3**, 159–168.

Friedman, D. & Alpert, P. 1991. Reciprocal transport between ramets increases growth of *Fragaria chiloensis* when light and nitrogen occur in separate patches but only if patches are rich. *Oecologia*, **86**, 76–80.

Gordon, D. M. 1995. The expandable network of ant exploration. *Animal Behaviour*, **50**, 995–1007.

Gordon, D. M. 1996. The organization of work in social insect colonies. *Nature*, **380**, 121–124.

Herbers, J. M. 1986. Nest-site limitation and facultative polygyny in the ant *Leptothorax longispinosus*. *Behavioral Ecology and Sociobiology*, **19**, 115–122.

Herbers, J. M. 1989. Community structure in north temperate ants: temporal and spatial variation. *Oecologia*, **81**, 201–211.

Hölldobler, B. 1983. Territorial behaviour in the green tree ant (*Oecophylla smaragdina*). *Biotropica*, **15**, 241–250.

Hölldobler, B. & Lumsden, C. J. 1980. Territorial strategies in ants. *Science*, **210**, 732–739.

Hölldobler, B. & Wilson, E. O. 1977. The number of queens: an important trait in ant evolution. *Naturwissenschaften*, **64**, 8–15.

Hölldobler, B. & Wilson, E. O. 1990. *The Ants*. Cambridge, Massachusettes: Belknap Press.

Holway, D. A. 1998. Effects of Argentine ant (*Linepithema humile*) invasions on ground-dwelling arthropods in northern California riparian woodlands. *Oecologia*, **116**, 252–258.

Holway, D. A. 1999. Competitive mechanisms underlying the displacement of native ants by the invasive Argentine ant. *Ecology*, **80**, 238–251.

Human, K. G. & Gordon, D. M. 1996. Exploitation and interference competition between the invasive Argentine ant, *Linepithema humile*, and native ant species. *Oecologia*, **105**, 405–412.

Human, K. G., Weiss, S., Weiss, A., Sandler, B. & Gordon, D. M. 1998. Effects of abiotic factors on the distribution and activity of the invasive Argentine ant (Hymenoptera: Formicidae). *Environmental Entomology*, **27**, 822–833.

Hutchings, M. J. & Wijesinghe, D. K. 1997. Patchy habitats, division of labour and growth dividends in clonal plants. *Trends in Ecology and Evolution*, **12**, 390–394.

Keller, L. 1988. Evolutionary implications of polygyny in the Argentine ant, *Iridomyrmex humilis* (Mayr) (Hymenoptera: Formicidae): an experimental study. *Animal Behaviour*, **36**, 159–165.

Lopez, F., Serrano, J. M. & Acosta, F. J. 1994. Parallels between the foraging strategies of ants and plants. *Trends in Ecology and Evolution*, **9,** 150–153.

McIver, J. D. 1991. Dispersed central place foraging in Australian meat ants. *Insectes Sociaux*, **38,** 129–137.

Markin, G. P. 1968. Nest relationships of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society*, **41,** 511–516.

Markin, G. P. 1970a. Seasonal life cycle of the Argentine ant, *Iridomyrmex humilis* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America*, **63,** 1238–1242.

Markin, G. P. 1970b. Foraging behavior of the Argentine ant in a California citrus grove. *Journal of Economic Entomology*, **63,** 740–744.

Markin, G. P. 1970c. Food distribution within laboratory colonies of the Argentine ant, *Iridomyrmex humilis* (Mayr). *Insectes Sociaux*, **2,** 127–158.

Newell, W. & Barber, T. C. 1913. The Argentine ant. *USDA Bureau of Entomology Bulletin*, **122,** 1–98.

Nonacs, P. & Soriano, J. L. 1998. Patch sampling behavior and future foraging expectations in Argentine ants, *Linepithema humile. Animal Behaviour*, **55,** 519–527.

Oster, G. F. & Wilson, E. O. 1978. *Caste and Ecology in the Social Insects.* Princeton, New Jersey: Princeton University Press.

Passera, L. 1994. Characteristics of tramp species. In: *Exotic Ants: Biology, Impact and Control of Introduced Species* (Ed. by D. F. Williams), pp. 23–43. Boulder, Colorado: Westview Press.

Pfeiffer, M. & Linsenmair, K. E. 1998. Polydomy and the organization of foraging in a colony of the Malaysian giant ant *Camponotus gigas* (Hym./Form). *Oecologia*, **117,** 579–590.

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

Slade, A. J. & Hutchings, M. J. 1987a. The effects of nutrient availability on foraging in the clonal herb *Glechoma hederacea. Journal of Ecology*, **75,** 95–112.

Slade, A. J. & Hutchings, M. J. 1987b. Clonal integration and plasticity in foraging behaviour in *Glechoma hederacea. Journal of Ecology*, **75,** 1023–1036.

Smallwood, J. 1982. The effect of shade and competition on emigration rate in the ant *Aphaenogaster rudis. Ecology*, **63,** 124–134.

Stuefer, J. F., DeKroon, H. & During, H. J. 1996. Exploitation of environmental heterogeneity by spatial division of labor in a clonal plant. *Functional Ecology*, **10,** 328–334.

Traniello, J. F. A. 1989. Foraging strategies of ants. *Annual Review of Entomology*, **34,** 191–210.

Traniello, J. F. A. & Levings, S. C. 1986. Intra- and intercolony patterns of nest dispersion in the ant *Lasius neoniger*: correlations with territoriality and foraging ecology. *Oecologia*, **69,** 413–419.

Tsuji, K. 1988. Nest relocations in the japanese queenless ant *Pristomyrmex pungens* Mayr (Hymenoptera: Formicidae). *Insectes Sociaux*, **35,** 321–340.

Vargo, E. L. & Passera, L. 1991. Pheromonal and behavioural queen control over the production of gynes in the Argentine ant *Iridomyrmex humilis* (Mayr). *Behavioral Ecology and Sociobiology*, **28,** 161–169.

Wilson, E. O. 1971. *The Insect Societies.* Cambridge, Massachusetts: Belknap Press.

Wilson, E. O. 1985. Sociogenesis of insect colonies. *Science*, **228,** 1489–1495.

Ydenberg, R. & Schmidt-Hempel, P. 1994. Modelling social insect foraging. *Trends in Ecology and Evolution*, **9,** 491–493.