# The effect of water on the ground nesting habits of the giant tropical ant, Paraponera clavata

Author: Elahi, Robin

Source: Journal of Insect Science, 5(34) : 1-7

Published By: Entomological Society of America

URL: https://doi.org/10.1673/1536-2442(2005)5[1:TEOWOT]2.0.CO;2

The BioOne Digital Library (https://bioone.org/) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (https://bioone.org/subscribe), the BioOne Complete Archive (https://bioone.org/archive), and the BioOne eBooks program offerings ESA eBook Collection (https://bioone.org/esa-ebooks) and CSIRO Publishing BioSelect Collection (https://bioone.org/csiro-ebooks).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 15 Jul 2025
Terms of Use: https://complete.bioone.org/terms-of-use

# The effect of water on the ground nesting habits of the giant tropical ant, *Paraponera clavata*

**Robin Elahi**

Center for Vertebrate Studies, Department of Biology, Northeastern University, 360 Huntington Ave, Boston, MA 02115
Present address: Department of Biology, California State University, 18111 Nordhoff St, Northridge, CA 91330-8303

## Abstract

The large predatory ant, *Paraponera clavata*, exerts measurable top-down effects in wet and moist Neotropical forests, and therefore its distribution has potential ecological implications. To determine how water affects the presence of this important predator, the ground nesting ecology of *P. clavata* was examined with respect to various habitat characteristics. Four hectares of disturbed Costa Rican lowland rain forest were surveyed for ant colonies to determine nest distribution patterns in wet and dry habitat; significantly more colonies were found in dry habitat. Seventeen of 19 nests built on slopes of > 5° inclination were positioned on the downward side of the tree, possibly using the trunk as a shield against runoff during rain showers. Moisture and pH inside nests were significantly different from adjacent soil. These results suggest that water influences the ground nesting habits of *P. clavata*, thus ecological differences between comparatively wet and dry portions of tropical forests may arise from the relative abundance of this ant species.

Cite this paper as:
Elahi R. 2005. The effect of water on the ground nesting habits of the giant tropical ant, *Paraponera clavata*. 7pp. *Journal of Insect Science* 5:34, available online: insectscience.org/5.34

Keywords: nest, distribution, microhabitat, flooding, tropical rain forest, Costa Rica
Correspondence: robin.elahi@csun.edu
Received 10 October 2004 | Accepted 9 June 2005 | Published 18 November 2005

## Introduction

Colonies of many ant species can be regarded as functionally sessile organisms because nests remain fixed in space and time for many years (Thurber et al., 1983; Wiernasz and Cole, 1995), with the dispersion patterns of nests resulting from initial queen settlement and subsequent mortality. The Neotropical ant *Paraponera clavata* (Hymenoptera: Formicidae), a conspicuous (2.5 cm length) inhabitant of lowland rain forests from Nicaragua to the Amazon Basin (Janzen and Carroll, 1983), provides one such example. Colonies consist of 1000-2500 individuals occupying nests built within soil at the base of trees (Janzen and Carroll, 1983), with nest tunnels occasionally extending from the base up the tree trunk. Several cases of completely arboreal colonies have also been reported (Breed and Harrison, 1989). Worker ants ascend to the canopy to forage for nectar and arthropods, and rarely descend to the forest floor (Bennett and Breed, 1985). *P. clavata* may protect trees from the activity of leaf-cutting ants (*Atta cephalotes*; Wetterer, 1994), and such indirect positive effects on plant biomass have recently been quantified (Dyer, 2002). At La Selva Biological Station, Costa Rica, randomly selected trees had significantly higher levels of leaf damage from folivory than trees harboring *P. clavata* nests (Dyer, 2002). Therefore, the distribution of this predatory ant in tropical forests has top-down ecological implications.

Several studies have found *P. clavata* colonies to be overdispersed, which is regarded as evidence of inter-colonial aggression (Bennett and Breed, 1985; Breed et al., 1991; Thurber et al., 1983; Pérez et al., 1999). However, nest dispersion patterns are not fully explained by mortality due to intraspecific competition, and are also due to selection by founding queens (Thurber et al., 1983). *P. clavata* queens may seek to colonize the bases of certain host species or life forms (*e.g.*, tree, shrub, palm, liana – see Belk et al., 1989), but studies examining such hypothetical nest-plant associations have yielded contrasting results (Bennett and Breed, 1985; Hölldobler and Wilson, 1990a; Thurber et al., 1983; Pérez et al., 1999). For example, Bennett and Breed (1985) suggested that *Pentaclethra macroloba*, a dominant tree species at La Selva, is a preferred nesting site for *P. clavata*, possibly due to the presence of buttresses and extra-floral nectaries. Conversely, large-scale studies on Barro Colorado Island, Panama, revealed that *P. clavata* nests were not significantly associated with buttressed trees or with species harboring extra-floral nectaries (Belk et al., 1989; Pérez et al., 1999).

In addition to host species attributes, microhabitat variables also affect nest site selection, thereby influencing nest dispersion patterns (Ryti and Case, 1986). The choice of nest location is the first step to maintaining individual and colonial homeostasis, because abiotic factors, such as temperature and humidity, are buffered from extreme fluctuations outside the nest (Seeley and Heinrich, 1980). Temperature affects individual ant metabolism (Calabi and Porter, 1989; Vogt and Appel, 1999), colony growth (Porter, 1988; Porter and Tschinkel, 1993), brood translocation (Brian, 1973; Roces and Nuñez, 1989) and larval growth and development (Brian, 1963). Although less well studied, humidity modifies survival (Kay and Whitford, 1975; Hood and Tschinkel, 1990) and worker behavior (Scherba, 1959; Potts et al., 1984; Cassill and Tschunkel, 2000). Brood development requires a specific range of moisture and temperature, which varies by species and developmental stage (Scherba, 1959; Brian, 1963; Wheeler and Wheeler, 1976; Porter, 1988; Roces and Nuñez, 1989). Furthermore, ants are sensitive to minute differences in moisture, which affects ant species diversity and abundance, foraging activity and nest distribution (Levings, 1983). Although the influence of abiotic factors on the nesting ecology of *P. clavata* has been sparingly investigated, seasonal flooding of flat terrain may hinder establishment and maintenance of *P. clavata* colonies (Thurber et al., 1983), suggesting that water significantly affects their distribution. The current investigation tested this hypothesis by quantifying various habitat characteristics of ant colonies.

This study examined patterns of *P. clavata* nest abundance in relation to moisture and topographic conditions over several hectares. Colonies were anticipated to be located on dry, hilly habitat, because Pérez et al. (1999) found nests to be positively associated with inclined terrain that could reduce flooding. Furthermore, the potential risk of flooding was expected to affect the specific location, or microhabitat, of the nest about the host tree. It was hypothesized that colonies on inclined terrain would be positioned on the side of the host plant facing downhill, using the trunk and/or buttresses as shields from rainwater flowing down the slope. To investigate the possibility that nest-building activities altered abiotic soil characteristics, moisture, temperature and pH were measured inside nests and within the surrounding soil. Differences were expected because the nests of soil dwelling ants buffer the physical fluctuations of the aerial environment (Seeley and Heinrich, 1980) and consequently alter soil chemistry (Culver and Beattie, 1983; Wagner et al., 1997; Frouz et al., 2003). To further describe the nesting habits of *P. clavata*, colony size, substratum slope and host plant were recorded for each nest.

## Materials and Methods

Fieldwork was conducted in two isolated patches of lowland rain forest in Heredia, Costa Rica. The forest remnants are approximately 80 ha in area and were surrounded by pasture. Both patches had been selectively logged, but were set aside as nature preserves approximately 35 years ago (A. Rothman, pers. comm.). The habitat is similar to lowland rain forest found at La Selva Biological Station, 40 km to the southwest (McDade et al., 1994). *P. macroloba*, a dominant tree in disturbed forests of Heredia (McDade et al., 1994), is common at the two sites.

In June and July 2002, eight 50 x 50 m contiguous plots were selected randomly at each site (4 ha total). To determine if nest abundance was related to moisture, plots were categorized as wet if the majority of the plot flooded at any time during the study, and remaining plots were labeled dry. The slope of each plot was estimated using a Silva Ranger (www.silva.se)clinometer (± 1°). Within each plot, the bases of all woody trees, palms and lianas greater than 1 cm diameter at breast height (DBH) were searched for nest entrances and active foragers. Potential nests without visible foragers were probed using a 1 m pole to determine if they were occupied by *P. clavata* (as in Belk et al., 1989; Pérez et al., 1999). Although *P. clavata* is primarily nocturnal (McCluskey and Brown, 1972; but see Young and Hermann, 1980), diurnal searches for nests are effective and have been commonly used (Bennett and Breed, 1985; Breed and Harrison, 1989; Belk et al., 1989; Thurber et al., 1983; Pérez et al., 1999).

Potential effects of flooding on microhabitat selection were examined by noting if colonies were oriented facing up or down the slope of the hill upon which they were built. The slope of the ground at each nest was measured using a Silva Ranger clinometer (± 1°). Abiotic differences between nests and the ambient environment were assessed by percent moisture, temperature and pH measurements inside each nest and within adjacent soil. Temperature was measured using a Weksler (www.wekslerglass.com) soil thermometer (± 1° C) that extended 20 cm into the ground, while moisture and pH were quantified using a Kelway soil moisture and pH meter (moisture ± 5%, pH ± 0.1), which extended eight cm into the ground. Soil measurements were taken randomly once at each nest between 1000 and 1600 h. Although soil moisture, temperature and pH measurements fluctuate daily and seasonally, such paired observations provide an instantaneous comparison between the nest interior and surrounding soil. Total nest surface area was calculated from the length and width of colonies.

To assess the type of host *P. clavata* utilized at this site, tree characteristics were recorded. Host plant DBH was measured and categorized into five size classes (1-7.9 cm; 8-15.9 cm; 16-31.9 cm; 32-63.9 cm; > 64 cm; after Belk et al., 1989). Height was visually estimated as one of four size classes (0-10 m; 11-20 m; 21-30 m; > 30 m). Host life form (e.g., tree, palm) was noted, as well as the presence/absence of buttresses.

### Statistical analyses

A *G* goodness of fit tested the hypothesis that large-scale differences in water prevalence affected nest distribution by comparing wet and dry plots with respect to nest frequency. Slopes of wet and dry plots were compared using a one-way analysis of variance (ANOVA) to determine if water prevalence was related to substratum inclination. To examine how water affected orientation of the colony with respect to the host, nest orientation was analyzed using a two-tailed binomial test ($H_0$: P = 0.5, downhill/uphill). Six nests were omitted because their substratum slopes were 5° or less, making nest orientation ambiguous with respect to slope. Moisture, temperature and pH differences between nests and ambient soil were analyzed using a paired *t*-test.

To determine whether tree size was related to nest size, planar nest surface area was compared by tree height class using a one-way ANOVA, and Pearson's correlation analysis was performed on nest surface area and host DBH. Data were graphically inspected to meet the assumptions of parametric testing, and transformations were unnecessary (Sokal and Rohlf, 1995). All analyses were completed using JMP 3.2 for the Macintosh.

## Results

Twenty-five *P. clavata* ground nests were found in 4 ha (6.25 nests/ha). Ten 50 x 50 m plots were characterized as dry, and six as wet. The ten dry plots harbored 23 colonies, but only two nests were found in the six wet plots. This observed distribution of nests differed significantly from expected frequencies of equal occurrence in dry and wet plots ($G = 11.61$, $P < 0.001$). The substratum was significantly steeper in dry plots (29 ± 6°, $N = 10$), than wet plots (2 ± 2°, $N = 6$) [ANOVA, F1, 15 = 13.62, $P < 0.01$]. Thus, most ground nests were found in dry and hilly habitat.

With regards to host plant microhabitat, the number of nests oriented downhill vs. uphill ($N = 17, 2$; respectively) differed significantly from an expectation of equal occurrence ($P < 0.001$). Percent moisture was significantly lower inside nests compared with adjacent soil, but nest temperature was statistically identical to adjacent soil temperature (Table 1). Nest pH was significantly higher than the pH of adjacent soil (Table 1).

**Table 1.** Abiotic factors measured inside 25 Paraponera clavata nests and within adjacent soil (mean ± SE). Paired t-tests compared nest and adjacent soil means, asterisks indicate significant differences.

| Abiotic factor | Nest | Soil | df | t | P |
|---|---|---|---|---|---|
| Temperature (°C) | 26 ± 1 | 26 ± 1 | 24 | 1.000 | 0.327 |
| Moisture (%) | 27 ± 2 | 37 ± 3 | 24 | 3.564 | 0.002* |
| pH | 6.1 ± 0.1 | 5.9 ± 0.1 | 24 | 3.110 | 0.005* |

The planar surface area of nests was 6280 ± 800 cm2 (mean ± SE), and no relationship existed between nest surface area and plant DBH ($N = 25$, $r = 0.036$, $P > 0.15$) or height class of host plant ($F_{3, 24} = 0.806$, $P > 0.5$). Thirteen host plants (52%) were taller than 30 m and the remaining 12 were evenly divided among the three other height classes (Table 2). Ten and eight host plants ranged between 32 – 63.9 cm and 16 – 31.9 cm DBH, respectively (72% total; Table 2). Twenty-one of 25 nests were found at the bases of trees, four of which were *P. macroloba*. The four remaining nests were found at the bases of palms. Thirteen host plants were buttressed. It is important to note that these are descriptive characteristics of the observed host plants, rather than explicit ant preferences, because the natural distribution of plant characteristics (e.g., height, DBH, species) was not determined at the study site.

**Table 2.** Number of host plants utilized by *Paraponera clavata* in five DBH classes and four height classes.

| Height (m) DBH (cm) | 0-10 | 11-20 | 21-30 | > 30 |
|---|---|---|---|---|
| 1 - 7.9 | 2 | - | - | - |
| 8 - 15.9 | 1 | - | - | - |
| 16 - 31.9 | 1 | 4 | 2 | 1 |
| 32 - 63.9 | - | - | 2 | 8 |
| > 64 | - | - | - | 4 |

## Discussion

Water prevalence was a significant determinant of *P. clavata*'s ground nesting ecology, because 23 of 25 colonies were located on dry and hilly habitat characterized by dense understory plant communities. On Barro Colorado Island, Panama, *P. clavata* nests are significantly associated with high plateaus and younger forest (Pérez et al., 1999). Inclined terrain may benefit ants during periods of heavy rainfall when nests on flat substrata are inundated, resulting in colony mortality. High densities of lianas and vines in younger forest provide these arboreal foragers increased access to the canopy. However, it should not be discounted that *P. clavata* infrequently nest in tree crotches as high as 14 m above the forest floor (Breed and Harrison, 1989). At their field site in La Selva Biological Station, Breed and Harrison (1989) estimated that minimally 5 – 15% of *P. clavata* nests are arboreal. Such a conservative estimate would not alter the conclusions drawn from this study given the preponderance of nests found in dry habitat. However, a thorough assessment of arboreal nesting is still needed to completely understand the ecological impact of this species (Breed and Harrison, 1989). Arboreal nests hypothetically alleviate the risks associated with swampy habitat, but due to logistical constraints they were not systematically searched for in this study.

At a microhabitat scale, *P. clavata* adjusted the orientation of the nest with respect to the host plant when the slope of the ground was > 5°. The majority of nests were situated on the downhill side of the tree, likely using the trunk as a shield against water flow to reduce the risk of inundation. Only two nests were wedged between their host tree and the ground facing uphill. Further increasing their potential to collect water, these two colonies were surrounded by large buttresses. Such uphill facing cavities could accumulate rainwater and flood the nest, but both colonies extended 50 cm up their trees, perhaps to provide refuge during a deluge. A different nest located in a wet plot also had the majority of entrances 60 cm above the ground, created in soil burrows within fissures of the host's trunk. In contrast, none of the 17 colonies oriented on the downhill side of the tree extended up the host.

Further supporting *P. clavata*'s preference for dry habitat was the observation that nest soil moisture was significantly lower than ambient soil moisture. Similarly, the colonies of *Formica ulkei*, which are found near sources of water within clearings and at the margins of midwestern American forests (Talbot, 1961), display lower moisture content (27.23 ± 0.66%) than adjacent soil (38.54 ± 0.77%) [Scherba, 1959]. However, harvester ant (*Pogonomyrmex* spp.) nests in xeric environments exhibit higher moistures than adjacent soil (Whitford, 1988; McGinley et al., 1994). These contrasting data are not surprising because nests buffer extreme abiotic fluctuations (Seeley and Heinrich, 1980), thus providing a narrow range of moisture regimes appropriate for brood development (Scherba, 1959). In this study, nest and ambient soil temperatures were identical, but a difference in temperature might have been detected deeper within the nest, as a wood ant (*Formica polyctena*) colony in a temperate forest had increased temperatures in the center of the nest compared with the periphery (Coenan-Staß et al., 1980). *P. clavata* colonies displayed significantly higher pH levels than the surrounding soil, corresponding closely to pH values for nests and adjacent soil (6.17 ± 0.15 and 5.92 ± 0.13, respectively) of the European common black ant, *Lasius niger* (Frouz et al., 2003). In contrast, *Pogonomyrmex barbatus* (Wagner et al., 1997) and *Formica canadensis* (Culver and Beattie, 1983) nests do not exhibit differences in pH from surrounding soil. The observed abiotic conditions within *P. clavata* nests warrant further investigation to determine if they match requirements for brood development.

The majority of host trees was taller than 30 m and ranged from 16 – 63.9 cm DBH. Although these data cannot suggest that *P. clavata* prefers host plants with these attributes, they are consistent with previous studies. Taller trees provide workers with enhanced access to the canopy, as Belk et al. (1989), found mid and over-canopy tree species to be favored by *P. clavata*. On Barro Colorado Island, trees greater than 8 cm DBH are utilized more often than expected (Belk et al., 1989; Pérez et al., 1999). However, in the current study, neither taller nor thicker trees harbored nests with greater surface areas, suggesting that colonies require hosts of a minimum size for canopy access, and achieve similar proportions when this threshold is surpassed. In other words, arboreal foragers such as *P. clavata* (Wetterer, 1994; Dyer, 2002) and other ponerines (Lachaud et al., 1984; Valenzuela-González et al., 1995) need sufficient connections between trees in the canopy to increase foraging territory, which likely explains the lack of a relationship between nest size and plant height or DBH class.

Bennett and Breed (1985) suggested that *P. clavata* nests were strongly associated with *P. macroloba* in La Selva because mature trees possess buttresses and extra-floral nectaries. Furthermore, Hölldobler and Wilson (1990a) showed that *P. clavata* queens are able to select *P. macroloba* based on the odor of bark and leaves alone. The current study cannot conclusively support these findings because data on *P. macroloba's* population density is unavailable for either site, although four nests were found at the bases of *P. macroloba*. The presence of extra-floral nectaries on other tree species was not determined. Buttresses were not a critical factor for host selection, because 12 (48%) nest plants lacked buttresses. However, three of four nest palms possessed stilt roots, which also present suitable nesting crevices. The fourth palm nest was located within a cluster of six individual understory palms. It may be that *P. clavata* does not prefer buttresses *per se*, but rather any sort of solid, protective architecture.

Ants are among the leading predators of insects and other small invertebrates in terrestrial habitats (Hölldobler and Wilson, 1990b). Arthropod prey, including dominant herbivores such as leaf-cutting ants and lepidopteran larvae, comprises 4 – 25% of the booty *P. clavata* workers return to the nest (Young and Hermann, 1980; Dyer, 2002). Furthermore, this species has indirect positive effects on plant biomass (Dyer, 2002). If the prevalence of water does indeed affect the nest distribution of *P. clavata*, potential ecological differences between relatively wet and dry lowland rain forests deserve future consideration. However, further research is still needed to determine how the prevalence of water affects colony distribution, including surveys for arboreal nests in swampy habitat, and manipulative experiments to investigate *P. clavata's* ability to cope with increased moisture in seasonally flooded habitats.

## Acknowledgements

G. S. Jones provided inspiration and invaluable advice throughout the entire project. J. Herrera (La Peninsula) and A. Rothman (Friends of the Great Green Macaw) supported my stay at El Retorno. S. Hocking and R. J. Guenther assisted with fieldwork. I thank M. D. Breed, S. L. Bush, P. J. Edmunds, D. A. Gray, R. J. Miller and an anonymous referee for thoughtfully reviewing the manuscript. The Northeastern University Honors Department and the Center for Experiential Education and Academic Advising funded this study.

## References

Belk MC, Black HL, Jorgensen CD. 1989. Nest tree selectivity by the tropical ant, *Paraponera clavata*. *Biotropica* 21: 173-177.

Bennett B, Breed MD. 1985. On the association between *Pentaclethra macroloba* (Mimosaceae) and *Paraponera clavata* (Hymenoptera: Formicidae) colonies. *Biotropica* 17: 253-255.

Breed MD, Harrison JM. 1989. Arboreal nesting in the giant tropical ant, *Paraponera clavata* (Hymenoptera: Formicidae). *Journal of the Kansas Entomological Society* 62: 133-135.

Breed MD, Stiller TM, Fewell JH, Harrison JM. 1991. Intercolonial interactions and nestmate discrimination in the giant tropical ant, *Paraponera clavata*. *Biotropica* 23: 301-306.

Brian MV. 1963. Studies of caste differentiation in *Myrmica rubra* L. *Insectes Sociaux* 10: 91-102.

Brian MV. 1973. Temperature choice and its relevance to brood survival and caste determination in the ant *Myrmica rubra* L. *Physiological Zoology* 46: 245-252.

Calabi P, Porter SD. 1989. Worker longevity in the fire ant *Solenopsis invicta*: ergonomic considerations of correlations between temperature, size and metabolic rates. *Journal of Insect Physiology* 35: 643-649.

Cassill DL, Tschinkel WR. 2000. Behavioral and developmental homeostasis in the fire ant, *Solenopsis invicta*. *Journal of Insect Physiology* 46: 933-939.

Coenan-Staß D, Schaarschmidt B, Lamprecht I. 1980. Temperature distribution and calorimetric determination of heat production in the nest of the wood ant, *Formica polyctena* (Hymenoptera, Formicidae). *Ecology* 61: 238-244.

Culver DC, Beattie AJ. 1983. Effects of ant mounds on soil chemistry and vegetation patterns in a Colorado montane meadow. *Ecology* 64: 485-492.

Dyer, LA 2002. A quantification of predation rates, indirect positive effects on plants, and foraging variation of the giant tropical ant, *Paraponera clavata*. *Journal of Insect Science*. 2: 18 (online) URL: http://www.insectscience.org/2.18

Frouz J, Holec M, Kalcik J. 2003. The effect of *Lasius niger* (Hymenoptera, Formicidae) ant nest on selected chemical properties. *Pedobiologia* 47: 205-212.

Hölldobler B, Wilson EO. 1990a. Host tree selection by the giant Neotropical ant *Paraponera clavata* (Hymenoptera: Formicidae). *Biotropica* 22: 189-190.

Hölldobler B, Wilson EO. 1990b. *The Ants*. Cambridge: Harvard University Press.

Hood WG, Tschinkel WR. 1990. Desiccation resistance in arboreal and terrestrial ants. *Physiological Entomology* 15: 23-35.

Janzen DH, Carroll CR. 1983. *Paraponera clavata*. In Janzen DH, editor. *Costa Rican Natural History* , 752-753. Chicago: University of Chicago Press.

Kay CA, Whitford WG. 1975. Influences of temperature and humidity on oxygen consumption of five Chihuahuan desert ants. *Comparative and Biochemical Physiology* 52A: 281-286.

Lachaud J-P, Fresneau D, García-Pérez J. 1984. Étude des strategies d'approvisionnement chez trios espéces de fourmis Ponérines (Hymenoptera, Formicidae). *Folia Entomológica Méxicana* 61: 159-177.

Levings SC. 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy distributions. *Ecological Monographs* 53: 435-455.

McCluskey ES, Brown Jr WL. 1972. Rhythms and other biology of the giant tropical ant *Paraponera*. *Psyche* 79: 335-347.

McDade LA, Bawa KS, Hespenheide HA, Hartshorn GS, editors. 1994. *La Selva: ecology and natural history of a Neotropical rain forest*. Chicago: University of Chicago Press.

McGinley MA, Dhillion SS, Neumann JC. 1994. Environmental heterogeneity and seedling establishment: ant-plant-microbe interactions. *Functional Ecology* 8: 607-615.

Peakin G, Nielsen MG, Syberg N, Pederson J. 1985. Respiration in the larvae of the ants *Myrmica scabrinodis* and *Lasius flavus*. *Physiological Entomology* 10: 205-214.

Pérez R, Condit R, Lao S. 1999. Distribución, mortalidad y asociación con plantas, de nidos de *Paraponera clavata* (Hymenoptera: Formicidae) en la isla de Barro Colorado, Panamá. *Revista de Biología Tropical* 47: 697-709.

Porter SD. 1988. Impact of temperature on colony growth and developmental rates of the ant, *Solenopsis invicta*. *Journal of Insect Physiology* 34: 1127-1133.

Porter SD, Tschinkel WR. 1993. Fire ant thermal preferences: behavioral control of growth and metabolism. *Behavioral Ecology and Sociobiology* 32: 321-329.

Potts LR, Francke OF, Cokendolpher JC. 1984. Humidity preferences of four species of fire ants (Hymenoptera: Formicidae: *Solenopsis*). *Insectes Sociaux* 31: 335-339.

Roces F, Nuñez JA. 1989. Brood translocation and circadian variation of temperature preference in the ant *Camponotus mus*. *Oecologia* 81: 33-37.

Ryti RT, Case TJ. 1986. Overdispersion of ant colonies: a test of hypotheses. *Oecologia* 69: 446-453.

Scherba G. 1959. Moisture regulation in mound nests of the ant, *Formica ulkei* Emery. *American Midland Naturalist* 61: 499–507.

Seeley T, Heinrich B. 1980. *Regulation of temperature in the nests of social insects*. In Heinrich B, editor. *Insect Thermoregulation*, 159-234. New York: John Wiley & Sons, Inc.

Sokal RR, Rohlf FJ. 1995. *Biometry*, 3rd edition. W. H. Freeman and Company.

Talbot M. 1961. Mounds of the ant *Formica ulkei* at the Edwin S. George Reserve, Livingston County, Michigan. *Ecology* 42: 202-205.

Thurber DK, Belk MC, Black HL, Jorgensen CD. 1993. Dispersion and mortality of colonies of the tropical ant *Paraponera clavata*. *Biotropica* 25: 215-221.

Valenzuela-González J, López-Méndez A, Lachaud J-P. 1995. Activity patterns and foraging activity in nests of *Ectatomma tuberculatum* (Hymenoptera: Formicidae) in cacao plantations. *Southwestern Entomologist* 20: 507-515.

Vogt JT, Appel AG. 1999. Standard metabolic rate of the fire ant, *Solenopsis invicta* Buren: effects of temperature, mass and caste. *Journal of Insect Physiology* 45: 655-666.

Wagner DM, Brown JF, Gordon DM. 1997. Harvester ant nests, soil biota and soil chemistry. *Oecologia* 112: 232-236.

Wetterer JK. 1994. Attack by *Paraponera clavata* prevents herbivory by the leaf-cutting ant, *Atta cephalotes*. *Biotropica* 26: 462-465.

Wheeler GC, Wheeler J. 1976. Ant larvae: review and synthesis. *Memoirs of the Entomological Society of Washington* 7: 82-83.

Whitford, WG. 1988. Effects of harvester ant (*Pogonomyrmex rugosus*) nests on soils and a spring annual. *Southwestern Naturalist* 33: 482-485.

Wiernasz DC, Cole BJ. 1995. Spatial distribution of *Pogonomyrmex occidentalis*: recruitment, mortality and overdispersion. *Journal of Animal Ecology* 64: 519-527.

Young AM, Hermann, HR. 1980. Notes on foraging of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). *Journal of the Kansas Entomological Society* 53: 35-55.