

Responding to a Variable Environment: Home Range, Foraging Behavior, and Nest Relocation in the Costa Rican Rainforest Ant *Aphaenogaster araneoides*

Terrence P. McGlynn,^{1,2} Melissa D. Shotell,¹ and Megan S. Kelly¹

Accepted July 16, 2003; revised August 4, 2003

*We studied how the tropical wet forest ant *Aphaenogaster araneoides* adjusted its home range and foraging behavior in response to changes in the leaf litter and food environments. We decoupled litter abundance and food availability by creating a factorial treatment design including litter removal and food supplementation. Leaf litter removal caused a decrease in the number of foraging trips but an increase in their duration. Over a 2-week experimental period, about half of the colonies relocated their nests. We found a strong effect of nearest neighbor distance upon the home range areas of colonies after they relocated their nests. In summary, short-term manipulations of resources resulted in changes in home range area and foraging behaviors that differed depending upon nest relocation and the competitive environment.*

KEY WORDS: home range; nest relocation; rainforest; resource abundance; environmental variation.

INTRODUCTION

When food abundance fluctuates, animals benefit from effective detection and responses to these changes. When the changes in the benefits and costs of

¹Department of Biology, University of San Diego, 5998 Alcalá Park, San Diego, California 92110.

²To whom correspondence should be addressed. Fax: (619) 260-6804. e-mail: tmcglynn@sandiego.edu.

foraging are predictable, animals can use endogenous and exogenous cues to respond to these changes. For instance, migratory birds travel in order to continue feeding throughout the winter, using day length and biological clocks as some of the triggers for migration (Cox, 1985). Brine shrimp use a decrease in daylight as a cue to move up the water column to feed at times of reduced predation risk (Forward and Hettler, 1992). However, when resource variability is unpredictable, relatively few external cues will be tied to resource abundance and it is possible that, as a result, animals may not be able to detect environmental changes reliably. As a result, animals in unpredictable environments may not be able to allocate their foraging effort efficiently.

Environmental stochasticity can have a strong effect on the evolution of behavior and life histories (Abrams, 1991; Chesson and Rosenzweig, 1991; Gordon, 1991). Ants foraging in the leaf litter of tropical rainforests experience unpredictable spatial and temporal fluctuations in resource abundance, driven by shifts in the abundance and moisture of leaf litter (Levings and Windsor, 1984; Kaspari, 1996; Soares and Schoereder, 2001; McGlynn *et al.*, 2002). In this and many other ant communities, competition for food through resource exploitation and direct interference is common (Bourke and Franks, 1995; Kaspari, 2000). Even though leaf litter ants are constrained by food abundance, their foraging and nesting behaviors are also shaped by other constraints, including nest availability, predation by army ants, topography, and spatiotemporal shifts in microclimate (Kaspari, 1993; Byrne, 1994; Powell and Mitchell, 1998).

When ant colonies change foraging behavior to improve the efficiency of locating food, they may be responding to the microclimate itself rather than directly assessing food abundance (McCoy and Kaiser, 1990). Because litter quantity and litter moisture are correlated with prey abundance for leaf litter ants (Levings and Windsor, 1984; McGlynn *et al.*, 2002), ants may indirectly assess prey abundance conditions within the leaf litter. In a laboratory manipulation, Durou *et al.* (2001) discovered that individual foragers of the rainforest leaf litter ant *Decamorium decem* changed the sinuosity of their foraging paths in association with the humidity in their foraging environment, which probably would result in more efficient foraging in the wild. However, it is not known whether ants may change foraging behavior in response to leaf litter quantity.

When food abundance, microenvironment, and competition change, ant colonies may respond by altering home range size, the frequency of foraging trips and the duration of foraging trips. An additional strategy to respond to environmental changes is relocation of the nest. Several ant taxa inhabiting tropical leaf litter have independently evolved some degree of nomadism or migration (Bourke and Franks, 1995). The foraging

behavior and nest movements in most genera with mobile nests are completely unknown but it is clear from existing studies that nest movements are quite common (Longhurst and Howse, 1979; Smallwood and Culver, 1979; Smallwood, 1982a; Levings and Franks, 1982; Diniz *et al.*, 1998; Banschbach and Herbers, 1999). Among most species with established nests that relocate periodically, the causes for nest relocation are unclear; earlier studies have not shown strong associations with competition, nest availability, nest quality, or food abundance (Tsuji, 1988; Byrne, 1994; Kaspari, 1996; Brown, 1999). Nest relocation will be profitable when the costs of relocation are offset by reduced competition or increased food abundance. We have performed a manipulative field experiment to determine how a nest relocating ant responds to changes in environmental quality. We created separate treatments to alter the abundance of litter and the abundance of food and measured how these changes affected foraging behavior.

METHODS

We studied the soil nesting and leaf litter foraging ant *Aphaenogaster araneoides* (long-necked ant), which is common in lowland wet forests of Costa Rica (McGlynn *et al.*, 2002). Little is known of its behavior or ecology, though its congeners in North America have been studied extensively (e.g., Holldobler *et al.*, 1995; Morales and Heithaus, 1998). This species has a relatively large body size, with workers about 5 mm in length. Our study site was La Selva Biological Station, located in the Caribbean lowlands of Costa Rica in Sarapiquí. La Selva is located in a tropical wet forest that receives ca. 4 m of rain annually (McDade and Hartshorn, 1994); detailed information about the field site is available on the Internet at www.ots.ac.cr. This study was conducted in May–June 2001, near the start of the wet season, in three old-growth forest sites. We selected locations that were relatively flat to reduce erosion caused by frequent traffic during experimentation, and those without large treefalls that would obstruct our ability to follow ants. The locations of the sites with respect to the La Selva trail system are as follows: site 1, 25 m N of CCL 210; site 2, 5 m SE of CES 410; and site 3, 5 m S of CCL 390.

We located nests by searching litter for foraging workers, and feeding them very small pieces of food (ca. 1 mg of oil packed tuna, with excess oil drained). We mapped the home ranges of the colonies by following foragers (see McGlynn *et al.*, 2002); we located and followed individual foragers back to their nests, marking and mapping polygons indicating home range areas. Treatments were assigned to colonies haphazardly. To facilitate mapping of complete home ranges, we used colonies that were located near one another,

often with adjacent home ranges. In all analyses, we use the colony as the unit of analysis, and the values for colonies were generated from at least ten measurements of individual colonies.

We employed a factorial design using two treatments: the removal of leaf litter (“no litter”) and the addition of supplemental food (“food”). We refer to the combined treatment as “no litter + food.” The leaf litter removal treatment was applied by removing all leaf litter from the soil (all material resting on the ground, excluding sticks with a diameter > 2 cm). The food addition treatment consisted of the daily addition of moderate quantities of food throughout the home ranges; this included protein, fat, and carbohydrate food, including termite workers and soldiers (*Nasutitermes corniger*), oilpacked tuna, and crushed cookies (Cremas, manufactured by Riviana Pozuelo). Termites used in the food treatments were collected from arboreal nests and frozen, and allowed to thaw before being placed as supplemental food. Two weeks after removing leaf litter and starting feedings, we reassessed home ranges using the same methods that we used before applying the treatments. We compared the amount of overlapping area between the initial and the final home ranges of the colonies.

Following the commencement of treatments, we evaluated the foraging behavior of marked colonies; each colony was observed for at least 9 h, with observations nested for equivalency in environmental conditions among treatments. To evaluate the number of foragers, we observed nest entrances and counted the number of individuals entering and leaving their nests, referred to as nest traffic. While performing these observations we also recorded the times of arrival and departure. We considered ants as foragers if they searched beyond the immediate nest area and were not carrying refuse away from the nest. We marked individuals by painting them with various colors of Testor’s Enamel; because the long legs of the workers obstructed the mesonotum, we painted single legs to discriminate among individuals. Painting individuals did not apparently disrupt foraging behavior, and some individuals kept their marks for several days. To account for potential environmental effects upon behavior, we measured temperature at the start and finish of each observational period.

Throughout the entire study, we performed daily checks of every marked nest to determine if the colonies had relocated in the intervening times. When we observed a nest movement in progress, we observed the event and recorded the details. When we did not observe the move, we were often capable of determining the new location of nests based on our maps of occupied and empty nests and marked workers; we excluded data when we were not confident of the identity of relocated colonies; this resulted in occasional differences in sample sizes of comparisons before and after treatments occurred. We calculated the frequency of nest relocation among

treatments by counting the number of nests that had moved throughout the experimental period, using only the colonies that we had observed from the start of treatments.

We refer to colonies that did not relocate during our experimental period as “stationary” and colonies those that relocated as “relocated.” These labels merely indicate whether these colonies had relocated during the course of our experiment, and whether our records on final nearest neighbor distance and final home range areas are from a new nest site. Because some nests on the edges of our experimental areas did not allow for full searches for nearest neighbor distances, sample sizes are not equal for all analyses.

To test whether the use of space and competition may have had an influence upon relocation, and how in turn relocation may have changed the use of space, we compared differences in home range area and nearest neighbor distance among relocated colonies and stationary colonies. We determined nearest neighbor distance using initial and final maps generated in the home range analyses. In the nearest neighbor analyses, we excluded nests that were located on the periphery of the mapped areas, because it is possible that these nests could have been positioned closer to an unmapped nest.

RESULTS

Foraging Frequency and Duration

Nest traffic was significantly different among the control and treatments (Fig. 1, Table I). Compared to the frequency of foragers entering and leaving the control nests, almost twice as many ants entered and left the food treatment nests, and there was a significant reduction in the nest traffic as a result of the litter removal. There was no individual colony-level effect upon the forager frequency (ANOVA, $F = 0.283$, $df = 23,8$, $P = 0.99$).

We compared the duration of foraging trips, to the temperature (calculated by the mean of the temperatures at the start and finish of the observation periods). Temperatures ranged from 24.3 to 26.7°C, and the relative humidity at 5 cm above ground level was always greater than 95%, in our field site in closed canopy forest. We found that the duration of the trips was significantly shorter at warmer temperatures, but with a very low correlation that was driven by a few outlying points of long foraging trips in cooler temperatures ($r^2 = 0.041$, $y = -242.4x + 7673$; ANOVA, $df = 1,158$, $F = 6.76$, $P = 0.01$). Because temperature accounted for less than 5% of the variation in foraging duration, we did not include temperature as a factor when comparing foraging durations among treatments. The duration of foraging trips was increased by the removal of leaf litter, though there was

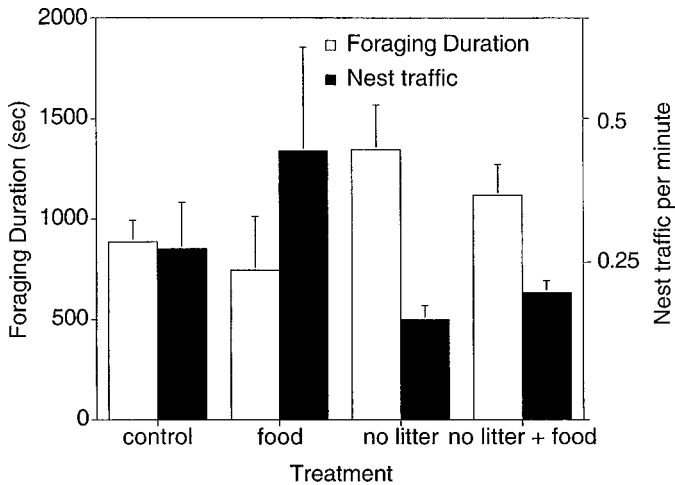


Fig. 1. Mean foraging duration and nest traffic to colonies subjected to each treatment. Nest traffic is the frequency of foragers entering and leaving the nest. Error bars represent one standard error. Analyses are presented in Tables I and II.

no significant effect of food addition (Fig. 1, Table II). There was no individual colony-level effect upon the foraging duration (ANOVA, $F = 1.174$, $df = 24, 133$, $P = 0.28$).

Home Ranges

Before the initiation of treatments, home range areas were not significantly different among the control and treatment colonies (Fig. 2, Table III). Because many colonies had relocated during the 1-week treatment period, we have separately analyzed the stationary colonies and the relocated colonies. Among the stationary colonies, home range area in the food treatments was twice as large as the mean home range area of the initial

Table I. Two-Factor ANOVA to Test the Effects of Litter Removal and Food Addition upon the Number of Ants Entering and Leaving Their Nests

Source of variation	df	MS	<i>F</i>	<i>P</i>
Food addition	1	0.05	1.62	0.22
Litter removal	1	1.54	4.73	<0.05
Food addition × litter removal	1	0.02	0.52	0.65
Residual	17	0.03		

Table II. Two-Factor ANOVA to Test the Effects of Litter Removal and Food Addition upon Foraging Duration

Source of variation	df	MS	F	P
Food addition	1	178,642.8	1.01	0.32
Litter removal	1	907,994.2	5.12	<0.05
Food addition × litter removal	1	9,969.8	0.06	0.81
Residual	18	177,252.2		

colonies. Because we were unable to find any of the food addition colonies that had relocated out of their original treatment areas, we removed food as a factor from the analyses involving both home range area and relocation. Among both the stationary and the relocated colonies, leaf litter removal had no affect upon home range areas (Fig. 2, Table III).

Because of frequent nest relocation, our sample sizes were inadequate for paired comparisons of initial and final home ranges among the treatments. Instead, we compared the amount of area shared by the initial and final home ranges of the colonies, which we refer to as overlap. Not surprisingly, the amount of overlap was highly correlated with the final home range areas (Fig. 3); to compare overlap areas independent of home range area, we performed a two-way ANOVA comparing the residuals of overlap area regressed with final home range area as an independent variable (Table II). Comparing residual overlap areas, we found that there was a significant

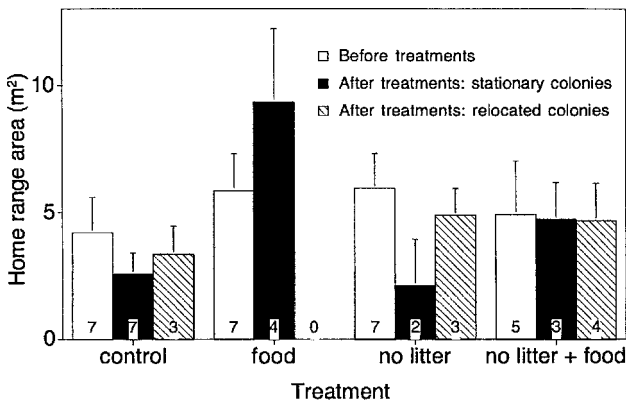


Fig. 2. Home range areas of ant colonies before and after treatments. Colonies that moved nest locations are shown with separate bars from colonies that did not move within the experimental period. Error bars represent one standard error; sample sizes are shown on bars. Analyses are included within Table III.

Table III. Results of Two-Factor ANOVA Testing Effect of Food Addition and Litter Removal on Home Range Areas^a

Source of variation	df	MS	F	P
Home range area before treatment				
Food addition	1	0.61	0.04	0.85
Litter removal	1	1.02	0.07	0.80
Food addition × litter removal	1	11.53	0.74	0.40
Residual	22	15.48		
Home range area after treatment—stationary colonies				
Food addition	1	71.57	6.06	<0.05
Litter removal	1	21.01	1.75	0.21
Food addition × litter removal	1	14.25	1.21	0.29
Residual	12			
Home range area after treatment—relocated colonies				
Litter removal	1	4.13	0.82	0.39
Residual	8	5.03		
Residuals of area overlapping between initial and final home ranges				
Food addition	1	0.45	0.28	0.60
Litter removal	1	2.28	1.41	0.25
Food addition × litter removal	1	8.84	5.44	<0.05
Residual	15		1.625	

^aSeparate analyses were performed for initial and final measurements; the stationary and relocated colonies were also analyzed separately. Food was not included as a factor in the analysis of relocated colonies because we could not find any nests subjected to the food treatment.

interaction effect of litter removal and food treatment, with the least overlap in areas with additional food and no leaf litter.

Nest Relocation

We kept daily records on the nest occupation of 36 colonies throughout the experimental period. Of the 16 colonies given supplemental food, 10 relocated; of the 20 without supplemental food, 10 relocated ($\chi^2 = 0.56$, $df = 1$, $P = 0.45$). Of the 17 colonies with removal of leaf litter, 12 relocated; of the 19 colonies with no litter removal, 8 relocated ($\chi^2 = 2.95$, $df = 1$, $P = 0.09$). Because we found no significant effects of treatment upon rates of relocation, we pooled all treatments for comparisons between stationary and relocated colonies. We found that stationary and relocated colonies expressed no significant differences in the initial or final measurements of home range and nearest neighbor distance (Table IV).

To examine the stability of home range area, we compared the initial home range of colonies with their final home ranges. We found that in

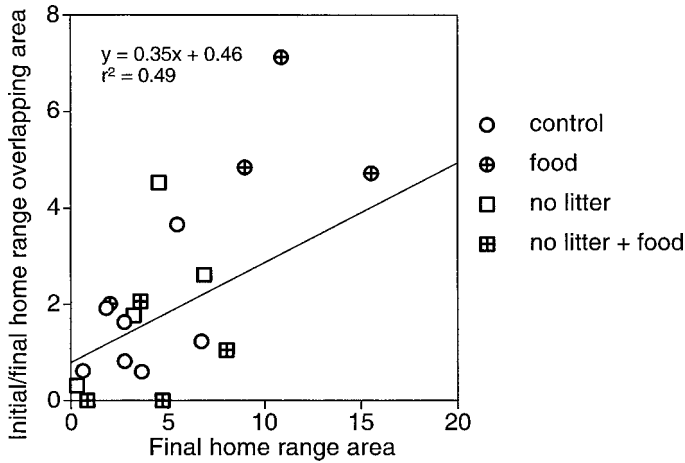


Fig. 3. The home range area overlapping in a comparison of the initial and final home ranges. By comparing the differences among the residuals of this regression, we found that the separate treatments resulted in the retention of the initial home ranges, but when coupled together, foragers shifted their home ranges to new areas during the experiment. The analysis is presented at the bottom of Table III.

colonies that had not relocated, initial home range was not a predictor of final home range, but for colonies that had relocated, initial home range around the original nest was a predictor of the area of the new home range (Figs. 4a and b).

To consider the proximity of neighborhood competitors, we compared initial nearest neighbor distances with initial and final home range areas. We found no association between initial nearest neighbor distance and

Table IV. Comparisons of Means of Four Variables Between Stationary and Relocated Colonies by *t*-Test

Source of variation	Stationary mean \pm SE (<i>N</i>)	Relocated mean \pm SE (<i>N</i>)	<i>t</i>	<i>P</i>
Initial home range area (m ²)	6.07 \pm 1.24 (10)	4.74 \pm 0.97 (16)	-0.88	0.39
Final home range area (m ²)	4.68 \pm 1.14 (15)	4.26 \pm 0.34 (11)	-0.29	0.77
Initial nearest neighbor distance (m)	1.77 \pm 0.20 (14)	1.74 \pm 0.13 (18)	-0.15	0.88
Final nearest neighbor distance (m)	2.11 \pm 0.20 (9)	2.10 \pm 0.40 (9)	-0.02	0.99

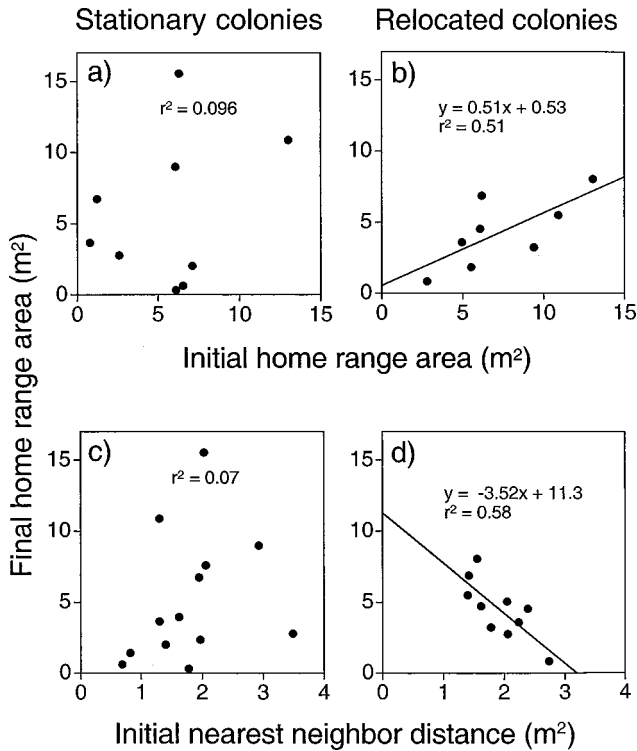


Fig. 4. Final home range area changes in response to initial conditions. The home range area is predicted by initial conditions only after the colonies relocate (b and d); if the colonies are stationary, the home range area is not associated with initial conditions (a and c).

initial home range area ($r^2 = 0.02$; ANOVA, $F = 0.48$, $df = 1,23$, $P = 0.50$). For the stationary colonies that had not relocated during our observation period, we found that initial nearest neighbor distance also failed to predict final home range area, but we found that initial home range area predicts final home range area in ants that relocated their nests (Figs. 4c and d).

We observed one event of a nest relocation caused by predaceous army ants, although epigeaic army ants were not in our research sites during the time of our experiment. In a separate location at least 200 m from our treatment plots, we observed an army ant (*Eciton hamatum*) raid upon an *A. araneoides* nest. Army ants entered the soil nest and removed brood, while *A. araneoides* workers were running away from the nest carrying brood into the leaf litter. The next day, the nest was unoccupied.

DISCUSSION

Aphaenogaster araneoides responds to changes in leaf litter abundance in a different fashion than it responds to changes in food abundance. Whereas more foragers are sent out in response to an increase in food abundance, foragers will spend more time searching for food in shallow of leaf litter regardless of food abundance. Because food abundance and litter abundance are normally coupled with one another, we infer that ant colonies send out relatively few foragers when resources are scarce, but these foragers have longer foraging trips. This finding helps explain an earlier finding that home range area was not associated with resource abundance (McGlynn *et al.*, 2002). While this species does not appear to change the size of the area it searches when resources are scarce, the frequency and duration of foraging trips change. Our results are consistent with the notion that colony-level responses to the food environment are the result of interacting individuals with flexible responses to their foraging environment (Herbers *et al.*, 1985; Dejean *et al.*, 1993; Cassill and Tschinkel, 1999).

If home range is not predicted by resource abundance, then what are the predictors of home range area? McGlynn *et al.* (2002) found a strong correlation between home range and colony size, and that home range was independent of habitat quality. The results from the present study show that home range is quite flexible, because there was only a weak relationship between initial and final home ranges of stationary colonies over a 2-week time span. While a single snapshot in time would suggest that competition has no effect on home range area, the tight negative correlation between nearest neighbor distance prior to relocation and home range area after relocation suggests that competition causes colonies to increase home range area after experiencing increased competition. The effects of competition upon home range area that we found in this study, combined with the established positive relationship between home range area and colony size, provide a more complete picture of how home range area is determined in this species.

Why does *A. araneoides* relocate its nests? We have present five non-mutually exclusive hypotheses. First, nest relocation may be driven by neighborhood competition (DeVita, 1979). Supporting evidence comes from the change in home range areas after relocation, but the frequency of relocation was independent of any direct measure of competition or home range quality. It may be possible that the trigger for relocation is independent of competition, and the observed changes in home range reflect the nutritional status of the colony as a result of neighborhood competition. It is possible that competition with other leaf litter ant species shapes the microhabitat preferences of *A. araneoides*, but the mechanisms of microhabitat selection have yet to be studied among these species (Martin, 1998). Rissing (1988)

found that neighboring colonies with permanent nest sites competed more heavily during times of resource depletion, but in his system the competing species inhabited an environment with seasonal fluctuations in food abundance. Overall, the hypothesis that competition drives nest relocation is difficult to evaluate given the existing evidence. The effect of nearest neighbor distance on home range size after relocation suggests that neighborhood competition is a strong interaction, but we first must find out whether nest relocation is associated with changes in the environment independent of competition.

Our second hypothesis is that nest relocation is driven by local resource depletion not caused by competing ant colonies (Holway and Case, 2000). If this hypothesis is true, then the diminishing returns of foraging effort may trigger nest relocation; in this study we did not collect enough data to adequately test whether foraging effort differed among stationary and relocated colonies.

Our third hypothesis for nest relocation concerns escape from predators, parasites, and parasitoids (Gordon, 1992). While we observed nest abandonment by *A. araneoides* during an army ant raid outside of our research plots, we observed many nest relocations in the absence of army ants. So far, our nest observations and excavations have not revealed clear evidence of parasites or parasitoids, though we have not conducted a formal survey.

The fourth hypothesis for nest relocation is a response to microclimate (Smallwood, 1982a). Smallwood (1982b) studied nest relocation in the temperate congener *Aphaenogaster rudis*. She found colonies increased nest relocation frequency in response to decreased insolation, but not in response to conspecific competition or reduced food availability. At the site of the present study, the amount of daylight penetrating to the leaf litter layer at this site is consistently between 1 and 7% of the light levels above the forest canopy, except within treefall gaps (McGlynn and Kirksey, 2000); therefore we are confident that these ants are not moving to increase insolation. It is conceivable that other abiotic factors at nest locations may be unfavorable and trigger relocation, though we have no particular candidate variable in mind. If an abiotic trigger for relocation is constant at a nest site (such as the tendency to flood), then one would expect that particular sites experience higher frequencies of relocation than other sites. One could evaluate this hypothesis by observing whether the frequency of relocation is associated with particular colonies or with particular nest sites.

The last hypothesis is that colonies outgrow their nests and locate new nests, as growing hermit crabs seek out new shells (Banschbach and Herbers, 1999). Because empty nest sites are frequently available, there are opportunities for colonies to occupy larger nests. This hypothesis assumes that nest enlargement is not possible, or is more costly than relocation.

The results from our experiment are insufficient to critically evaluate the hypotheses for the causes of nest relocation in *A. araneoides*. One might suspect that the derived phenomenon of nest relocation would readily demonstrate its adaptive advantage upon investigation. However, the costs of relocation are not known and in many cases the benefits of relocation are unclear. It is our opinion that the difficulty in finding the benefits of nest relocation is not caused by the shortcomings of experimental design. Instead, we simply lack the foundation of natural history and sociometry available for the interpretation of our results (Tschinkel, 1991). Once we learn more about the natural history of *A. araneoides* and the overall pattern of nest relocation, it may be possible to design experiments to understand why nest relocation has evolved.

ACKNOWLEDGMENTS

This research was supported by USD College of Arts and Sciences Faculty Research Grant and Enhanced Student–Faculty Interaction Fund awards to T.P.M. and USD Summer Undergraduate Research Experience awards to M.S.K. and M.D.S. Tierney Berger assisted with fieldwork. We thank OTS and the staff of La Selva Biological Station. We thank Amelia Chapman, Bonnie Ripley, and anonymous reviewers for assistance with analyses and composition.

REFERENCES

- Abrams, P. A. (1991). Life history and the relationship between food availability and foraging effort. *Ecology* **72**: 1242–1252.
- Banschbach, V. S., and Herbers, J. M. (1999). Nest movements and population spatial structure of the forest ant *Myrmica punctiventris* (Hymenoptera: Formicidae). *Ann. Entomol. Soc. Am.* **92**: 414–423.
- Bourke, A. F. G. (1999). Colony size, social complexity and reproductive conflict in social insects. *J. Evol. Biol.* **12**: 245–257.
- Bourke, A. F. G., and Franks, N. R. (1995). *Social Evolution in Ants*, Princeton University Press, Princeton, NJ.
- Brown, M. J. F. (1999). Nest relocation and encounters between colonies of the seed-harvesting ant *Messor andrei*. *Insectes Soc.* **46**: 66–70.
- Byrne, M. M. (1994). Ecology of twig-dwellings ants in a wet lowland tropical forest. *Biotropica* **26**: 61–72.
- Cassill, D. L., and Tschinkel, W. R. (1999). Effects of colony-level attributes on larval feeding in the fire ants, *Solenopsis invicta*. *Insectes Soc.* **46**: 261–266.
- Chesson, P., and Rosenzweig, M. (1991). Behavior, heterogeneity, and the dynamics of interacting species. *Ecology* **72**: 1187–1195.
- Cox, G. W. (1985). The evolution of avian migration systems between temperate and tropical regions of the new world. *Am. Nat.* **126**: 451–474.

- Dejean, A., Beugnon, G., and Lachaud, J. (1993). Spatial components of foraging behavior in an African ponerine ant, *Paltothyreus tarsatus*. *J. Insect Behav.* **6**: 271–285.
- De Vita, J. (1979). Mechanisms of interference and foraging among colonies of the harvester ant *Pogonomyrmex californicus* in the Mojave Desert. *Ecology* **60**: 729–737.
- Diniz, J. L. M., Brandão, C. R. F., and Yamamoto, C. I. (1998). Biology of *Blepharidatta* ants, the sister group of the Attini: A possible origin of fungus-ant symbiosis. *Naturwissenschaften* **85**: 270–274.
- Durou, S., Lauga, J., and Dejean, A. (2001). Intensive food searching in humid patches: Adaptation of a myrmicine ant to environmental constraints. *Behaviour* **138**: 251–259.
- Forward, R. B., Jr., and Hettler, W. F., Jr. (1992). Effects of feeding and predator exposure on photoresponses during diel vertical migration of brine shrimp larvae. *Limnol. Oceanogr.* **37**: 1261–1270.
- Gordon, D. M. (1991). Variation and change in behavioral ecology. *Ecology* **72**: 1196–1203.
- Gordon, D. M. (1992). Nest relocation in harvester ants. *Ann. Entomol. Soc. Am.* **85**: 44–47.
- Herbers, J. M., Adamowicz, S. C., and Helms, S. D. (1985). Seasonal changes in social organization of *Aphaenogaster rudis* (Hymenoptera: Formicidae). *Sociobiology* **10**: 1–16.
- Holldobler, B., Oldham, N. J., Morgan, E. D., and König, W. A. (1995). Recruitment pheromones in the ants *Aphaenogaster albisetosus* and *A. cockerelli* (Hymenoptera: Formicidae). *J. Insect Physiol.* **41**: 739–744.
- Holway, D. A., and Case, T. J. (2000). Mechanisms of dispersed central-place foraging in polydomous colonies of the Argentine ant. *Anim. Behav.* **59**: 433–441.
- Kaspari, M. (1993). Body size and microclimate use in Neotropical granivorous ants. *Oecologia* **96**: 500–507.
- Kaspari, M. (1996). Testing resource-based models of patchiness in four Neotropical litter ant assemblages. *Oikos* **76**: 443–454.
- Kaspari, M. (2000). A primer in ant ecology. In Agosti, D., Majer, J., Alonso, E., and Schultz, T. (eds.), *Ants: Standard Methods for Measuring and Monitoring Biodiversity*, Smithsonian Institution Press, Washington, DC, pp. 9–24.
- Levings, S. C., and Franks, N. R. (1982). Patterns of nest dispersion in a tropical ground ant community. *Ecology* **63**: 338–344.
- Levings, S. C., and Windsor, D. M. (1984). Litter moisture content as a determinant of litter arthropod distribution and abundance during the dry season on Barro Colorado Island, Panama. *Biotropica* **16**: 125–131.
- Longhurst, C. P., and Howse, E. (1979). Foraging, recruitment and emigration in *Megaponera foetens* (Fab.) (Hymenoptera: Formicidae) from the Nigerian Guinea savanna. *Insectes Soc.* **26**: 204–215.
- Martin, T. E. (1998). Are microhabitat preferences of coexisting species under selection and adaptive? *Ecology* **79**: 656–670.
- McCoy, E. D., and Kaiser, B. W. (1990). Changes in foraging activity of the southern harvester ant *Pogonomyrmex badius* (Latreille) in response to fire. *Am. Midl. Nat.* **123**: 112–123.
- McDade, L. A., and Hartshorn, G. S. (1994). La Selva Biological Station. In McDade, L. A., Bawa, K. S., Hespeneide, H. A., and Hartshorn, G. S. (eds.), *La Selva: Ecology and Natural History of a Neotropical Rain Forest*, University of Chicago Press, Chicago, pp. 6–14.
- McGlynn, T. P., and Kirksey, S. E. (2000). The effect of food presentation and microhabitat upon resource monopoly in a ground-foraging ant (Hymenoptera: Formicidae) community. *Rev. Biol. Trop.* **48**: 629–642.
- McGlynn, T. P., Hoover, J. R., Jasper, G. S., Kelly, M. S., Polis, A. M., Spangler, C. M., and Watson, B. J. (2002). Resource heterogeneity affects demography of the Central American ant *Aphaenogaster araneoides*. *J. Trop. Ecol.* **18**: 231–244.
- Morales, M. A., and Heithaus, E. R. (1998). Seed dispersal mutualism shifts sex ratios in colonies of the ant, *Aphaenogaster rudis*. *Ecology* **79**: 739.
- Powell, R. A., and Mitchell, M. S. (1998). Topographical constraints and home range quality. *Ecography* **21**: 337–341.
- Rissing, S. W. (1988). Dietary similarity and foraging range of two seed-harvester ants during resource fluctuations. *Oecologia* **75**: 362–366.

- Smallwood, J. (1982a). Nest relocations in ants. *Insectes Soc.* **29**: 138–147.
- Smallwood, J. (1982b). The effect of shade and competition on relocation rate in the ant *Aphaenogaster rudis*. *Ecology* **63**: 124–134.
- Smallwood, J., and Culver, D. C. (1979). Colony movements of some North American ants. *J. Anim. Ecol.* **48**: 373–382.
- Soares, S. M., and Schoereder, J. H. (2001). Ant-nest distribution in a remnant of tropical rainforest in southeastern Brazil. *Insectes Soc.* **48**: 280–286.
- Tschinkel, W. R. (1991). Insect sociometry, a field in search of data. *Insectes Soc.* **38**: 77–82.
- Tsuji, K. (1988). Nest relocations in the Japanese queenless ant *Pristomyrmex pungens* Mayr (Hymenoptera: Formicidae). *Insectes Soc.* **35**: 321–340.