

Frequent nest relocation in the ant *Aphaenogaster araneoides*: resources, competition, and natural enemies

Terrence P. McGlynn, Ryan A. Carr, Johnny H. Carson and Johnathan Buma

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Sessile and vagile organisms differ from one another in some fundamental ways, including methods of resource acquisition and competition. Ant colonies are typically studied as sessile entities, even though a large fraction of ant species frequently relocate their nests in the course of their life history. Little is known about the causes and consequences of nest relocation, but it is likely that the costs and benefits of relocation are driven by nest quality, neighborhood competition, or resource availability. In this paper, we document several cycles of nest relocation in a population of the Central American ant *Aphaenogaster araneoides*. In our first experiment, we tracked the pattern of relocation, testing whether environmental characteristics and colony demography were associated with relocation behavior. In our second experiment, we manipulated resource availability by adding or subtracting leaf litter, which is known to predict colony growth. We found that colonies relocated their nests once per week on average and colonies often reoccupied nests from which they had once emigrated. Larger colonies relocated more frequently than smaller colonies, and quickly growing colonies utilized a greater number of nests within their home range compared to slowly growing colonies. Relocation events were most likely to occur in periods when vapor pressure deficits were greatest. Nearest neighbor distance and other measures of environmental conditions were not associated with relocation behavior and there was no significant effect of litter removal or supplementation. We found evidence that multiple natural enemies attacked *A. araneoides* colonies. Based on the demographic correlates of relocation and our rejection of other plausible hypotheses, we propose that nest relocation is driven by the escape from natural enemies.

T. P. McGlynn, R. A. Carr, J. H. Carson and J. Buma, Dept of Biology, Univ. of San Diego, 5998 Alcalá Park, San Diego, CA 92110, USA (tmcglynn@sandiego.edu).

Ants are dominant members of terrestrial ecosystems. Ant colonies most strongly influence the environment immediately around nest entrances, through the cycling of soil, competitive exclusion, seed dispersal, and mutualisms with plant predators (Hölldobler and Wilson 1990, Andersen 1992, Schultz and McGlynn 2000). Ants are typically regarded as sessile organisms, rooted into their nests as plants are rooted into the ground (Andersen 1991, 1995). Nomadism has not evolved often in the evolutionary history of ants (Gotwald

1995, Brady 2003), and all of the non-nomadic ants occupy nests as central locations for food sharing and raising brood, as well as specialized functions such as cultivating fungus gardens and homoperans (Schultz and McGlynn 2000). Spatial distributions of ant nests are widely considered to be the product of neighborhood competition and are measured by the distance between colonies and the stability of nest locations (Levings and Traniello 1981, Ryti and Case 1992). In general, many studies of ant ecology are based upon the explicit or

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implicit assumption that colony locations are temporally stable, though this assumption is invalid for many species.

There is a growing body of evidence to suggest that periodic nest relocation is an integral component of the life history of many ant species, perhaps the majority of all ants. Observations of nest relocation in ants document broad prevalence of the phenomenon (Darwin 1859, Van Pelt 1976, De Vita 1979, Droual 1981, Smallwood 1982a, Tsuji 1988, Gordon 1992, Byrne 1994, Freitas 1995, Banschbach and Herbers 1999, Brown 1999). Hölldobler and Wilson's 1990 seminal tome on ant biology called attention to the "startling" number of species that perform nest relocation (p. 171), and prominently highlighted the lack of information about the phenomenon. Nest relocation is not a spurious evacuation, but rather is a highly coordinated process emerging from the division of labor among colonymates, involving complex decisions made at the colony level (Hölldobler 1984, Mallon et al. 2001, Pratt et al. 2002, Franks et al. 2002, 2003). Because nest relocation is largely unexplored, there are major gaps in our understanding of the basic ecology of ants. For example, polygynous colonies of the most intensively studied ant species in the world, *Solenopsis invicta* (Vinson 1997), relocate their nests frequently (Fuller et al. 1984) but little is known how relocation is associated with colony and population demography (Adams and Tschinkel 2001).

Why does nest relocation occur? What are the consequences of nest relocation for relocating colonies and their neighbors? Unfortunately, the answers to both of these questions have been elusive. In most cases, researchers failed to find a major endogenous or exogenous factor associated with nest relocation (Longhurst and Howse 1979, Smallwood and Culver 1979, Fuller et al. 1984, Tsuji 1988, Gordon 1992, Byrne 1994, Freitas 1995, Banschbach and Herbers 1999). In a few cases, researchers tied relocation events to environmental conditions, including adjustments to promote insolation (Harrison and Gentry 1981, Smallwood 1982b), efficient foraging (Holway and Case 2000), and increasing the distance from competing colonies (De Vita 1979, Brown 1999). Aron et al. (1986) showed that *Leptothorax unifasciatus* increased in foraging effort after relocation. Because competition and food availability are considered to have a strong effect upon distancing between colonies and how colonies forage and use space around their nests, changing the position of nests will change competitive interactions for space and food. When food availability is known to limit the growth of colonies, then it is likely that nest relocation occurs to increase access to food (McGlynn et al. 2002).

We present two experiments designed to search for correlates and causes of nest relocation in ants. First, we describe the spatiotemporal pattern of frequent nest

relocation in a common ground-nesting ant species, with emphases upon the environmental and demographic correlates of relocation events. Second, we present the results of a manipulation to alter food abundance around ant nests to determine whether food abundance could result in a change in relocation behavior. In this paper, we present results of the most thorough experimental investigation of nest relocation in a social insect.

Methods

Natural history

Aphaenogaster araneoides Emery is a myrmicine ant with a generalized diet of leaf litter arthropods that nests in tropical wet forests in Central America. Colonies are monodomous and monogynous, with ergatoid queens and relatively small colony sizes (mean = 123; McGlynn et al. 2002). Colonies grow and produce sexuals continuously throughout the year (Kaspari et al. 2001, T. P. McGlynn, unpubl.). *Aphaenogaster araneoides* had been observed relocating its nests in the course of earlier experiments (McGlynn et al. 2002). We conducted this study from June through August 2002 at La Selva Biological Station. La Selva is located in the Atlantic lowland wet forest of Costa Rica, Heredia Province, Sarapiquí Canton. La Selva receives ca 4 m of rain annually, with the majority of rain falling during the wet season between June and December. Maps, weather records, and other information about La Selva are available on the internet at www.ots.ac.cr.

We use the term "nest" to describe the soil structure that contains the ant colony, and the ants themselves comprise "colonies". Nest entrances of *A. araneoides* are rather wide, about 2 cm in diameter, so we were able to determine whether nests were occupied without disturbing the colony. We used a low-powered flashlight to look into the uppermost chamber. In nearly all cases, nests with workers inside had at least few individuals easily observed just beneath the nest entrance. Even when colonies were inactive, we could still observe workers inside. When a nest that was previously active appeared to contain no ants, we confirmed this by gently disturbing the first chamber of the colony with a piece of wire without damaging the nest. Based on several excavations of several recently vacated nests, we are wholly confident in this method to determine nest occupation. This disturbance did not increase the frequency of nest relocation (McGlynn et al. 2002), but nevertheless the status of nests was typically unambiguous and we rarely performed such a disturbance.

Experiments were designed and statistical analyses were performed with the assistance of Dytham's (1999) dichotomous key and Mitchell (2001); analyses were performed on SPSS (SPSS Inc., 2000, Version 10 for Macintosh, Chicago IL), SAS, Statview (SAS Institute

Inc., 1998. Version 5, Cary NC), and Piste (Vaudor, A., 2000, English version 3.1.2, Univ. of Montreal, Canada). We confirmed with Komolgorov-Smirnoff tests that all variables used in parametric tests had distributions that were not significantly different from normal; only weather data required a transformation to conform to a normal distribution.

Experiment one

Spatiotemporal tracking of nest relocation

We established a single observation plot of 600 m² to follow the movements of nests through space and time. The site was located north of the Camino Experimental Sur at 300 m on the La Selva Trail system. We searched exhaustively for 50 person-hours to locate occupied nests by feeding and following foragers, and by directly searching for nest entrances. All nests were marked with wire flags; nests and colonies, as defined above, each received unique designations. We located 33 colonies in the plot and kept track of relocation events for 34 days, and then we started to collect colonies by excavating the nests. By the end of the observation period, 108 separate nests had been occupied and marked.

Once per morning, we checked the nests to see whether ants were inside; if no ants were present we searched for the nest newly occupied by the colony. We inferred relocation events when we discovered a previously occupied nest was vacant, and a previously unoccupied nest was occupied or a new nest was discovered. This method was sound because we had found all of the nests within the plot, relocation events usually occurred within 1 m of the initial nest, and adjacent colonies rarely moved simultaneously. In earlier studies (unpubl.), the reliability of the method was confirmed by the marking of workers. We mapped nests to an accuracy of 1 cm using a bi-variate grid laid throughout the plot.

At the end of the observation period, we completely collected 24 colonies over five days; the remaining colonies were located within inaccessible nests. We collected colonies using a trowel to excavate, extracting adults and brood using forceps and aspirators. All colonies are stored in 95% ethanol at the Univ. of San Diego. We observed that some of the colonies housed mites (Arachnida: Acari), usually found in the lowest chambers, and always in chambers containing brood. Mite abundance was recorded as "absent," "few," or "many." Because mites might have negatively affected colony performance, we tested whether demography or behavior differed among the colonies with and without mites. To test whether the duration of nest occupation was associated with an increased load of mites within the nest, we compared the mean duration of nest occupation

among the mite abundance categories prior to nest collection.

Demography and nest relocation

We used colony size and colony growth as demographic measurements. We measured colony size using the number of adult workers in each nest, and measured colony growth by dividing the number of worker pupae by the number of adult workers (sensu Kaspari 1996, McGlynn et al. 2002). Because these two variables were not associated with one another ($r^2 = 0.02$) we regard them as independent measures of colony status. Sexual caste production was uncommon and not useful for demographic comparisons among colonies, except for comparing the presence or absence of male reproductives.

To our knowledge there is no standardized method to quantify frequency and timing of nest occupation and emigration in social animals. Thus, we created two measures of colony relocation behavior. The first variable, "relocation frequency," is the number of relocation events divided by the number of days of observation. The reciprocal of relocation frequency is the mean duration of nest occupation of the focal colony. We created a second measure of relocation behavior, "nest infidelity," to account for the variation among colonies in the reuse of previously occupied nests. During the observation period, nests were often used more than once by a colony. Nest infidelity values are the residuals of the linear regression of the number of nests occupied per colony dependent upon the number of relocation events by the colony ($y = 0.29x + 1.9$; $r^2 = 0.46$). Colonies with high nest infidelity were more likely to use nests only once during the observation period; colonies with low nest infidelity moved among nests that they have previously occupied during our observations. Relocation frequency and nest infidelity were not associated with one another ($r^2 < 0.001$).

The proximity to neighboring conspecific colonies may have influenced colony demography or relocation. We used nearest neighbor distances (NND) to indicate levels of competition among neighbors. Some colonies experienced consistently greater NND than other colonies, even as colonies relocated throughout their home ranges. For analyses applied to colonies (as opposed to measures of discrete relocation events), we employed a "colony centroid" incorporating of all of the nests occupied by a focal colony during our observations to be used for measuring the distance to neighboring colonies. We calculated the colony centroid with the mean x-coordinate value of all of the nests occupied by the colony and the mean y-coordinate of all of the nests occupied by the colony. This method of calculating nearest neighbor distances was created for time-independent analyses of colony demography and nest relocation behavior. To test whether nearest

neighbor distance affected relocation behavior, we compared changes in nearest neighbor distance before and after relocation events. We identified the relocation events in our plot for which we had complete information about nearest neighbors; relocation events near the periphery of the plot were excluded.

Multiple correlations among demography, nearest neighbor distance, and relocation behavior were confounded by intercorrelation. To infer effects of demography and nearest neighbor distances upon relocation behavior, we created an a priori path model to calculate path coefficients indicating direct effects among variables accounting for the paths in the diagram.

Experiment two

Effect of resource availability upon relocation

To determine how colonies may relocate in response to changes in resource abundance, we located nests throughout the forest to be designated for treatments and controls. It is known that there is a strong correlation between litter abundance and prey availability (McGlynn et al. 2002). Therefore, we were able to manipulate litter abundance to change resource availability. We created 30 sites along several trails in the old growth forest of La Selva, ranging over a distance greater than 2 km. At each of the 30 sites, we found at least three nests to be designated to each of the treatments and as controls. Two treatments were created: leaf litter removal ("removal") and leaf litter supplementation ("addition"). Treatments were designated randomly and nests were at least 6 m apart. At some sites, we located additional nests and used them as controls. A small number of nests were removed from the study because they were destroyed or obscured by treefalls, branchfalls, or apparent vertebrate predation.

For the removal treatments, we removed leaf litter from a circle of 7 m² area around the center of the nest. The area of leaf litter that we removed was greater than the mean area of *A. araneoides* home ranges plus two standard deviations, as reported by McGlynn et al. (2002). We removed all leaf litter above the soil excluding sticks and pieces of wood greater than 2 cm in diameter. The litter from the leaf litter removal treatment nest was added to the leaf litter supplementation treatment nest at the same site. Every day, we checked whether the nests were still occupied; observations continued for 34 days. We removed some nests from the study because they became obscured or destroyed by treefalls, branchfalls, or apparent vertebrate predation.

We created two variables to measure relocation behavior of the colonies using the focal nests in this experiment. The first variable was occupation frequency, calculated as the number of days the nest was observed with a colony inside divided by the total number of days

the nest was observed. (The results from experiment one support the assumption that only a single colony occupied each nest in this experiment.) The second variable was nest continuity. We calculated nest continuity using the residuals of the regression of the duration of the longest continuous nest occupation against the occupation frequency. Nests with high nest continuity values were occupied for long durations, while nests with low nest continuity were occupied for shorter periods of time. Nest occupation frequency and nest continuity were not associated with one another ($r^2 < 0.001$).

Environmental characteristics associated with nest relocation

We measured many environmental variables related to nest locations and compared them to the relocation variables. Nest opening area was calculated by taking perpendicular measurements of the diameter of the nest opening and calculating area using the equation for the area of an oval. We used a clinometer to measure the slope of the sites, and also to calculate the angle of the entrance into the first chamber. We measured the distance of the nest to the bole of the nearest canopy tree; we regarded a canopy tree as any individual whose crown was incorporated into the canopy of the forest (≥ 15 m). We calculated the canopy cover using the mean of values obtained from taking spherical densiometer readings at the cardinal compass points above each nest at breast height. Measurements of mean leaf litter depth around each nest were taken from measuring the depth of penetration through leaf litter until the wire hit bare soil at four points located 0.20 m from the nest. We created a separate a priori path model to determine significant interactions between environment and relocation behavior; we used this model separately for the control and each of the treatments.

The microhabitat locations of nests were classified into two additional sets of categories: nest substrate and flood protection. We created three nest substrate categories: 1) against the buttresses of canopy trees (buttress), 2) at the base of understory stems (stems) or 3) exposed and not adjacent buttresses or plant stems (exposed). We also examined the local topography and nest architecture to consider whether the location and construction of nests would provide protection from localized flooding during periods of heavy rain. We classified nests as either flood sheltered or flood vulnerable. This measure was subjective, though performed in a consistent fashion by one of the authors (RAC). Because the ants evacuated from nests to sites above ground when flooding occurs, we also measured the distance to the closest refuge above ground.

Weather effects upon relocation

Our nest observations were separated by 24 hours; we use weather data from the intervening 24 h for comparison with changes in the occupation of nests. Because we performed nest monitoring between 7:00 am and 11:00 am and rainfall during those hours was not appreciable during the study, we use 10:00 am as the boundary time between observation periods. We use cumulative rainfall over 24 h to compare against the daily frequency of nest relocation.

To assess the dessicating power of air, we calculated air vapor pressure deficit (VPD) using temperature, relative humidity, and saturated air pressure (as in Kaspari 1993). We calculated the mean VPD, the maximum VPD during the 24 hour period, and also the difference between the maximum VPD and the mean VPD in each 24 hour period. Weather records were provided by La Selva Biological Station in hourly intervals. These data were compiled from sensors above the forest canopy located within 1.5 km of all of the sites. We compared rainfall and VPD against the frequency of observed relocation events per day, using all nests from experiments one and two over 25 continuous days when all nests had been monitored on a daily basis. To consider whether the treatments in experiment two affected the how ants responded to weather conditions, we calculated separate daily relocation frequencies for each of the treatments.

Results

Experiment one

Pattern of relocation

The mean relocation frequency was 0.131 ($SD \pm 0.072$). On average, colonies relocated their nests every 7.6 days. The range of relocation frequency was broad, ranging from 0 (in a single colony) up to 0.297. Throughout the entire study, nests were never shared among colonies. Colonies often reoccupied nests from which they had previously emigrated; this frequency was measured using nest infidelity. In some cases, we observed that unoccupied nests were maintained by the colony that had occupied the nest earlier in the observation period.

We discovered several relocation events in progress; nest relocation events required at least 15 minutes for

completion. Our observations of nest relocations suggest that in most cases nests are completely deserted; collections of nests from this and an earlier study (McGlynn et al. 2002) are consistent with monodomy. In a few instances, we infer from our observations of nest occupation that there were occasional events of colony fission followed by fusion back to the initial status within 1–3 days. Many relocation events required no excavation of nests, and based on the quantity of excavated soil it appears when excavation was performed the cavity was previously available and required some maintenance. The mean nearest neighbor distances between the colony centroids was 2.19 m ($n = 15$, $SE = 2.40$, nests on periphery of plot excluded), ranging from 0.25 m to 3.51 m.

Colony level analyses

The correlations among relocation behavior, demography, and nearest neighbor distance variables are presented in Table 1. The path diagram supports direct effects of demography upon relocation behavior, though there were not significant direct effects of nearest neighbor distance (Fig. 1). The very high path coefficients support the model's effects of colony size on nest relocation frequency, and of colony growth on nest infidelity. Larger colonies relocated their nests more frequently, and faster growing colonies were more likely to relocate into previously unoccupied nests.

We found that the nests with many mites had been occupied for the longest period of time (13.67 d, $N = 3$, $SE \pm 3.48$), while the nests with few mites were occupied for an intermediate duration (6.88 d, $N = 8$, $SE \pm 1.42$), and the nests with no observed mites were occupied for the shortest duration (4.63 d, $N = 14$, $SE \pm 1.28$). The mean occupation duration of the nests with many mites was significantly different than in the nests with few or no mites, with no significant difference between the nests with few mites and those without mites (ANOVA, $F = 4.64$, $DF = 2,22$, $P = 0.02$; LSD post-hoc tests).

We tested whether adult reproductive male ants avoided colonies containing mites. Out of 27 colonies evaluated for mites, 12 colonies hosted mites and five contained males; all of the colonies with males lacked mites. The absence of males from nests with mites was significantly different from the frequency of males in nests with mites (Fisher's exact test, $p < 0.05$). Because

Table 1. Correlations (r^2) of relocation behavior, demography, and nearest neighbor distance.

	Colony size	Colony growth	Relocation frequency	Nest infidelity	Nearest neighbor distance
Colony size	1	-0.336	0.696	-0.217	-0.216
Colony growth	-	1	0.028	0.792	-0.178
Relocation frequency	-	-	1	0.116	-0.106
Nest infidelity	-	-	-	1	-0.056

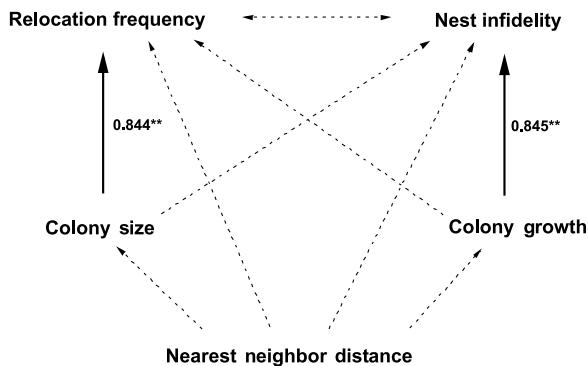


Fig. 1. Path diagram of relocation behavior, nest demography, and nearest neighbor distances. All effects in model are shown as arrows; bold arrows indicate significant results of direct effects. Values indicate path coefficients. ** indicates the p-values associated with the path coefficients were <0.01 .

the mating system of this species is undescribed, it is not yet known whether the males were produced within the colonies that we collected or if they originated from a foreign colony. We found that the frequency of male pupae within colonies was not associated with the presence of mites. Two of the 15 nests without mites contained male pupae; 3 of the 12 nests with mites contained male pupae (Fisher's exact test, ns).

Relocation event analyses

The mean nearest neighbor distance before relocation was 2.69 m, while the mean nearest neighbor distance after relocation was 2.65 m (paired t-test, $t = 0.36$, $df = 49$, ns). We treated each relocation event as an independent variate, even though the analysis incorporated relocation events from 17 colonies, including a maximum of four events for each colony. The mean distance traveled between nests was 0.93 m ($SD \pm 0.74$), with a range from 0.01 m to 2.44 m. The relocations across the short distance of 0.01 m occurred for a single colony that had two nests with entrances arranged directly above one another under an elongated canopy tree buttress; during nest excavations we confirmed that these nests were not connected underground.

Table 2. Microhabitat characteristics and relocation behaviors of colonies located in buttress, stem, and exposed nests. Post-hoc results of ANOVAs indicate LSD $p < 0.05$.

Microhabitat	Buttress		Stem		Exposed		df, F	p
	mean (\pm SE)	n	mean (\pm SE)	n	mean (\pm SE)	n		
Distance to refuge (m)	0.244 ^{ab} (0.07)	7	0.247 ^a (0.05)	38	0.439 ^b (0.05)	37	2.79; 3.91	0.024
Nest opening size (cm^2)	1.86 (0.31)	12	2.31 (0.30)	38	2.14 (0.31)	40	2.87; 0.30	0.074
Nest angle (degrees)	35.5 (7.4)	10	40.4 (3.3)	34	35.3 (3.2)	34	2.75; 0.63	0.535
Leaf litter depth, control only (mm)	32.9 (8.1)	6	20.9 (3.8)	9	20.8 (3.3)	17	2.29; 1.69	0.202
Canopy cover (%)	94.8 ^{ab} (0.38)	12	95.6 ^a (0.26)	38	94.5 ^b (0.33)	40	2.87; 3.13	0.049
Distance to canopy tree bole (m)	1.86 ^a (0.50)	12	4.31 ^b (0.41)	38	4.11 ^b (0.34)	39	2.86; 5.72	0.005
Time to decay after vacancy (d)	6.00 (1.53)	3	8.14 (1.73)	14	7.48 (1.27)	21	2.35; 0.17	0.842
Occupation frequency	0.45 (0.71)	12	0.44 (0.04)	38	0.48 (0.04)	40	2.87; 0.27	0.765
Continuity index	1.62 (1.1)	12	0.62 (0.58)	38	-0.26 (0.69)	39	2.86; 1.19	0.301

Experiment two

Nest site selection and architecture

The entrance cavities were round to oval in shape; the mean size of the nest opening was $2.16 cm^2$ ($n = 93$, $s = 1.81$). Beyond the entrances, all nests had a passage of similar diameter to the opening up to 8 cm in length. The angle of the passage into the nest was highly variable. At the end of entrance passage was a chamber that usually contained both brood and adults. We found 0–3 additional chambers that branched off the first chamber serially; larger colonies were located in nests with more chambers.

Among the 94 nests that we located at the start of the experiment, 12.7% (12) of the nests were located against the buttresses of canopy trees (buttress); 41.5% (39) were located at the base of understory stems (stem), and 44.7% (42) were not adjacent buttresses or plant stems (exposed). One nest (1.1%) was located inside the leaf litter of an understory palm. We observed that foragers leaving and returning to the aerial nest foraged on the ground in the leaf litter layer, and did not forage above the leaf litter layer. As the locations of the buttress, exposed, and stem nests appeared qualitatively different, we compared the microhabitat characteristics of these nests (Table 2). While nests located in the buttresses of canopy trees were closer to the boles of such trees, there was no significant difference in the mean distances to canopy trees between the stem and exposed nests. There were no significant interaction effects of treatments with microhabitat variables, except of course with leaf litter depth.

Effects of leaf litter treatments

We directly tested for the effects of leaf litter treatments upon relocation behavior and nest condition (Table 3). Leaf litter treatments had no effect upon the frequency of nest occupation or the longest duration of occupation. However, nests in the leaf litter removal treatments filled in with mud in a shorter period of time than those that filled in with mud in the controls (Table 3).

Table 3. Effects of treatments upon nest occupation. Means are presented \pm SE (post-hoc results indicate LSD, $p > 0.05$).

Treatment	Occupation frequency	Continuity index	Time to nest decay
Control	0.44 ± 0.04 (35)	0.155 ± 0.68 (35)	$22.57^a \pm 1.52$ (14)
Litter addition	0.44 ± 0.03 (28)	0.638 ± 0.67 (28)	$19.90^{ab} \pm 2.12$ (10)
Litter removal	0.51 ± 0.05 (29)	-0.280 ± 0.89 (29)	$15.57^b \pm 2.07$ (14)
ANOVA	$F = 0.79$; DF = 2,89; ns	$F = 0.21$; DF = 2,89, ns	$F = 3.77$; DF = 2,35; $p = 0.033$

Because many of the microhabitat variables were intercorrelated with relocation behavior variables, we created a path model to determine direct effects (Fig. 2). We performed separate analyses using the same path model on the three datasets of nests subjected to each treatment. There was a generalized effect of the slope of a site upon the angle of the nest entrance passage. The removal of leaf litter resulted in a positive association between the distance to refuge and nest continuity.

are: $r^2 = 0.37$, $y = 0.81x + 0.08$; ANOVA, $F = 13.50$, df = 1,23; $p < 0.01$.

We examined the daily frequency of relocation events of the nests in experiment two to determine whether response to weather was altered by the treatments (Fig. 4). Control nests demonstrated a significant positive association between $VPD_{max} - VPD_{mean}$ and daily relocation frequency, while the pattern was absent from both treatments.

Effects of weather on relocation behavior

The open and exposed nature of the nests suggested vulnerability to changes in rainfall and VPD. We converted rainfall to normality with a square root transformation. We found that rainfall in the 24 h between monitoring events had no association with relocation frequency per day (Fig. 3). However, we did find a strong positive association with VPD and the daily frequency of nest relocations. The relationships were similar and significant for all three measures of VPD, which is not surprising as VPD_{mean} , VPD_{max} , and $VPD_{max} - VPD_{mean}$ were all correlated with one another (all $r^2 > 0.7$). Because $VPD_{max} - VPD_{mean}$ demonstrated the most robust association with nest relocation frequency, we present these results in Fig. 4. The results for the nest relocation frequency per day dependant upon VPD_{mean} are: $r^2 = 0.21$, $y = 1.2x + 0.12$; ANOVA, $F = 6.08$, df = 1,23; $p < 0.05$). The results for the nest relocation frequency per day dependent upon VPD_{max}

Discussion

Four major products of these experiments make significant progress in understanding the ecology of nest relocation. First, we are reporting the phenomenon that a soil-nesting ant species moves its colonies among nests at an astoundingly high frequency. Second, we provide the first detailed description of spatiotemporal pattern of nest relocation, by tracking the timing and location of several relocation events for many adjacent colonies. Third, our experiments lead us to reject food availability and neighborhood competition as reasons for nest relocation. Last, we have found intriguing demographic and environmental correlates suggesting that nest relocation is a response to parasitism or predation.

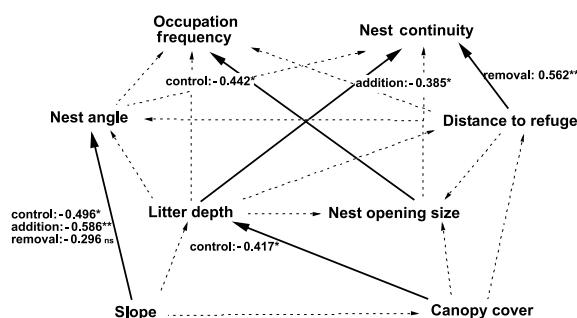


Fig. 2. Path diagram presenting results of a path model applied to three separate datasets on control, litter addition, and litter removal nests. Significant direct effects are indicated with bold arrows and path coefficients presented with significance (* denotes $p < 0.05$; ** denotes $p < 0.01$).

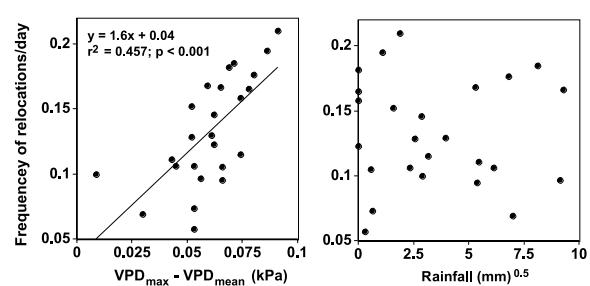


Fig. 3. Relationships between frequency of relocation events over a 24 h period and the weather conditions during that period. Vapor pressure deficit (VPD) of air is a composite measure of relative humidity, temperature, and the saturated vapor pressure of air at a given temperature. Relocation events were more frequent on days with greater peaks of high temperature and low humidity. Cumulative rainfall over the 24 h period was converted to normality with a square root transformation. Frequency of relocation events was calculated using all observed nests.

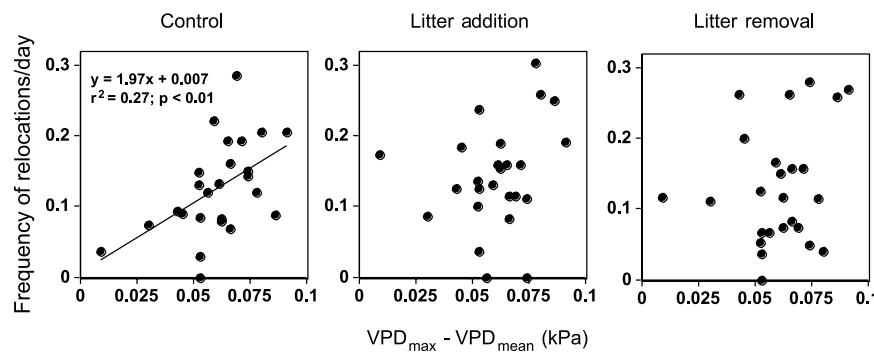


Fig. 4. Association between vapor pressure deficit and relocation event frequency compared among treatments in experiment two. The positive relationship between VPD and relocation event frequency is present in the control nests but disappears when nests are subjected to leaf litter addition or removal.

Inferences based upon the pattern of relocation

We were quite surprised to find that colonies of *A. araneoides* move among nests at such a high frequency without a trauma to nests or an appreciable change in the position of the nest. Nests used by one colony were never used by adjacent colonies, nor were colonies capable of increasing their distance from competitors by relocating. Relocation did not appear to change access to resources or the level of competition.

Structural integrity is a component of nest quality. It is possible that much of the biology of relocation could be simply explained by the costs and benefits of occupying new nests and maintaining old nests. It is plausible that the costs of relocation are less expensive than the costs of maintaining continuously occupied nests. Indeed, the next logical step in studying this phenomenon is to quantify the costs and benefits of relocation in both field and laboratory settings. However, we think that the cost of maintaining the physical structure of the nest is not the major selective force because colonies often leave and subsequently reoccupy the same nest multiple times, often with no maintenance performed on the nest. While it is true that the duration of occupation varies based on the physical characteristics of the nest (for example, the size of the nest entrance), it does not make sense that the cost of nest maintenance is the reason ants relocate when colonies leave structurally suitable nests, only to reoccupy them later.

Colonies appear to move in time periods when the risk of desiccation is greatest. Why does the frequency of relocation increase in periods of time with high vapor pressure deficits? Relocation events become more risky during the rain. Even though these ants are relatively large bodied, they cease foraging during heavy rainfall and we observed individuals stuck in muddy puddles in the rain. Though the decision to relocate is not solely caused by a change in VPD, the timing of relocation may occur when the probability of rainfall is lowest. Note that relocation events are independent of rainfall in a

24 h period, and relocation events are known to occur when VPDs are relatively low.

The most robust results demonstrated a link between colony demography and relocation behavior. It was surprising to find that larger colonies relocated more frequently than smaller colonies. Brown (1999) argued that species with larger colonies probably have greater relocation costs than species with smaller colonies, and this comparison probably holds true for conspecific comparisons. Therefore, if nest relocation is adaptive, then one would predict that the benefits of nest relocation are also greater for large colonies. Similarly, we found that quickly growing colonies use more nests than colonies growing more slowly.

Our experiments provide data that lead us to reject some hypotheses that might have explained nest relocation behavior in *A. araneoides*. These include response to neighborhood competition, localized resource depletion, unfavorable microenvironment or microclimate near the nest, and that colonies simply outgrow their nests.

We can reject resource availability and competition as the driving force behind nest relocation. We have several reasons to reject food availability and other correlates of litter quality as reasons for nest relocation. First, our treatments had no direct effect upon nest occupation frequency. We know that litter abundance predicts growth (McGlynn et al. 2002). While colonies subjected to reduced litter grow more slowly, this does not cause them to move their nests. If the decline of food in the environment caused nest relocation, we would have detected so in our experiment. The spatiotemporal pattern of nest relocation reinforces this interpretation that food and competitors do not matter. Relocation distances are very short and relocation events easily fall within the home ranges of these colonies. Even though colonies occupied multiple nests in serial, there was no sharing of nests among colonies. One could attempt to argue that relocation was driven by localized resource depletion near the nest, but this fails to explain that many of the relocation events were within 0.25 m of the

initial nest – once with two unconnected nests less than one cm apart – a small fraction of the home range of the colonies, with previously reported means ranging from 1.23 m² to 6.07 m² (McGlynn et al. 2002, 2003).

Nest relocation is probably driven by top-down regulation: two hypotheses

It is possible that colonies would relocate with high costs and no benefits, if precipitated by a traumatic event (such as an army ant raid or flooding) that gives the ants no choice but to move. However, we observed many relocation events when this was not the case. The obvious conclusion is that there is a hidden benefit or cost to nest relocation that we have yet to measure.

Colonies that are doing better are moving more frequently compared to those that are struggling to get by. Large colonies move more frequently than smaller colonies. Colonies that are growing more rapidly use more nests than colonies that are growing slowly. In addition, colonies in litter supplementations stay in their nests for shorter durations when resources are added. What could colonies have to gain from relocating, if not a change in their resources, microenvironment, or competition? All of our data are consistent with predictions made by top-down hypotheses.

There are a number of natural enemies that attack *A. araneoides*. The association between nest occupation duration and the number of mites inside the nest is suggestive, though the activity of this mite has yet been documented. Because mites are known to act as parasites of ant larvae (Eickwort 1990, Gotwald 1996), relocation may be driven by this mite. However, *A. araneoides* experiences other strong top-down influences. Above ground foraging army ants are known predators of *A. araneoides*. We have observed colonies raided by several species of army ants in the genera *Eciton*, *Labidus*, and *Neviamyrmex*, including the generalist swarm raider *E. burchellii*. When these raids occurred, *A. araneoides* workers abandoned the nest with brood and hid within the litter and often aggregated at the closest refuge above the litter layer. Other possible predators of *A. araneoides* include vertebrates such as the coati mundi (*Nasua narica*) and the vested anteater (*Tamandua mexicana*). Three of the nests that we followed throughout the course of the study (but none in the observational plot) were apparently excavated by vertebrate predators. The frequency of this type of event may be a strong force of selection if relocation can reduce the risk of depredation by these vertebrates. Even though *A. araneoides* is a rather large and common ant, we have not found any evidence of dipteran or hymenopteran parasitoids.

We propose two hypotheses to explain nest relocation that are consistent with all of our results: the parasitic

load hypothesis and the attractant hypothesis. In the parasitic load hypothesis, colonies relocate to reduce the cost of parasitism within their current nest. The attractant hypothesis proposes that colonies relocate their nests to decrease the probability that parasites or predators will be attracted to the nest because of an odor that accumulates over time. These hypotheses are not mutually exclusive and both may be acting simultaneously. We have no preference for a particular hypothesis, as we have some evidence supporting both hypotheses.

Under both the parasitic load and attractant hypotheses, the colony size/relocation frequency correlation makes sense. In the parasitic load hypothesis, larger colonies are likely to experience a greater cost of parasitism because they can support a larger burden of parasites. Under the attractant hypothesis, larger colonies are more likely to accumulate odors more quickly and thus will experience a greater risk of being detected by natural enemies.

The cumulative evidence points toward the importance of temporal variation in nest quality. The ants move because they have a problem with a nest they had been occupying for a brief period of time. Moving out of a nest of poor quality would provide a benefit to the colony. But how could a nest be a poor home today but become acceptable within a few weeks? It makes sense that if colonies leave nests because of nest condition, then the decline in nest condition is temporary and the nest becomes suitable while the colony occupies another site.

We can offer brief explanations of the temporal variability of nest quality that are consistent with top-down regulation. In the parasitic load hypothesis, the parasite load may increase with increased occupation duration and relocation may then reduce parasite load. In the attractant hypothesis, the potency of the attractant may dissipate as nests remain unoccupied. The high frequency of nest relocation on days with high vapor pressure deficits makes sense under the attractant hypothesis, because aromatic compounds will diffuse into the air at higher rates on these days.

The negative correlation between litter depth and nest continuity in food addition treatments seems counter-intuitive, but makes sense in light of the top-down hypotheses. It is helpful to remember that resources do not directly cause nest relocation, and that resources were added not only to the focal nest, but also to the other nests that the colony uses within its home range that we did not track during the study. In addition, the negative correlation between litter and continuity occurred only among colonies that had just received about twice as much litter as they had previously lived with. Thus, this comparison is not between starving and sated colonies, but between sated and feasting colonies. Feasting colonies have lower nest continuity relative to

controls, but other colonies show no difference. If one views the decision to relocate as a balance of the costs and benefits, then the supplementation of resources probably alters this balance to decrease the cost of relocation because of the reduced risk of resource deprivation after relocation. This is supported by the observation that home ranges temporarily shrink after relocation, probably as a result of the cost of relocation (McGlynn et al. 2003). Additionally, if relocation is a benefit to the colonies, then one would expect that colonies with luxury consumption would reside within their nests for briefer periods of time.

The role of natural enemies in the nesting biology of social insects is underappreciated, though it is known that predators and parasites can change nesting habits. In a study of the wasp *Polistes bellicosus*, Strassmann et al. (1988) found that in a single season most colonies moved their nests due to destruction by predators. Another wasp species, *P. exclamans*, occupies satellite nests to reduce the cost of parasitoids that attack the brood (Strassmann 1981). While army ants are also known to drive ants out of their nests (McDonald and Topoff 1986, Ward 1999), there is no documented cycle of continual relocation in a population of social insects in response to natural enemies. If nest relocation is a strategy employed by *A. araneoides* in an evolutionary arms race with its predators and parasites, then the ants appear to have lost the battle. Given the energetic resources invested into relocating nests and maintaining the structures of multiple nests, these ants are paying a high cost. However, it is possible that the ants might have lost the evolutionary arms race battle, but have won the war. This animal is highly abundant and has arguably the most uniform distribution in the forest, with colonies less than three meters apart throughout the forest. It is possible that constantly abandoning nests is an adaptive strategy compared to other species that maintain permanent nests under the burden of high rates of parasitism and predation.

It is difficult to learn about the ecology of vagile organisms, relative to compared to those with long-term nesting affinities. It is simpler to track temporal variation changes in the condition of organisms and their environments when there is no spatial change (Gordon 1991). Some pragmatic restrictions have prevented researchers from learning more about nest relocation. In most species, the observation of the inner workings of nests in the field is likely to disrupt relocation behavior. Just as physiologists can only kill an animal once, demographic data on field colonies can only be collected once. A more challenging constraint is that it is often impossible to differentiate between inactive nests and those that have been abandoned. Field-oriented ant ecologists have traditionally chosen species with long-lived permanent nests, which allow repeated sampling with confidence of colony identity. It is likely that

investigation into the life histories of ants demonstrating nest relocation will reveal that many concepts applied to sessile organisms are not applicable.

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