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# Resource heterogeneity affects demography of the Costa Rican ant *Aphaenogaster araneoides*

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ABSTRACT. How do animals respond to an unpredictably heterogeneous environment? Ants foraging in the leaf litter of tropical wet forests experience unpredictably fluctuating food resources. To study how an ant species responds to these changes, foragers were tracked to determine home ranges of 51 colonies of *Aphaenogaster araneoides*, in three sites in a Costa Rican tropical wet forest. Of these colonies 16 were excavated to measure colony size, colony growth, and reproductive investment. These demographic variables were compared with two measures of home range quality: leaf litter dry weight and mass of arthropods. Home range areas of colonies were highly correlated with colony size, and moderately correlated with resource abundance. Colony growth was independent of colony size, as is found in other ants in unpredictable environments. The growth of colonies was closely associated with resource abundance. Production of the male reproductive caste was closely tied to the size of a colony rather than growth, but male production in slow-growing colonies was limited. Colonies foraging within high-quality environments grew at a faster rate, but reproduction was mainly correlated with colony size. Furthermore, it was found that the frequency of foragers in long-term treatment plots with supplemental food and reduced leaf-litter quality was not significantly different from the frequency of foragers in control plots. This rainforest ant does not modify its home range areas in response to poor environments, and as a result, small-scale environmental heterogeneity strongly determines growth and reproduction.

KEY WORDS: colony size, foraging, home range, leaf litter, rain forest, resource limitation, territory

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## INTRODUCTION

How do animals change their home ranges, growth, and reproduction when times of scarcity and high productivity do not change predictably within the seasons? In several tropical environments such as coral reefs (Ebersole 1980), rain-forest canopies (Rodgers & Kitching 1998) and rain-forest leaf litter (Kaspari 1996a, b; Levings & Windsor 1984), resource availability is unpredictable. In these environments one may predict that home range sizes are correlated with resource quality, but this is not the case for many animals that maintain large home ranges even when resources are plentiful (Carpenter 1987). The effect of food variability on optimal home ranges is pronounced, and depends upon the cost of maintaining the home range (McNair 1987). What remains to be understood is how animals with an unpredictable resource base control their home ranges.

Ants are arguably the most abundant animals on the planet, with the greatest abundance found in tropical ecosystems (Wilson 1987). We know much more about the ecology of temperate ants than tropical ants (Gordon & Kulig 1996, Ryti & Case 1986, 1992; reviews by Carroll & Janzen 1973, Hölldobler & Wilson 1990); and ecological comparisons between tropical and temperate ants are not very informative. In temperate environments, colonies often grow quickly and shift energy towards sexual reproduction after reaching a threshold size. However, Kaspari (1996a, b) found that the onset of tropical leaf-litter ant reproduction is often independent of colony size. McGlynn (1999) found that tropical leaf-litter ant colonies increase reproduction in response to supplemental food regardless of colony size. The best explanation for the early onset of reproduction in tropical leaf-litter ants is that the risk of colony death probably does not decrease much as colonies grow. Established colonies in more predictable environments may have a higher fitness by delaying reproduction until the colony reaches a mature size. In many rain forests, the quantity of litter in a given location is unpredictable both temporally and spatially (Didham *et al.* 1998). Because colony growth and reproduction in this fluctuating environment are different from temperate model systems, it is important to discover whether the use of space also differs.

What is known about the effects of variation in resource quality upon home ranges mainly comes from studies of birds (Armstrong 1991). When competition is not important, some species will extend their home ranges in times of low resource availability (Ewald & Bransfield 1987). However, we do not know whether ants with fluctuating food availability also adjust their home ranges accordingly to compensate for low resource availability. Frequent flooding, branch falls and litterfall, and army-ant invasions consistently threaten tropical forest leaf-litter-foraging ants (Byrne 1994). Expanding foraging ranges in this complex environment holds greater risks than for animals in less topographically variable environments (Kaspari & Weiser 1999, Powell & Mitchell 1998).

In this study, we explore how resource quality affects demography in the

Central American leaf-litter-foraging ant *Aphaenogaster araneoides* Emery. Our goal is to determine how home range, foraging behaviour, and colony demography are affected by resource availability.

## METHODS

*Aphaenogaster araneoides* is a conspicuous soil-nesting ant that forages for food in tropical leaf litter. Throughout Costa Rica, *A. araneoides* is a very common species in undisturbed forests, though there is little known of its ecology or behaviour. While it does not defend absolute territories against other species, it will fight for quality foods (McGlynn & Kirksey 2000). There are no other published reports on the behaviour or ecology of this species to our knowledge.

We chose three locations to study the biology of *A. araneoides*. All sites were located in old-growth tropical wet forest at La Selva Biological Station in the Caribbean lowlands of Costa Rica. La Selva receives *c.* 4 m of rain annually (McDade & Hartshorn 1994). We performed this component of the study during May–June 2000. At each of the three sites, we set up a 10-m × 10-m plot.

According to the La Selva trail system, site 1 was located 5 m south of the 200 m mark on the Camino Experimental Sur. Site 2 was located 50 m east of the 650 m mark on the Camino Circular Cercano. Site 3 was located 10 m north of the 220 m mark of the Camino Circular Lejano. Sites 1 and 3 were on alluvial soils, while site 2 was on volcanic soil. We compared the light environment of the three plots by creating a 2-m sampling grid at each site containing 36 points, and estimated canopy cover over 1 m with a spherical densiometer. We also compared understorey vegetation (under 1 m in height) by ranking sampling points into three categories: heavy cover (> 70%), medium cover (30–70%), or light cover (< 30%).

We mapped the colonies and their home ranges by marking the movements of foragers with wire flags placed in the ground. We hand-fed foragers bits of food small enough to be carried by a single forager. After accepting the food items, the foragers always returned directly to their nests. We fed them either cream filling from biscuits or oil-packed tuna to avoid saturating colonies with one type of food. By locating and following foragers rather than using baits, we were able to track the normal home ranges of the ants. In many cases, we observed ants carrying naturally occurring prey items, which were other leaf-litter arthropods representing a wide variety of taxa, including Coleoptera, Diptera, Odonata and Orthoptera. We also tracked foragers leaving their nest and marked the furthest extent of their foraging trips. We exhaustively searched for nests and home ranges for 7 d. Plots were considered to be complete when home ranges remained consistent after 10 person-h searching during times of active foraging. We spent approximately 70 person-h in each plot searching for nests and home ranges. We excluded home ranges from our analyses if less than ten foragers were used to determine the home range of a

nest, or if the home range extended more than 2 m outside our plots, where we did not search intensively.

We collected leaf litter from the home ranges of colonies by removing all decomposing leaves, twigs, seeds, seed pods, and organic material, though we did not collect wooden debris. We extracted arthropods from the leaf litter using Berlese funnels under 25 W bulbs for 48 h, with animals collected in 95% ethanol. We measured arthropod mass to estimate prey density. The dry mass of the litter arthropods was measured on an electronic balance to 0.01 g accuracy. The leaf-litter samples were placed in drying ovens at 70 °C for 24 h after arthropod extraction, and then were weighed to 0.01 accuracy on an electronic balance.

We completely excavated colonies to gather demographic information including colony size, growth, and the number of reproductive caste members within the colonies. We calculated colony growth as the number of worker pupae divided by the total number of workers (as in Kaspari 1996a). We arbitrarily selected site 3 for the emphasis of nest collections to increase our understanding of fine-grain spatial relationships. In addition to collecting 11 nests at site 3, we collected two colonies at site 1 and three colonies at site 2, for a total of 16 colonies among the three sites. Sample sizes for comparisons between demography and environmental variables were smaller because we lacked environmental data for some of the excavated colonies, resulting from unintentional disturbance of the leaf-litter during the experiment. During the time we were excavating colonies, there were no mating flights of this species to our knowledge; thus we can reliably compare the number of males among the colonies. We started excavations by removing all workers in the entrance, and chased many individuals out of the nests before we used forceps and a trowel to excavate the nest. Workers and brood were collected from within the nest, and as they exited the nest opening. We removed all soil around the nest until we were confident that the entire nest was collected. We counted the contents of the nest and identified all adult castes and brood. Colonies were stored at −20 °C in 95% ethanol at the University of San Diego.

We addressed the relationship between food availability and forager abundance by collecting all stray foraging ants within 1-$m^2$ food-supplementation and physical-disturbance plots over a period of 4 mo, between January and May 1997. We created 300 1-$m^2$ plots randomly assigned to controls and four treatments: clumped food supplementation, diffuse food supplementation, removal of leaf litter, and trampled leaf litter. Both food treatments received approximately 5 g of *Nastutitermes corniger* termites, applied every 2 d. Termites were collected directly from arboreal carton nests at La Selva, then frozen in a −70 °C freezer. Termites were lightly coated with vegetable oil to attract a wide variety of foraging ants in the leaf-litter community. In the clumped food plots, termites were placed in a single pile in an arbitrarily selected location inside a 20-cm circle located at the centre of the plot. In the diffuse food plots,

the same quantity of food provided in the clumped food plots was distributed equally among four quarters of the plot. In the trampled plots, the leaf litter within the plots was trampled at weekly intervals with ten footsteps by a researcher wearing rubber boots. In the leaf-litter-removal plots, approximately 3/4 of the leaf litter within the plot was removed at the start of the experiment. Throughout the study, *A. araneoides* workers were observed transporting the supplemental food back to their nest several times within the treatment plots. We collected all of the foraging ants within the plots between 08h00 – 10h00.

## RESULTS

We compared the spatial coverage of home ranges within 100-$m^2$ sites by determining the presence or absence of a home range at 36 points located on a 2-m sampling grid. The home ranges in site 3 covered more area than sites 1 and 2 (site 1: 6 of 36 points were within a home range; site 2, 5 of 36; site 3, 20 of 36; $\chi^2 = 20.3$, df = 2, $P < 0.0001$). While home ranges were generally non-overlapping and not adjacent, the dense home ranges in site 3 occasionally overlapped on the edges while this was never the case in sites 1 and 2.

The sites had small yet significant differences in canopy cover. The mean cover values in the sites were site 1, 91.3%; site 2, 92.3%; site 3, 92.5% (Kruskal–Wallis test, H = 6.36, df = 2, $P < 0.05$). The level of understorey cover also differed among sites, with high, medium, and low cover in sites 1, 2, and 3, respectively as 0, 18, 18; 2, 14, 20; 2, 24, 10 ($\chi^2 = 6.24$, df = 2, $P < 0.05$; the four high understorey datapoints were excluded from the analysis to meet the requirements of the $\chi^2$ test). Despite the differences in understorey cover among the sites, the frequencies of understorey cover at the nest sites among the sites were equivalent (site 1: 2 high, 12 medium, 4 low; site 2: 1, 8, 4, site 3: 0, 15, 7; $\chi^2 = 0.29$, df = 2, $P = 0.87$, excluding three high-cover datapoints to meet the requirements of the $\chi^2$ test). We compared the two measures of home range quality. Because arthropod mass and litter mass were highly correlated ($r^2 = 0.62$; ANOVA, $F = 24.4$, df = 1, 15; $P < 0.001$), we used multiple regressions (with arthropod mass and litter mass as independent variables) to compare home range quality with colony demographics.

### *Demography*

Among the 16 excavated colonies, the number of workers ranged from 55 to 235 (mean = 123.0; SD = 50.9). All but three of the colonies contained a single ergatoid queen. One colony contained two queens, and two colonies lacked queens. Because the queens closely resembled workers, it is likely that the two missing queens were removed for a separate study without detection. The queens are identified by slightly enlarged gasters and three whitish ocelli. Social structure and the phenology of growth and reproduction in this species is currently under investigation.

*Were home ranges overlapping?*

The degree of home range overlap in site 3 was slight, and there was absolutely no overlap in sites 1 and 2. In site 3 (Figure 1), home range areas were larger than in sites 1 and 2 (site 1: mean = 1.23 $m^2$ (SE = 0.29); site 2: 1.48 (0.30); site 3: 3.36 (0.71); ANOVA, F = 5.14, df = 2, 45; $P < 0.01$; Bonferroni post-hoc comparisons $P < 0.05$).

As the study progressed during and after home range mapping, we detected 13 out of 35 nests among all three plots that moved from one nest location to a very close but separate location, usually within 0.5 m of the original nest. In two of these cases, we observed the transfer of brood above ground from one nest to another. We had previously removed individuals from eight of these 13 colonies for a separate study. The proportion of our nest disturbances was not significantly different from the proportion of the total number of relocated

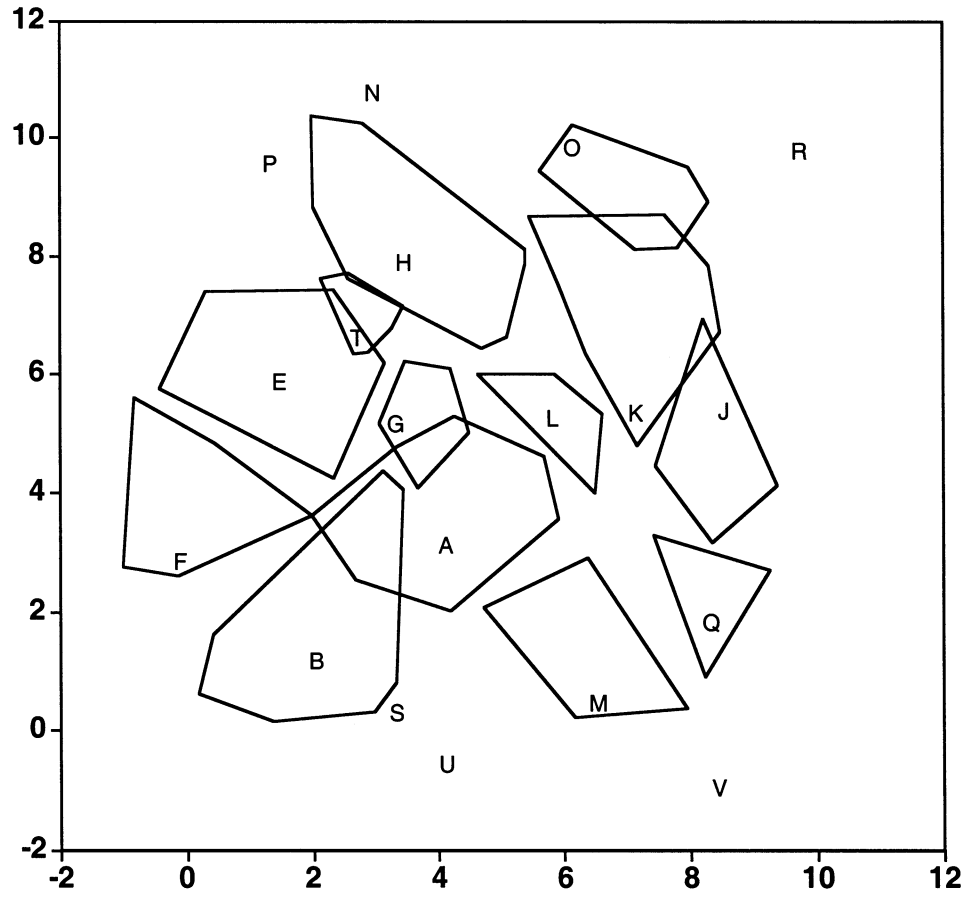


Figure 1. Map of site 3. Letters indicate the locations of nests. Nests without mapped home ranges extended significantly out of the plot and were not completely mapped. Eleven of these colonies were excavated.

nests ($\chi^2 = 2.29$, df = 1, ns), suggesting that nest movements were independent of our sampling. We did not observe any change in the home ranges of colonies after relocation, though we did not systematically quantify these movements; workers foraged in the same locations before and after nest movements. While these ants moved into an unoccupied location, the new nests were in pre-existing holes with no signs of new excavation activity. Nest movements were complete, as there was no activity in the new nest prior to movement, or in the initial nest after movement.

*How were home range and habitat quality associated with colony size?*

We compared colony size against three environmental variables: home-range area, weight of litter within the home range, and the mass of arthropods extracted from the litter within the home range. We used the total numbers of workers in the colony to measure colony size. Colony size was highly correlated with the size of the home range (Figure 2). Even though home-range size and home-range quality were positively correlated (multiple regression ANOVA, $F = 12.9$, df = 2, 14, 16; $P < 0.001$; $r^2 = 0.59$), the relationship between home-range size and home-range quality was more pronounced. The weaker correlation between colony size and home-range quality resulted from one to three outliers of larger colonies with large home ranges of poor quality. These outlying colonies are important because they reinforce the observation that colony size is a better predictor of home range, regardless of resource abundance.

*How were home range and habitat quality associated with colony growth?*

We found that colony growth was most closely associated with the quality of the home range, rather than the size of the home range (Figure 3). There was a non-significant trend associating home-range area with colony growth, but the significant relationship with habitat quality was a better estimator of colony growth (Figure 3).

*Did large colonies or fast-growing colonies reproduce?*

Colony growth was not linearly associated with the production of the male sexual caste, but colony size was significantly correlated with male production (Figure 4). The phenology of the sexual-caste production is still unknown in this species. Like many temperate ant species, *A. araneoides* produced most of its sexual caste in mature colonies. However, slow-growing colonies were less likely to produce sexuals than fast-growing colonies. Like other tropical litter ant species, the production of sexuals occurred in small-sized colonies, but these individuals are a small proportion of the total number of new individuals produced within the colonies. There was no clear shift of energetic effort from colony growth into sexual reproduction as colonies grew, because colony growth was absolutely independent of colony size (Figure 5).

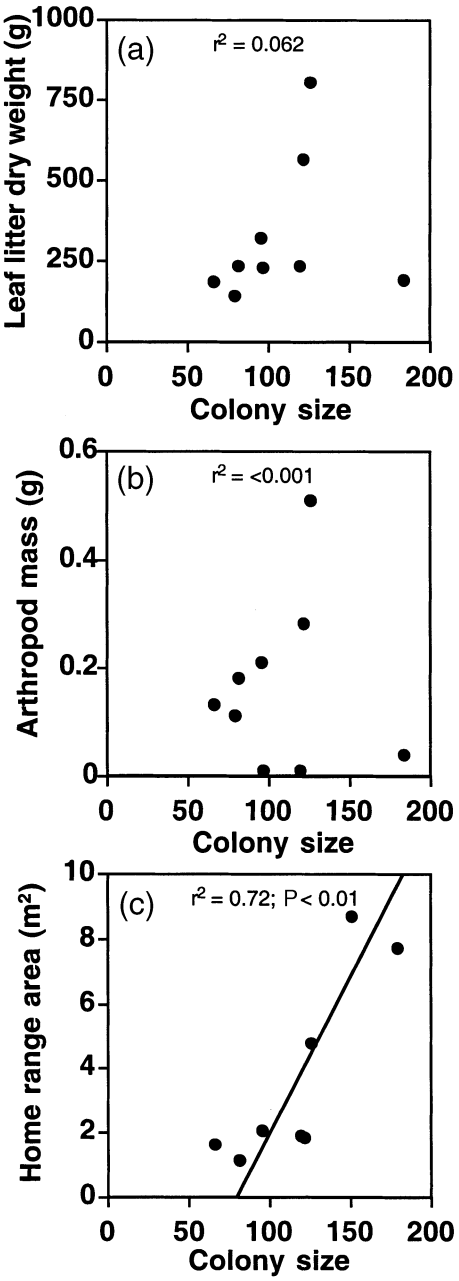


Figure 2. Colony size compared against environmental variables. Colony size is not associated with litter weight (a) and arthropod mass (b) (multiple regression ANOVA, $F = 1.31$, df = 2, 6, 8; $P = 0.34$; $r^2 = 0.072$). Colony size and home range (c) are highly correlated (ANOVA, $F = 6.95$, df = 1, 6; $P < 0.05$; $r^2 = 0.717$).

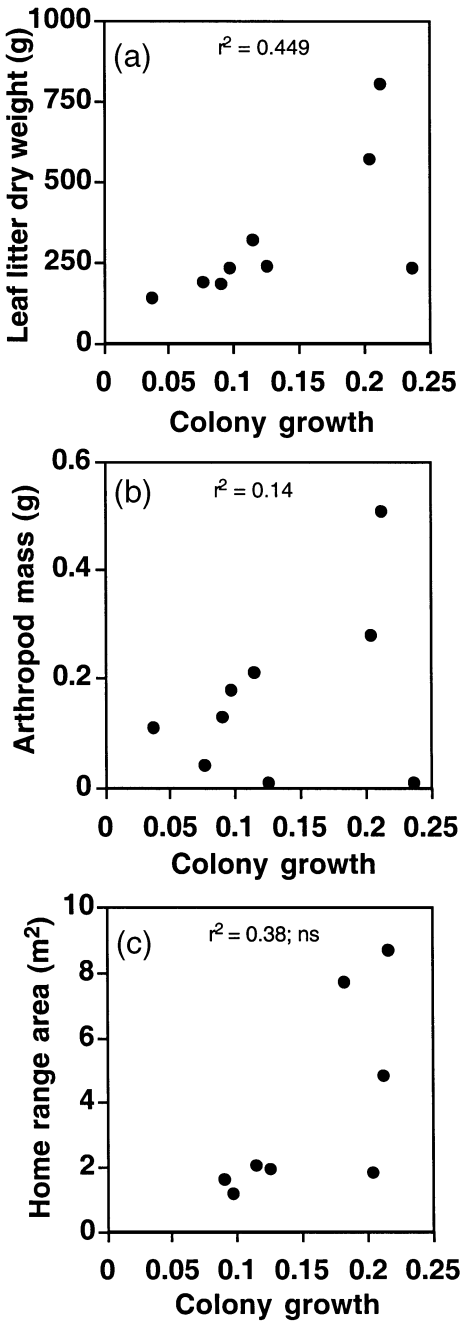


Figure 3. Colony growth compared against environmental variables. The litter weight (a) and arthropod mass (b) are correlated with growth rate (multiple regression ANOVA, $F = 7.735$, df = 2, 6, 8; $P < 0.05$; $r^2 = 0.63$), with a high univariate correlation for litter weight. Despite a moderate correlation, growth was not linearly associated with home range (c) (ANOVA, $F = 4.33$, df = 1, 12; $P = 0.08$; $r^2 = 0.38$).

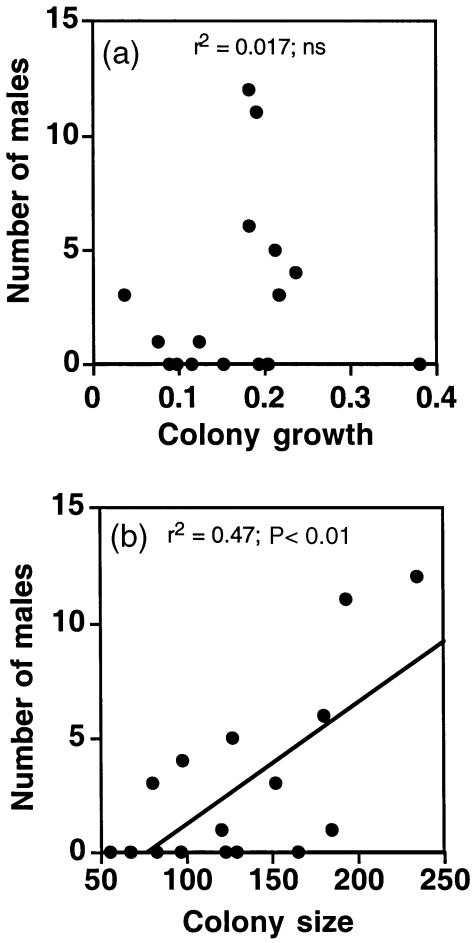


Figure 4. Male production compared against colony size and colony growth. Male production is not linearly associated with colony growth rate (a) (ANOVA, F = 0.25, df = 1, 14; P = 0.63), but colony size is a predictor of the number of males found within a colony (b) (ANOVA, F = 12.51, df = 1,14; P < 0.01). There was no significant linear relationship between growth and male production even after an outlying variate was removed from the analysis.

*Did forager abundance change with long-term increases or decreases in resources?*

Foragers did not occur at a significantly higher frequency in the food-supplementation plots, nor at a lower frequency in the plots with reduced leaf-litter volume or biomass (Table 1). The frequency of *A. araneoides* was 6.7% in the control plots, and 12.5% among the two food-supplementation treatments, but this was not a significant difference. The removal of leaf litter had no effect upon the frequency of foragers compared with control plots; these results are consistent with the stability of home ranges based on colony size, rather than resource abundance. It may be possible that the treatments had a slight effect that could not be detected, despite a sample size of 60 plots per treatment, because the probability of finding foragers was relatively low for all treatments.

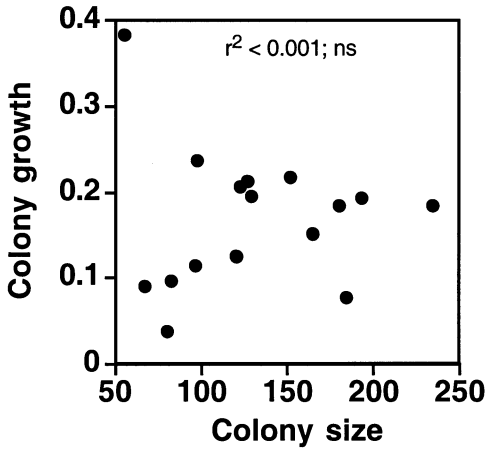


Figure 5. Rates of growth among nests of different sizes. Colony growth was independent of colony size (ANOVA, F = 0.019, df = 1, 14; P = 0.89).

Table 1. The frequency of *A. araneoides* foragers detected within plots subjected to environmental changes over a period of 4 mo. The frequency of *A. araneoides* in the treatment plots was not different from the control plots ($\chi^2 = 2.14$, df = 4, P = 0.71).

| Treatment | n | Plots with *A. araneoides* foragers |
|---|---|---|
| Control | 60 | 4 |
| Food supplementation – clumped | 60 | 7 |
| Food supplementation – diffuse | 60 | 8 |
| Trampled plots | 60 | 5 |
| Leaf litter removal | 60 | 4 |

## DISCUSSION

Habitat quality is the best estimator of growth rate in this litter-foraging species. Large colony size is no assurance for future colony maintenance and growth, as the abundance of prey items in leaf litter exerts a strong influence on colony success. The quality of a home range is dependent upon the quantity of leaf litter, which is a patchy resource that changes throughout the life of a colony. Colonies located in patches of reduced leaf litter slow their growth rate, while colonies located in deep leaf litter grow at a much greater rate, independent of colony size. *Aphaenogaster araneoides* did not extend its home range in poor leaf litter, even though in some cases there was a large area that remained unexplored by these colonies. While colony growth is a function of the quantity of litter within the home range, the home range itself is simply determined by the size of the colony.

What can explain the failure of *A. araneoides* to increase its home range when few resources are available? The existing work on the ecology of tropical wet forest litter-nesting ants suggests they are quite responsive to environmental changes and do not wait to produce sexuals until colonies are large in size (Kaspari 1996a). Strict application of optimal foraging theory results in the

conclusion that this species is constrained from increasing its home ranges (e.g. Hixon 1980). Indeed, there are numerous constraints on the foraging activity of tropical wet-forest leaf-litter ants, especially leaf-litter humidity (Kaspari 1993). While it is no surprise that colonies with more ants forage greater distances (Figure 3), this fact reduces the power of environmental constraints to explain the failure of resource-poor colonies to increase their home ranges. The foraging distance of workers does not appear to be influenced by the amount of energy stored within colonies, because fast-growing colonies and slow-growing colonies of the same size have equivalent home ranges.

There are several possibilities to explain the close correlation between colony size and home-range size. It is quite possible that the behaviours tying home range with colony size are phylogenetically constrained. The genus *Aphaenogaster* is far more diverse in temperate North America, while our study site has only one species of *Aphaenogaster*. It is possible that *A. araneoides* was recently derived from temperate ancestors. Unfortunately, no species-level phylogenies of *Aphaenogaster* are available. An attractive explanation for the inability of *A. araneoides* to respond to the rain-forest environment is that its ancestors were subject to the selection pressures of seasonal resource availability rather than unpredictably fluctuating resources, and this species has not yet evolved foraging strategies that match its rain-forest environment. Another more adaptive explanation is that colonies of *A. araneoides* could maintain large home ranges to prevent large competitors from establishing colonies near their own nests. Even though the size of the home range may not vary as resources change, the foraging strategies may change to increase the efficiency of capturing prey (Durou *et al.* 2001). These hypotheses are consistent with our data on the equivalent frequency of encountering foragers in food-supplementation and leaf-litter-removal plots. Other species in this litter environment are capable of changing nesting and foraging behaviours in response to resource availability. For instance, McGlynn (1999) found that a typically arboreal *Crematogaster* species moved its colonies into leaf litter in response to food supplementation.

Leaf-litter weight showed a higher correlation with colony growth than with arthropod mass (Figure 3). There is a good reason to expect litter quantity to show a more robust association with growth. Collecting arthropods presents a momentary measure of potential prey items that fluctuates as the litter becomes wet and dries out (Levings & Windsor 1984). Because litter arthropods are more mobile than the litter itself, the mass of arthropods probably fluctuates at a faster rate than litter quantity. A single sample of arthropod mass does not accurately represent the recent history of the ant colonies, but the fluctuations in litter quantity are as slow as the fall of new litter and decay of old litter. Also, arthropod mass is less effective at estimating colony growth because the ant colonies already consumed some of the arthropods missing from our samples.

It is difficult to understand why nest movements occurred, as they moved

very short distances and did not change home ranges. Because leaf litter is so critical to growth, movements to higher quality patches would be advantageous. It is useful to consider that litter-nesting species in this forest also frequently move their nests (Byrne 1994), as well as a temperate *Aphaenogaster* species (Smallwood 1982). We found that *A. araneoides* moved its soil nest sites at a rate similar to that found in litter-nesting species (Byrne 1994). Authors have surmised that the frequent nest movement by leaf-litter ants was a response to the flooding or deterioration of nests in decaying twigs and seed pods (Byrne 1994, Kaspari 1996b). Other potential explanations included escape from predatory army ants and the location of better food resources. Our observations do not support the ideas that nest movements are caused by deteriorating nest quality, or army-ant predation. While we were collecting colonies, we caused disturbances at nest entrances that would often cause several individuals to flee the nest with brood and return to the nest within several seconds. Longino (www.evergreen.edu/ants) has observed the same phenomenon. Though these anecdotes support the case that physical disturbances could result in nest movements, several colonies that we did not disturb also moved into new nest locations as well. It may be possible that nest movements resulted in improved resources within the core area of the home range, even though the colonies maintained the same home ranges.

While ants are often considered to be the masters of adaptive resource exploitation, we have found that *A. araneoides* uses a fixed-home-range strategy in a highly variable environment. As we learn more about the foraging behaviour, niche breadth, and reproductive biology of this species, we will be able to gain more insights from the interaction between life history and environmental heterogeneity. Because this species inhabits a diverse community of ants presenting a variety of competitive strategies, exploring how *A. araneoides* interacts with other species may suggest the costs and benefits of its life history.

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