

Ants on the Move: Resource Limitation of a Litter-nesting Ant Community in Costa Rica¹

Terrence P. McGlynn²

Department of Biology, University of San Diego, 5998 Alcalá Park, San Diego, California 92110, U.S.A.

ABSTRACT

The leaf litter of tropical wet forests is replete with itinerant ant nests. Nest movement may help ants evade the constraints of stress and disturbance and increase access to resources. I studied how nest relocation and environmental factors may explain the density, size, and growth of leaf litter ant nests. I decoupled the relationships among litter depth, food abundance, and nest availability in a 4-mo manipulation of food and leaf litter in a community of litter-nesting ants in a lowland wet forest in Costa Rica. Over 4 mo, 290 1 m² treatment and control plots were sampled without replacement. Nest densities doubled in response to food supplementation, but did not decrease in response to litter removal or stress (from litter trampling). The supplementation of food increased the utilization of less favored nesting materials. In response to food supplementation and litter trampling, arboreal ants established nests in the litter, and growth rates of the most common ants (*Pheidole* spp.) increased. Colony growth was independent of colony size and growth rates of the most abundant ants. In general, I conclude that litter-nesting ant density is driven primarily by food limitation, that nest relocation behavior significantly affects access to resource and the demographic structure of this community, and that nest fission may be a method to break the growth–reproduction trade-off.

RESUMEN

La hojarasca de bosques húmedos tropicales está repleta de nidos itinerantes de hormiga. El movimiento de nido puede ayudar a las hormigas a evadir las limitaciones producidas por tensión y perturbación y a la vez aumentar el acceso a recursos. Las relaciones entre la profundidad de la hojarasca, la abundancia de alimento y la disponibilidad de nido fueron desconectadas durante 4 meses debido a la manipulación de hojarasca y de alimento en un bosque húmedo bajo en Costa Rica. Durante 4 meses, 290 parcelas de tratamiento y control de 1 m² fueron muestreadas sin reemplazo. Las densidades de nido doblaron en respuesta al alimento suplementario, pero no disminuyeron en respuesta a la eliminación de la hojarasca y la tensión (causada al pisotear la hojarasca). El alimento suplementario aumentó la utilización de materiales menos favorecidos para anidar. Debido al alimento suplementario y la tensión en la hojarasca, las hormigas arbóreas establecieron nidos en la hojarasca y las tasas de crecimiento de las hormigas más comunes (*Pheidole* spp.) aumentaron. El crecimiento de la colonia era independiente del tamaño de la colonia, y de las tasas de crecimiento de las hormigas más abundantes. En términos generales, se concluye que la densidad de las hormigas en la hojarasca es gobernada primordialmente por la limitación de alimento, que la conducta de trasladar nido afecta significativamente el acceso a recursos y a la estructura demográfica de esta comunidad, y que la fisión de nido puede ser un método para romper el intercambio entre crecimiento y reproducción.

Key words: competition; Costa Rica; density; leaf litter; nest relocation; *Pheidole*; resource limitation; *Solenopsis*; tropical rain forest.

IN TROPICAL RAIN FORESTS, nest relocation is a regular part of the life history of most ant species, particularly those nesting within leaf litter (Byrne 1994). When resource quality declines, ants may move their nests to patches of higher resource abundance or reduced densities of competitors. Because litter is highly patchy within the scale of ant home ranges, one might expect that nest relocation may be an important mediator of competition (McGlynn *et al.* 2004).

To date, little is known about the resources limiting litter ants, mainly because they move their nests (but see Kaspari 1996a,b). Food, nests, or territories are limiting for many species (Carroll & Janzen 1973, Ryti & Case 1992, Sanders & Gordon 2003), often observed through competitive interactions among species (Savolainen & Vespäläinen 1988, Porter & Savignano 1990, Andersen & Patel 1994, Adams & Tschinkel 1995, Tschinkel & Hess 1999, Sanders *et al.* 2003). It is difficult to determine which resources are limiting (Andersen 1995, Bestelmeyer & Wiens 1996, Morrison 1996) and hence determine density and demography of ant nests (Fernandez Escudero & Tinaut 1999, Brown & Gordon 2000, McGlynn *et al.* 2002).

In a community of ants that moves nests frequently, what regulates density and growth? Within the leaf litter environment, potential regulators include nest availability, food abundance, food distribution, and microclimate (Kaspari 1996a, Bansbach *et al.* 1997, McGlynn & Kirksey 2000, Durou *et al.* 2001). All of these variables are in turn mediated by the depth of leaf litter, which provides nests, retains humidity, and forms the foundation of the detrital food web (Moore *et al.* 2004). Manipulative experiments can decouple the natural correlations among litter abundance, food abundance, and microclimate (Levings & Windsor 1984). Even though field researchers cannot alter microclimate and natural food resources *in situ* without confounding environmental changes, manipulations of resources and microhabitat nevertheless will provide new insights into the environmental factors that limit leaf litter ants.

In this study, I use experimental manipulations to assess how food and leaf litter affect the density and demography of ants that move their nests within the leaf litter of a tropical wet forest. I created four alterations of food or leaf litter at the spatial scale of a single square meter to be sampled over 4 mo. Because ants in this community move their nests on the scale of weeks, nest relocation may be inferred by increases or decreases in nest density.

¹Received 18 February 2005; revision accepted 28 June 2005.

²Corresponding author; e-mail: tmcglynn@sandiego.edu

METHODS

This study was conducted from January to June 1997 in an old growth forest at La Selva Biological Station, Sarapiquí Canton, Heredia Province, Costa Rica. La Selva is a lowland wet tropical forest in the Caribbean Lowlands of Costa Rica, and receives *ca* 4 m of rain annually, with the majority falling in the wet season from June to December (McDade & Hartshorn 1994). The 4-ha site was near the intersection of the Camino Circular Cercano and Sendero Suroeste on the La Selva trail system. Using the La Selva GIS, the site was bounded by 1100 and 1300 on the 32° axis, and 600 and 800 on the 122° axis. I demarcated 290 plots of 1 m² size using wire flags and plastic flagging. These plot locations were at least 5 m apart and at least 20 m away from trails. In similar habitat at the same field station, Kaspari (1996b) found that 1 m² plots placed 5 m apart from one another were far enough to ensure independent sampling of leaf litter-nesting ant species. Plots were randomly assigned in equal proportion among the control and four treatment categories.

I created four treatments altering food abundance, food distribution, and leaf litter quantity and quality. I refer to these treatments as clumped food, split food, removal, and trampling. Both litter treatments caused a reduction in the depth of leaf litter, but trampling caused the destruction of potential nests and litter compaction, and removal caused a drop in prey abundance without reduction in the number of nests. Each of the food treatments received approximately 5 g (about 20 individuals) of *Nasutitermes corniger* termites, applied every 2 d. Termites were collected directly from arboreal carton nests at La Selva, and then frozen in a -20°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 center of the plot. In the split food treatments, the same quantity of food was distributed equally among four quarters of the plot. The leaf litter removal treatment was designed to increase stress, through removal of prey biomass and reducing humidity. I applied this treatment once, at the beginning of the experiment; I removed approximately three-fourths of the leaf litter from the ground, without removing any ant nests. I only removed leaf matter, without removing any twigs, sticks, nuts, seeds, or seedpods. Any leaves containing ant nests were replaced to the plot. The trampling plots received a weekly treatment, stepping firmly ten times in rubber wading boots, size 10–11 (US). When a research assistant with size 7 (US) boots stepped in the plots, she stepped 12 times, to result in an equivalent surface area subjected to trampling.

The experiment was designed to prevent any disturbance or stress upon the field colonies. Consequently, plots were sampled continuously without replacement, with collections distributed over the course of 4 mo after the start of treatments. Approximately every 2 d, one plot per treatment was sampled. I collected leaf litter ant nests from the plots using the “intensive sampling” protocol described by Bestelmeyer *et al.* (2000). In the field, all matter resting upon the ground inside the plot was collected and brought into the laboratory in plastic bags. Immediately following collection, I sorted

TABLE 1. Frequency of common nest materials among treatment plots. Nest material rarely used within control plots was used more frequently by ants in the food supplementation plots ($\chi^2 = 47.18$, $df = 28$, $P = 0.013$).

Nest material	Clumped		Split	Removal	Trampled	Total
	Control	food	food			
Diffuse	3	10	11	8	8	40
Leaf	6	25	25	14	9	79
Palm leaf or petiole	2	11	12	4	9	38
<i>Pentaclethra</i>	3	13	15	0	6	37
<i>macroloba</i> Pod						
Hard seed	3	2	11	6	4	26
Subtotal: nonwoody nests	17	61	74	32	36	220
Stick	72	78	75	48	73	346
Twig	134	172	175	114	142	737
Wood	12	15	20	13	12	72
Subtotal: woody nests	218	265	270	175	227	1155
Total	235	326	344	207	263	1375

through the leaf litter breaking every single twig, stick, nut, piece of wood, panicle, bark, and seedpod to ensure that every single litter-dwelling ant was collected. In nearly all cases, nests remained intact and all of the contents were collected into a single vial. Throughout the first month since the treatments started, I collected 80 plots, equally distributed among five treatment categories. During the second, third, and fourth months, I collected 85, 70, and 55 plots, respectively, for a total of 290 plots.

Nest materials were sorted into several categories (Table 1). “Diffuse” nests were not located in a discrete cavity and may have been enclosed between two types of materials or exposed to the surface. Leaf nests were found inside curled up leaves or between two leaves. Nests on the surface of the common dehiscent pods of *Pentaclethra macroloba* (Mimosaceae) were relatively exposed compared to other nests. “Hard seeds” represented a variety of plant taxa and were not identified. Twigs had a diameter of <1 cm, while sticks were thicker than twigs. Pieces of “wood” were noncylindrical pieces of decomposing wood that were neither sticks nor twigs. I excluded 74 nests from the contingency analysis of nest materials. The excluded nest categories included those that were so decomposed that the materials were not identifiable, and infrequently used materials, such as infructescences of the palm *Welfia regia* and the fruit capsules of *Apeiba membranacea* (Tiliaceae).

Nests were brought to the laboratory for sorting, identification, and counting of ants. I counted the number of workers, worker pupae, dealate queens, winged queens, pupal queens, males, pupal males, and larvae. For the dimorphic genus *Pheidole*, I distinguished between major and minor workers and pupae; these results are presented elsewhere (McGlynn & Owen 2002). I identified every ant to species or morphospecies, according to Bolton (1994), Longino and Hanson (1995), Longino and Cover (pers. comm.

TABLE 2. Nest frequencies per treatment sorted by functional group. Functional group composition was significantly heterogeneous among control and treatment plots ($\chi^2 = 61.89$, $df = 24$, $P < 0.0001$).

Functional group	Control	Clumped food	Split food	Removal	Trampled	Total
Arboreal	0	6	5	0	5	16
Dacotine	40	51	43	37	35	206
<i>Paratrechina</i>	2	16	20	6	8	52
<i>Pheidole</i>	114	151	164	89	128	646
<i>Solenopsis</i>	47	47	74	46	76	290
<i>Wasmannia</i>	8	19	20	12	2	61
Others	28	54	39	36	22	179
Total	239	344	365	226	276	1450

and <http://www.evergreen.edu/ants>), and Wilson (2003). I use the nest as the unit of analysis in this study, because colony boundaries could not be reliably determined by species-level identification or by queen number.

Because of high species richness, no species was sufficiently abundant (despite the collection of 1450 nests overall) to allow for meaningful species-level comparisons among the treatments, even though there were 58 plots per treatment. To facilitate comparisons of community members, I grouped species together on the bases of taxonomy and functional role in the community (Table 2). Such “functional groups” are parallel to those of Andersen (1995), Bestelmeyer and Wiens (1996), and McGlynn (1999a), and represent a reasonable approach to evaluating components of a “hyperdiverse” community. Here I list the criteria for designating functional groups. “Arboreal” consists of species that are known mainly from sampling of canopy ants and have been rarely or never observed within leaf litter, according to sampling of the Arthropods of La Selva project (www.evergreen.edu/ants). Arboreal ants included *Azteca* spp., *Crematogaster* spp., and *Pheidole christopherseni*. Members of the genera *Pyramica* and *Strumigenys* constitute the “Dacotine” group; they are generally believed to be specialized predators of arthropod microfauna (Hölldobler & Wilson 1990, Dejean 1991). The two abundant genera *Pheidole* and *Solenopsis* were each designated to their own functional groups; little is known about their natural history and there was little basis for analyzing these genera by species groups. Two species, sole representatives of their genus in this study, have been assigned to their own groups: *Paratrechina steinheli* and *Wasmannia auropunctata*. The foraging ecology of these two species differs from the other litter-nesting species. *P. steinheli* is an opportunist that does not defend food resources to which it recruits (McGlynn & Kirksey 2000). *W. auropunctata* has a diffuse colony structure and is an invasive species in other parts of the world (LeBreton *et al.* 2003). Some taxa were relatively uncommon or not primarily litter-nesting species and were simply excluded from analyses other than those of total nest density. These species included: two *Camponotus*, one *Adelomyrmex*, one *Megalomyrmex*, two *Gnamptogenys*, one *Anochetus*, two *Discothyrea*, four

Cyphomyrmex, one *Cerapachys*, and over two dozen *Hypoponera* nests that could not be completely collected. A complete list is available in another publication (McGlynn 1999b).

After counting the contents of each identified nest, I measured demographic variables for each colony. Colony size is defined by the number of adult workers. Growth may be defined by the ratio of pupal workers to adult workers (as in Michener 1964, Kaspari 1996b, McGlynn & Owen 2002, McGlynn *et al.* 2004). Reproduction is the sum of pupae and adults of reproductive castes.

Statistical tests were informed by the use of Dytham’s dichotomous key (1999). I tested whether nesting habits changed in response to treatments by comparing the frequency of nest types among the treatments using a chi-square test. I tested the effects of treatments upon nest size, growth, and reproduction using analysis of variance (ANOVA). The demographic responses were tested for time dependent effects using two-way ANOVAs with month of treatment duration as the second factor, using separate analyses for each functional group. The Arboreal and *Wasmannia* groups have been excluded from several analyses because sample sizes were not adequate for the appropriate statistical tests.

To rule out the possibility that increases in nest density were purely the result of nest fission instead of nest relocation, I performed correlation analyses for each treatment, comparing the number of nests in each plot with the mean number of workers per nest. If changes in nest density were only attributable to nest fission, then nest fission events would simultaneously increase nest density and decrease nest sizes, resulting in a negative relationship between nest density and colony size. I tested whether the density of nests in each plot was independent among functional groups; one would expect negative associations if one functional group displaced another. Because the distribution of nest frequencies was not normal, I created used rank correlations. To explain additional variance in the density of ant nests, I evaluated the effects of leaf litter depth upon nest density using linear regression. To determine how the treatments affected nest growth rates, I performed polynomial regression on the number of worker pupae relative to the number of workers.

RESULTS

NEST MATERIAL.—Over the course of the experiment, 1450 nests were collected from control and treatment plots. The frequencies of nest material significantly differed among treatments. Marginal nest materials that rarely were occupied in the control plots often contained ant nests in the food supplementations (Table 1).

NEST DENSITY.—Over 4 mo, both food supplementation treatments caused an increase of the number of nests, compared to the control plots, while removal and trampled treatments showed no change relative to the controls (Fig. 1). A two-way ANOVA on nest density demonstrated significant effects of treatment ($F_{4,280} = 5.31$, $P < 0.001$), month of treatment duration ($F_{4,280} = 3.95$, $P < 0.01$), and an interaction between month and treatment ($F_{4,280} = 1.80$, $P < 0.05$). To determine whether the increase in density was caused by increases in particular functional groups, I examined the changes in

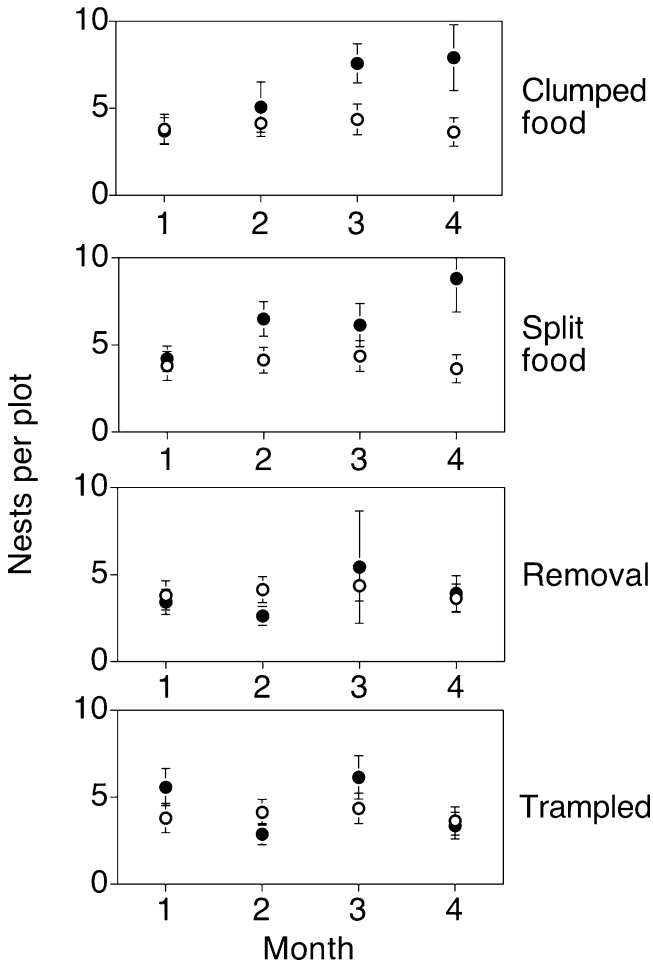


FIGURE 1. The response of nest density (per m²) to treatments applied to 1 m² plots. Open circles indicate control plots and error bars represent ±1 standard error.

nest density among groups (Table 2). The increase in nest density occurred in both food treatments among *Arboreal*, *Paratrechina*, *Pheidole*, and *Wasmannia*. None of these groups changed in nest density with trampling. *Solenopsis*, on the other hand, experienced increased nest densities in the split food and trampling treatments, but not in the clumped food treatment.

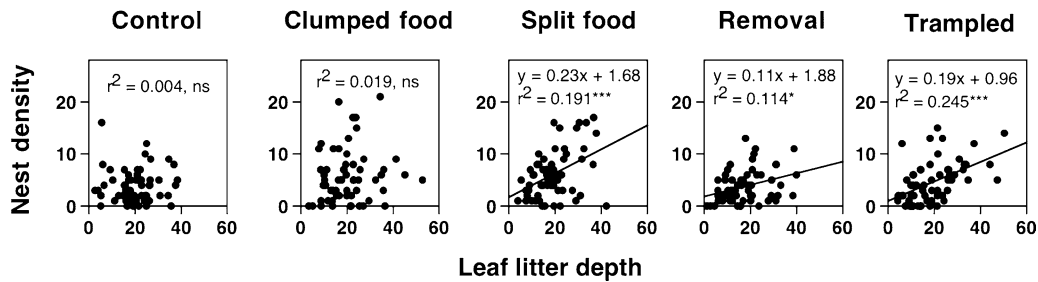


FIGURE 2. The relationship between the density of litter ant nests and the depth of leaf litter in 1 m² plots, among control and treatment plots. Linear regression, ** $P < 0.01$; *** $P < 0.001$.

TABLE 3. Comparisons of nest density per plot, using Kendall's rank-order correlation coefficients, T, * $P < 0.05$ after Bonferroni correction for multiple comparisons.

Functional group	Arboreal	Dacetine	<i>Paratrechina</i>	<i>Pheidole</i>	<i>Solenopsis</i>	<i>Wasmannia</i>
Arboreal	—	-0.002	0.006	0.016	0.015	-0.001
Dacetine		—	0.021	0.184*	0.136*	-0.017
<i>Paratrechina</i>			—	0.046	0.066*	0.019*
<i>Pheidole</i>				—	0.171*	-0.025
<i>Solenopsis</i>					—	-0.006
<i>Wasmannia</i>						—

I found no association between nest size and nest density; the highest R^2 value was 0.026, indicating that the changes in the number of nests could not have resulted solely from fragmentation. Functional groups did not apparently displace one another, as nest density among functional groups was independent of one another; the greatest tau value was 0.18 (Table 3). Most associations were weakly positive, which was likely caused by a general increase in nest density with deeper leaf litter. I found that leaf litter depth did not affect nest density in the control plots. Leaf litter depth was positively correlated with nest density in three of the treatments, but not the clumped food (Fig. 2).

DEMOGRAPHIC RESPONSES TO TREATMENTS.—I compared demographic responses to the treatments using nest size (number of workers), growth rate (worker brood/workers), and reproduction (number of reproductives) as metrics. Table 4 presents the effects of treatments on the nest demographic parameters in each functional group. The treatments caused significant effects on the size, growth, or reproduction of *Pheidole* nests only. There were no effects of month of treatment duration or interacting effects between the demographic factors and the treatment duration.

In all of the treatments, among all the four functional groups considered, the maximum colony size was larger than in the controls. In the large nests of *Paratrechina*, *Pheidole*, and *Solenopsis*, the shapes of the curves indicated greater growth in the split food treatments compared to the clumped food treatments, often driven by a few outlying observations (Fig. 3). In many cases, large colonies continued to grow as quickly, if not more quickly, than small colonies.

TABLE 4. Demographic responses to treatments among functional groups. ANOVA comparisons were performed within each functional group between each treatment and control; * $P < 0.05$ and ** $P < 0.01$ after Bonferroni correction. Two-way ANOVA results in every functional group indicated no interacting effects of treatment duration, using four categories designated for the months of treatment duration.

Functional group	Treatment	Number of adults, mean \pm SE (N)	Alates, mean \pm SE (N)	Growth, mean \pm SE (N)
Arboreal	Control	(0)	(0)	(0)
	Clumped food	57.8 \pm 26.1 (6)	0 \pm 0 (6)	0.23 \pm 0.15 (6)
	Split food	103.6 \pm 46.0 (5)	0.6 \pm 0.4 (5)	0.54 \pm 0.22 (5)
	Removal	(0)	(0)	(0)
	Trampled	5.8 \pm 3.2 (5)	0 \pm 0 (5)	0 \pm 0 (3)
Dacetine	Control	13.7 \pm 1.5 (40)	1.85 \pm 0.68 (40)	0.40 \pm 0.06 (37)
	Clumped food	13.5 \pm 2.7 (51)	1.43 \pm 0.66 (51)	0.45 \pm 0.11 (48)
	Split food	20.1 \pm 4.2 (43)	1.81 \pm 0.56 (43)	0.23 \pm 0.05 (41)
	Removal	23.35 \pm 5.4 (37)	1.65 \pm 0.46 (37)	0.31 \pm 0.08 (32)
	Trampled	17.0 \pm 2.7 (35)	0.80 \pm 0.28 (35)	0.30 \pm 0.05 (33)
<i>Paratrechina</i>	Control	13 \pm 4.0 (2)	0 \pm 0 (2)	0.14 \pm 0.08 (2)
	Clumped food	28.7 \pm 5.3 (16)	0.19 \pm 0.10 (16)	0.28 \pm 0.07 (16)
	Split food	20 \pm 3.6 (20)	2.10 \pm 0.93 (20)	0.18 \pm 0.06 (20)
	Removal	27.5 \pm 8.8 (6)	0 \pm 0 (6)	0.20 \pm 0.08 (6)
	Trampled	36.5 \pm 12.7 (8)	1.5 \pm 0.93 (8)	0.28 \pm 0.09 (8)
<i>Pheidole</i>	Control	46.4 \pm 4.1 (114)	0.73 \pm 0.32 (114)	0.27 \pm 0.03 (112)
	Clumped food	54.7 \pm 4.7 (151)	2.52 \pm 0.62 (151)*	0.44 \pm 0.06 (151)*
	Split food	62.9 \pm 5.0 (164)*	2.87 \pm 0.73 (164)**	0.33 \pm 0.03 (163)
	Removal	41.9 \pm 5.6 (89)	1.10 \pm 0.39 (89)	0.46 \pm 0.07 (85)*
	Trampled	40.6 \pm 4.3 (128)	1.31 \pm 0.46 (128)	0.33 \pm 0.4 (125)
<i>Solenopsis</i>	Control	29.2 \pm 5.2 (47)	0.04 \pm 0.3 (47)	0.37 \pm 0.05 (47)
	Clumped food	30.7 \pm 5.2 (47)	0.11 \pm 0.09 (47)	0.40 \pm 0.05 (47)
	Split food	30.2 \pm 4.4 (74)	1.10 \pm 0.83 (74)	0.37 \pm 0.05 (74)
	Removal	26.9 \pm 2.5 (46)	0.44 \pm 0.23 (46)	0.55 \pm 0.12 (45)
	Trampled	30.9 \pm 3.2 (76)	0.37 \pm 0.17 (76)	0.43 \pm 0.05 (76)
<i>Wasmannia</i>	Control	80.3 \pm 55.6 (8)	0.50 \pm 0.50 (8)	0.70 \pm 0.49 (8)
	Clumped food	84.2 \pm 18.0 (19)	0 \pm 0 (19)	0.58 \pm 0.28 (19)
	Split food	105.6 \pm 27.8 (20)	0.25 \pm 0.18 (20)	0.54 \pm 0.30 (20)
	Removal	72.6 \pm 16.1 (12)	0 \pm 0 (12)	0.12 \pm 0.07 (12)
	Trampled	237.0 \pm 231.0 (2)	0 \pm 0 (2)	0 \pm 0 (2)

The majority of nests did not produce reproductive caste members (Table 5). In *Pheidole*, one of few groups where reproductive caste members were present, the frequency of the production of reproductive caste members was significantly greater than in the controls.

DISCUSSION

NEST RELOCATION.—The increase in nest density of the food supplementation treatments was primarily caused by nest relocation. We can eliminate nest fission as a major cause of the increase in density because nest size did not decline with increases in nest density. It is not possible to know whether ants relocated outside the plots during the treatment period, but it is clear that the net influx of ants into these plots was greater than the net rate of departure. Nests in

food supplementation plots may choose to move less frequently, or move short distances to remain within the plot. Alternatively, nests that relocate may be more likely to select the areas subjected to food treatment.

LIMITATION OF NEST DENSITY.—It appears that both food and nests can be limiting. When food is limiting, nest sites are not limiting. When food is added, nest sites appear to become the limiting factor. Two lines of evidence support this hypothesis. First, when food was added, ants shifted to suboptimal nesting habitats. Second, leaf litter depth and nest density positively correlated in the supplemental food treatments but not in the control.

Because nest availability and food availability are often coupled in nature (even if loosely), it would have been difficult to evaluate these relationships without supplemental food. Even though relocation brings more ants into areas with supplemental food, there is

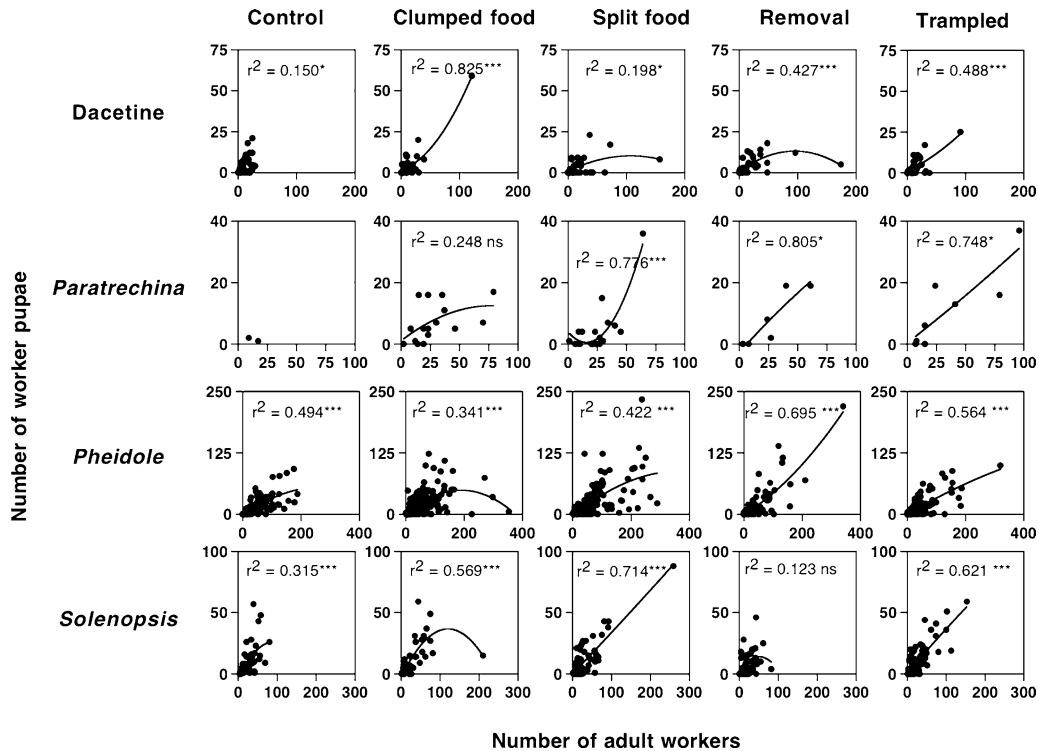


FIGURE 3. Worker–worker pupae curves measure investment into growth as nest sizes increase. Second order polynomial regression, * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

no evidence that ants emigrate away from bad conditions or poor food quality. There was no decline in the nest density in the litter (and hence food) removal treatment, or in the trampling treatment which resulted in the destruction of many potential nests. Considering that the depth of leaf litter is closely associated with the number of available nests, the release of food constraint may then reveal nest constraint. In the trampling treatment, resulting in the destruction of some potential nests, there was no decline in nest density, although litter depth was correlated with nest density.

If nests are limiting, then the apparent abundance of potential and unoccupied nests begs explanation. Many potentially high quality nests are unoccupied at any given moment. While picking through leaf litter, ants often are found nesting in the most paltry locations while hollow sticks and twigs remain unoccupied. In another study, when supplemental nests were added to the litter, nest densities were found to increase even though few of the supplemental nests were occupied (Kaspari 1996a). It appears as if the existence of empty nests may have value, even if they are unoccupied.

I suggest that the value of unoccupied nests is a function of the frequent relocation of litter-nesting species. Although nest relocations are frequent in the litter, no selective force driving a regular pattern of nest relocation has yet to be determined in any species (McGlynn *et al.* 2004). Nest relocation could occur to improve access to resources or avoid competition, because relocations often place nests in more favorable locations (Smallwood 1982). However, at least one ant species at La Selva, the common ground-nesting *Aphaenogaster araneoides*, apparently relocates its nests about once

per week independent of resource availability and environmental conditions (McGlynn *et al.* 2004). *Aphaenogaster araneoides* may move in response to army ants (McGlynn *et al.* 2004). Under the army ant predation hypothesis, ant nests accumulate odors, which attract army ants. It is assumed that army ants use short-distance olfactory cues to locate prey, though no such experiment has been conducted (Gotwald 1995). Even though there is no direct evidence for the army ant predation hypothesis yet, other hypotheses are not supported and the circumstantial evidence is intriguing.

GROWTH AND REPRODUCTION.—Social insects are typically thought to resolve the trade-off between growth and reproduction by initially investing in growth when nests are small, then shifting to reproductive castes when more workers are in the nest (Oster & Wilson 1978). In most social insect nests, which grow and reproduce in modular units, this switch in energetic allocation is easily evaluated by counting the number of members of each caste (Bourke & Franks 1995). Surprisingly, in the present study, there is no evidence that ants defer reproduction until reaching a threshold nest size.

Kaspari (1996b) proposed that the independence of nest size and relative allocation toward sterile and reproductive castes is caused by a constant rate of mortality. According to this argument, because death might arrive at any minute, selection does not favor a delay in the production of reproductive caste members. I offer an alternative explanation for the fixed allocation to reproductive and sterile castes: namely, that frequent colony fission breaks the trade-off between growth and reproduction. At least some and perhaps

TABLE 5. Percentage of nests containing reproductive caste members. Chi-square values were calculated on frequency values used to determine significant differences among treatments within functional groups. The observed frequency values in each category are in parentheses. *df* for all tests is 12.

Functional group	Treatment	Percent reproductive castes absent	Percent only males	Percent only females	Percent both sexes	<i>N</i>	χ^2	<i>P</i>
Dacotine	Control	70.0 (28)	5.0 (2)	12.5 (5)	12.5 (5)	40	10.47	0.57
	Clumped food	76.5 (39)	2.0 (1)	13.7 (7)	7.8 (4)	51		
	Split food	53.5 (23)	9.3 (4)	18.6 (8)	18.6 (8)	43		
	Removal	64.9 (24)	2.7 (1)	13.5 (5)	18.9 (7)	37		
	Trampled	74.3 (26)	2.7 (2)	14.3 (5)	2.7 (2)	35		
<i>Paratrechina</i>	Control	100 (2)	0	0	0	2	12.01	0.45
	Clumped food	81.3 (13)	12.5 (2)	6.3 (1)	0	16		
	Split food	70.0 (14)	10.0 (2)	15.0 (3)	10.0 (2)	20		
	Removal	100 (6)	0	0	0	6		
	Trampled	62.5 (5)	0	37.5 (3)	0	8		
<i>Pheidole</i>	Control	82.5 (94)	7.0 (8)	7.9 (9)	2.6 (3)	114	12.13	0.049
	Clumped food	69.5 (105)	13.2 (20)	14.6 (22)	2.6 (4)	151		
	Split food	68.3 (112)	14.0 (23)	11.6 (19)	6.1 (10)	164		
	Removal	84.3 (75)	5.6 (5)	7.9 (7)	2.2 (2)	89		
	Trampled	78.9 (101)	12.5 (16)	7.0 (9)	1.6 (2)	128		
<i>Solenopsis</i>	Control	95.7 (45)	2.1 (1)	2.1 (1)	0	47	7.90	0.79
	Clumped food	95.7 (45)	0	2.1 (1)	2.1 (1)	47		
	Split food	89.2 (66)	2.7 (2)	4.1 (3)	4.1 (3)	74		
	Removal	89.1 (41)	0	8.7 (4)	2.2 (1)	46		
	Trampled	82.1 (70)	1.3 (1)	3.9 (3)	2.6 (2)	76		

most litter ant species can reproduce by fission. Colonies of animals that reproduce via fission have broken the growth–reproduction trade-off, by allocating growth units toward reproduction at the time of fission. It is hard to estimate rates of fission in the field, because of the difficulty differentiating fission and relocation events (Peeters & Ito 2001). Sterile workers are a prerequisite for fission, and the number of successful fission events is tied to the number of sterile workers produced within a nest. As a result of translating nest growth into reproductive potential, fission-reproducing ants greatly restrict the range of dispersal from the natal nest.

Changes in the distribution of colony size with food supplementation offer indirect evidence as to how fission rate and relocation relate. In plots where food was supplemented, the maximum colony size consistently increased. While maximum colony size may be a function of the size at which colonies die, it is more likely to be a function of the size at which colonies split. Thus, the upper limit on observed nest sizes may be determined by the behavioral decision to split one nest into two. This decision to split a nest is probably based on foraging efficiency (*e.g.*, Garb *et al.* 2000). At the size at which foraging efficiency declines with increasing colony size, colonies can be expected to split (they do not just slow their growth since we know that growth rate is independent of colony size). The greater nest sizes in the food supplementation treatments may thus demonstrate that colonies have decided to split at a larger threshold size due to a higher rate of payoff for larger colonies when resources are plentiful.

Whereas work at other sites makes clear predictions as to how allocation to reproduction varies with colony size, predictions for how growth rate (worker/pupae curves) scales with colony size come largely from other work in the tropics. Two aspects of colony growth rate can be compared, the mean growth rate (mean worker/pupae ratio) and the relationship between growth rate and colony size. Our results apparently contradict “Michener’s paradox”: that per capita worker production declines with the number of adult workers in the nest (Michener 1964). Kaspari (1996a) found that colony growth rates are generally independent of colony size. In the present study, within the stress and disturbance treatments, colony growth rates were greater or equal to those in the controls. In the food supplementation plots, colony growth rates increased as colonies grew in the split food plots, but nests in the clumped food plots showed slower growth in large colonies. Large nests in the clumped food plots slow down their growth. The opposite pattern occurred for the food supplementation for the dacetines, but this makes sense as the dacetines are probably specialized predators who were competing for nest space with the other functional groups, but not for the supplemental food.

NESTING HABITS OF THE LITTER ANT COMMUNITY.—Changes in the abundance of food in the litter created several changes in nesting behavior. In both food treatments, ants were found within nest materials that were rarely occupied in the control plots. Moreover, nests of arboreal species increased in density. Whereas arboreal ants

are occasionally found at traps and baits on the ground (McGlynn & Kirksey 2000, T. McGlynn, pers. obs.), these ants were thought to access the litter while foraging from aboveground nests. Because arboreal ants are probably nitrogen-limited (Davidson *et al.* 2003), then a predictable source of nitrogen-rich food apparently is adequate to entice some ants to nest within the litter.

ACKNOWLEDGMENTS

Mark Springer volunteered 5 mo of fieldwork. Several undergraduates assisted with the field experiment and colony processing, including Jeb Owen, Fielding Arnold, Bobby Bascomb, Erica Brady, Jess Burlason, Rob Ickes, Candice Kelley, Eben Kirksey, Sarah Lamond, and Lloyd Rowland. Mike Breed, Jeb Owen, Nate Sanders, Bonnie Ripley, and two anonymous reviewers helped with the interpretation of results and editing of the manuscript, and Rob Dunn was instrumental in its completion. Emily Barker translated the abstract into Spanish. This project was funded by a University of San Diego Faculty Research Grant, an Organization for Tropical Studies Dissertation Grant, the Andrew Mellon Foundation, and Amelia.

LITERATURE CITED

- ADAMS, E. S., AND W. R. TSCHINKEL. 1995. Spatial dynamics of colony interactions in young populations of the fire ant *Solenopsis invicta*. *Oecologia* 102: 156–163.
- ANDERSEN, A. N. 1995. A classification of Australian ant communities, based on functional groups which parallel plant life-forms in relation to stress and disturbance. *J. Biogeogr.* 22: 15–29.
- , AND A. D. PATEL. 1994. Meat ants as dominant members of Australian ant communities: An experimental test of their influence on the foraging success and forager abundance of other species. *Oecologia* 98: 15–24.
- BANSCHBACH, V. S., N. LEVIT, AND J. M. HERBERS. 1997. Nest temperatures and thermal preferences of a forest ant species: Is seasonal polydomy a thermoregulatory mechanism? *Insectes Soc.* 44: 109–122.
- BESTELMEYER, B. T., D. AGOSTI, L. ALONSO, C. R. BRANDÃO, W. L. BROWN, JR., J. H. C. DELABIE, AND R. SILVESTRE. 2000. Field techniques for the study of ground-dwelling ants: An overview, description and evaluation. *In* D. Agosti, L. Alonso, J. Majer, and T. Schultz (Eds.). *Ants: Standard methods for measuring and monitoring biodiversity*, pp. 122–144. Smithsonian Institution Press, Washington, District of Columbia.
- , AND J. A. WIENS. 1996. The effects of land use on the structure of ground-foraging ant communities in the Argentine chaco. *Ecol. Appl.* 6: 1225–1240.
- BOLTON, B. 1994. *Identification guide to ant genera of the world*. Harvard University Press, Cambridge, Massachusetts.
- BOURKE, A. F. G., AND N. R. FRANKS. 1995. *Social evolution in ants*, p. 529. Princeton University Press, Princeton, New Jersey.
- BROWN, M. J. F., AND D. M. GORDON. 2000. How resources and encounters affect the distribution of foraging activity in a seed-harvesting ant. *Behav. Ecol. Sociobiol.* 47: 195–203.
- BYRNE, M. M. 1994. Ecology of twig-dwelling ants in a wet lowland tropical forest. *Biotropica* 26: 61–72.
- CARROLL, C. R., AND D. H. JANZEN. 1973. Ecology of foraging by ants. *Annu. Rev. Ecol. Syst.* 4: 231–257.
- DAVIDSON, D. W., S. C. COOK, R. R. SNELLING, AND T. H. CHUA. 2003. Explaining the abundance of ants in lowland tropical rainforest canopies. *Science* 300: 969–972.
- DEJEAN, A. 1991. Gathering of nectar and exploitation of Aphididae by *Smithistruma emarginata* (Formicidae: Myrmicinae). *Biotropica* 23: 207–208.
- DUROU, S., J. LAUGA, AND A. DEJEAN. 2001. Intensive food searching in humid patches: Adaptation of a myrmecine ant to environmental constraints. *Behaviour* 138: 251–259.
- DYTHAM, C. 1999. *Choosing and using statistics: A biologist's guide*. Blackwell Science, Oxford.
- FERNÁNDEZ ESCUDERO, I., AND A. TINAUT. 1999. Factors determining nest distribution in the high-mountain ant *Proformica longiseta* (Hymenoptera: Formicidae). *Ethol. Ecol. Evol.* 11: 325–338.
- GARB, J., B. P. KOTLER, AND J. S. BROWN. 2000. Foraging and community consequences of seed size for coexisting Negev Desert granivores. *Oikos* 88: 291–300.
- GOTWALD, W. H. 1995. *Army ants: The biology of social predation*. Comstock Publishing Associates, Ithaca, New York.
- HÖLDOBLER, B., AND E. O. WILSON. 1990. *The ants*. Belknap Press, Cambridge, Massachusetts.
- KASPARI, M. 1996a. Testing resource-based models of patchiness in four Neotropical litter ant assemblages. *Oikos* 76: 443–454.
- . 1996b. Litter ant patchiness at the 1-m² scale: Disturbance dynamics in three Neotropical forests. *Oecologia* 107: 265–273.
- LEBRETON, J., J. CHAZEAU, AND H. JOURDAN. 2003. Immediate impacts of invasion by *Wasmannia auropunctata* (Hymenoptera: Formicidae) on native litter ant fauna in a New Caledonian rainforest. *Aust. Ecol.* 28: 204–209.
- LEVINGS, S. C., AND D. M. WINDSOR. 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.
- LONGINO, J. T., AND P. E. HANSON. 1995. The ants (Formicidae). *In* P. E. Hanson and I. D. Gauld (Eds.). *The Hymenoptera of Costa Rica*, pp. 588–620. Oxford University Press, London.
- MCDADE, L. A., AND G. S. HARTSHORN. 1994. La Selva biological station. *In* L. A. McDade, K. S. BAWA, H. A. Hespenheide, and G. S. Hartshorn (Eds.). *La Selva: Ecology and natural history of a Neotropical rain forest*, pp. 6–14. University of Chicago Press, Chicago, Illinois.
- MCGLYNN, T. P. 1999a. The worldwide transport of ants: Geographic distribution and ecological invasions. *J. Biogeogr.* 26: 535–548.
- . 1999b. *The biogeography, behavior, and ecology of exotic ants*. Ph.D. dissertation, University of Colorado, Boulder, Colorado.
- , R. CARR, J. CARSON, AND J. BUMA. 2004. Frequent nest relocation in the ant *Aphaenogaster araneoides*: Resources, competition, and natural enemies. *Oikos* 106: 611–621.
- , J. R. HOOVER, G. S. JASPER, M. S. KELLY, A. M. POLIS, C. M. SPANGLER, AND B. J. WATSON. 2002. Environmental heterogeneity affects demography of the Central American ant *Aphaenogaster araneoides*. *J. Trop. Ecol.* 18: 231–244.
- , AND S. E. KIRKSEY. 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.
- , AND J. P. OWEN. 2002. Food supplementation alters caste allocation in a natural population of *Pheidole flavens*, a dimorphic leaf-litter dwelling ant. *Insectes Soc.* 49: 8–14.
- MICHENER, C. D. 1964. Reproductive efficiency in relation to colony size in hymenopterous societies. *Insectes Soc.* 11: 317–341.
- MOORE, J. C., E. L. BERLOW, D. C. COLEMAN, P. C. DE RUITER, Q. DONG, A. HASTINGS, N. COLLINS JOHNSON, K. S. MCCANN, K. MELVILLE, P. J. MORIN, K. NADELHOFFER, A. D. ROSEMOND, D. M. POST, J. L. SABO, K. M. SCOW, M. J. VANNI, AND D. H. WALL. 2004. Detritus, trophic dynamics and biodiversity. *Ecol. Lett.* 7: 584–600.
- MORRISON, L. W. 1996. Community organization in a recently assembled fauna: The case of Polynesian ants. *Oecologia* 107: 243–256.
- OSTER, G. F., AND E. O. WILSON. 1978. *Caste and ecology in the social insects*. Princeton University Press, Princeton, New Jersey.

- PEETERS, C., AND F. ITO. 2001. Colony dispersal and the evolution of queen morphology in social Hymenoptera. *Annu. Rev. Entomol.* 46: 601–630.
- PORTER, S. D., AND D. A. SAVIGNANO. 1990. Invasion of polygyne fire ants decimates native ants and disrupts arthropod community. *Ecology* 71: 2095–2106.
- RYTI, R. T., AND T. J. CASE. 1992. The role of neighborhood competition in the spacing and diversity of ant communities. *Am. Nat.* 139: 355–374.
- SANDERS, N. J., AND D. M. GORDON. 2003. Resource-dependent interactions and the organization of desert ant communities. *Ecology* 84: 1024–1031.
- , N. J. GOTELLI, N. E. HELLER, AND D. M. GORDON. 2003. Community disassembly by an invasive ant species. *Proc. Natl. Acad. Sci. USA* 100: 2474–2477.
- SAVOLAINEN, R., AND K. VESPALAINEN. 1988. A competition hierarchy among boreal ants: Impact on resource partitioning and community structure. *Oikos* 51: 135–155.
- SMALLWOOD, J. 1982. Nest relocations in ants. *Insectes Soc.* 29: 138–147.
- TSCHINKEL, W. R., AND C. A. HESS. 1999. Arboreal ant community of a pine forest in northern Florida. *Ann. Entomol. Soc. Am.* 92: 63–70.
- WILSON, E. O. 2003. *Pheidole* in the new world: A dominant, hyperdiverse ant genus. Harvard University Press, Cambridge, Massachusetts.