



HAL
open science

Nest Distribution and Food Preferences of *Ectatomma ruidum* (Hymenoptera: Formicidae) in Shaded and Open Cattle Pastures of Colombia

Carlos Santamaría, Inge Armbrrecht, Jean-Paul Lachaud

► **To cite this version:**

Carlos Santamaría, Inge Armbrrecht, Jean-Paul Lachaud. Nest Distribution and Food Preferences of *Ectatomma ruidum* (Hymenoptera: Formicidae) in Shaded and Open Cattle Pastures of Colombia. *Sociobiology*, 2009, 53 (2B), pp.517-541. hal-02131957

HAL Id: hal-02131957

<https://hal.science/hal-02131957>

Submitted on 16 May 2019

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

Nest Distribution and Food Preferences of *Ectatomma ruidum* (Hymenoptera: Formicidae) in Shaded and Open Cattle Pastures of Colombia

by

Carlos Santamaría¹, Inge Armbrrecht¹ & Jean-Paul Lachaud^{2,3}

ABSTRACT

Ectatomma ruidum is a common ground-dwelling ant species in the Neotropics which has been reported as a potential biocontrol agent in maize and coffee-cocoa agroecosystems in Mexico and Nicaragua. Its spatial distribution and food preferences were evaluated between February and May 2007, both in shaded (with tree cover) and sunny (open) cattle pastures in the Pesca-dor and El Palmar regions of southwestern Colombia. Two sunny and two shaded cattle pasture plots were selected at each region. Twenty consecutive, equilateral 25 m² parcels were established at each plot. Nest locations were found by following trails from 20 equidistant tuna baits per parcel. The procedure was repeated during the wet and dry seasons with a total of 16 plot records. For determining food preferences, a paper disk providing five live ticks, five honey droplets and five *Passiflora ligularis* seeds was placed 30 cm away from the nest entrance, at one nest for each of 15 parcels per plot. Nest distribution was aggregated in shaded pastures, with an average nest density of 568 nests/ha, whereas it was mainly random in sunny pastures, with an average nest density of 1945 nests/ha. Whatever the season, *E. ruidum* nested preferentially in open places in both regions, apparently avoiding soil surfaces under the tree canopy cover in shaded pastures. This could explain the aggregated pattern recorded in these pastures despite some intraspecific competition. Foragers demonstrated a high capacity as seed dispersers, the myrmecochoric *P. ligularis* seeds representing 74.7% of the total weight of

¹Biology Department, Universidad del Valle, Apartado Aéreo 25360. Cali, Colombia.

²Centre de Recherches sur la Cognition Animale, CNRS-UMR 5169, Université Paul-Sabatier, 118 route de Narbonne, F-31062 Toulouse cedex 09, France

³El Colegio de la Frontera Sur, Dpto Entomología Tropical, Apdo Postal 36, Tapachula 30700, Chiapas, Mexico

Corresponding author: Inge Armbrrecht, Universidad del Valle, Departamento de Biología, Calle 13 # 100-00. Cali, Colombia e-mail: inge@univalle.edu.co, ingeparallel@gmail.com

all food items removed. Comparatively, they were significantly less attracted by honey and ticks which were retrieved in similar quantities (14.3% and 11.0% of the total weight removed, respectively). In the course of this study, individual workers were observed carrying in their mandibles wild, natural ticks, captured in the field. This is the first report of ants naturally preying on ticks in Colombia. Our data confirm the status of *E. ruidum* as an important natural biocontrol agent which could be properly managed for ecological services in Neotropical agroecosystems.

Key words: Andean mountains, ant spatial distribution, *Ectatomma ruidum*, land management, open pastures, predation on ticks, shaded pastures, seed dispersion.

INTRODUCTION

The presence of trees in agroforestry, cattle pastures, and silvopastoral systems is very common in Latin America. Some of the most important agronomic functions of trees are: a) providing a proper microclimate for certain crops or pasture systems, b) the incorporation of organic matter to soil through leaf litter and root growth, c) nitrogen fixation (Leguminae), d) nutrient circulation, and e) preventing or decreasing soil erosion (Beer *et al.* 1998). Plant species richness and canopy cover are also variables that have explained the relatively high diversity of silvopastoral systems (Ibrahim *et al.* 1999). The Colombian Andes exhibit highly fragmented landscapes, in which the last remnants are constantly being transformed into cattle pastures or intensively managed crops, a phenomenon that is causing wild species extinction and the disruption of ecological characteristics (Galindo-González *et al.* 2000). Nowadays, about 35% of the land used for cattle ranching is in conflict with the conservation of natural resources in Colombia (Gómez 2007). It is therefore necessary to search for a sustainable cattle-raising system and an ecologically friendly agriculture, mainly by introducing and managing shrubs and trees in these systems (Kang & Akinnifesi 2000). One aspect in the search of sustainable productive systems is to understand how keystone associated species behave when shade or agronomic management changes.

Ants (Hymenoptera: Formicidae) are frequently considered as ecosystem engineers because of their role in moving large amounts of matter and energy throughout the ecosystem's compartments and trophic webs (Lavelle *et al.*

2006). Because they are eusocial insects, their colonies tend to occupy or construct nests, which confers on them a certain spatio-temporal stability (Hölldobler & Wilson 1990). One of the factors affecting nest stability is their spatial location (Bernstein & Gobbel 1979). Nest sites may provide indications of appropriate environments for brood development and also of places for food collection (Bernstein & Gobbel 1979). It is likely that the selective indication of an enemy or competitor is a general phenomenon for ants, and perhaps the factor that triggers the behavioral mechanism regulating ant distribution, and consequently, nest distribution. This means that nest distribution of ants reflects intra- and interspecific interactions (Hölldobler & Lumsden 1980, Levings & Franks 1982).

Three types of spatial distributions can be recognized for a given population: random, uniform and aggregated (or contagious). Because social insects may be also predators, mutualists, and competitors, their distribution patterns play an important role in ecosystems (Wilson 1985, Crist 1998, Jouquet *et al.* 2004, Alinvi *et al.* 2008). The most frequent distribution recorded for ants is the uniform (also known as regular or overdispersed) one, and this is generally explained as the result of intra- or interspecific competition for food among colonies (Bernstein & Gobbel 1979, Levings & Traniello 1981). This distribution may be also the result of preferential predation on founding queens or young colonies by already-established ant colonies belonging to the same or different species (Levings & Franks 1982).

Ant nests can also show random or aggregated distribution, albeit in a lower frequency (Ryti & Case 1984, Herbers 1985, Soares & Schoereder 2001, Braschler & Baur 2003). A random distribution means that the probability of finding an individual or a nest is similar at any spatial or temporal point. It also implies that the presence of an individual (or nest) does not affect the chance to find another one, even sharing the same resource. In the aggregated distribution, the probability of finding an individual or a nest increases if there is another one, and they can even distribute in groups (Bolaños 1999, Soares & Schoereder 2001). The spatial distribution of populations is one of the most important ecological characteristics to be taken into account, in order both to carry out effective sampling (Wilson 1985), and to consider ants as possible biological control agents (Way & Khoo 1992, Philpott & Armbrrecht 2006).

Ectatomma ruidum Roger (Formicidae: Ectatomminae) is a widely distributed solitary predator throughout South and Central America. It is abundant in agricultural systems, savannas and forests (Weber 1946, Brown 1958). Its latitudinal distribution range goes from Michoacan and Veracruz in Mexico towards southeastern Ecuador and northern Brazil at the Amazonian basin (Brown 1958, Kugler & Brown 1982). The species is common and abundant in coffee, cocoa and maize plantations (Lachaud 1985, 1990, Perfecto 1991). Its altitudinal range varies between sea level up to 1600 m a.s.l. (Weber 1946). Nest density may be as high as 10,600 nests/ha in Panama (Pratt 1989) and 11,500 nests/ha (Schatz *et al.* 1998, Schatz & Lachaud 2008) in Mexico. Schatz & Lachaud (2008) in Mexico, Breed *et al.* (1990) in Costa Rica, and Levings & Franks (1982) in Panama found significantly overdispersed populations of this species for a broad range of nest densities varying from 1400 to 11,500 nests/ha.

Ectatomma ruidum usually exhibits terrestrial habits, although it is also commonly observed foraging on understory vegetation. In spite of its presence in a large range of habitats, *E. ruidum* prefers open places, that is, those exposed to solar radiation (Brown 1958, Kugler & Brown 1982, Rivera 2003, Domínguez & Fontalvo 2005, Osorio García 2007). Additionally, *E. ruidum* has sometimes been found as the dominant species in agroecosystems and matrices surrounding forest fragments (Perfecto 1990, Domínguez & Fontalvo 2005).

This ant is an efficient predator on other arthropods, leading several researchers to identify it as a potentially outstanding biocontrol agent (Weber 1946, Lachaud 1990, Perfecto 1991, Ibarra-Núñez *et al.* 2001). Nevertheless, the species uses a wide variety of resources, especially sweet secretions from extrafloral nectaries and hemipterans, and also collects seeds from soil, so it is also considered a generalist consumer (Passera *et al.* 1994, Lachaud *et al.* 1996, Dalling *et al.* 1998, Apple & Feener 2001, Escobar *et al.* 2007). A physiological explanation for these variable feeding habits is that predatory ant colonies need large quantities of animal protein for rising immature stages, while the adult stages need large quantities of carbohydrates for their maintenance activities (Medina 1995). Diet can also interact with climate to determine the extent of ant foraging (Lachaud 1990). Seasonal changes, that is, the distribution of rainfall, constitute another factor that might influence

the spatial dispersion of ants (Levings 1983); Colombia, a tropical country, shows a bimodal system, with two wet periods alternated with two dry periods throughout the year. Investigating the spatial distribution of ant nests at the local scale will provide information about their foraging activities and their role in both the agroecosystems and the natural systems (Bernstein 1975).

Even though *E. ruidum* has been the focus of several detailed studies in agricultural and natural systems (Lachaud *et al.* 1984, 1996, 1999, Perfecto 1990, 1991, Breed *et al.* 1990, 1999, Windsor *et al.* 1996, Altshuler 1999, de la Fuente & Marquis 1999, Ibarra-Núñez *et al.* 2001, Lachaud & Lachaud-Pérez 2009), there is still a lack of information about both its distribution and food preferences in changing management systems and in changing seasonality. This study aimed to describe the changes in the distribution of *E. ruidum* nests in shaded *vs.* open pastures along a wet *vs.* dry season in an Andean landscape in the Colombian Southwest. Food preferences (prey, carbohydrates and seeds) were also tested in this scenario, hypothesizing that energy-protein requirements might change according to the type of habitat which the ant population was inhabiting.

MATERIALS AND METHODS

The study was conducted in two types of cattle pastures: pastures with tree cover ('shaded') and open pastures without trees ('sunny'), during both dry and wet seasons. Intensive samplings were carried out in February and May 2007 in two regions or municipalities: (1) Pescador, Cauca Department (2° 56' 16" N; 76° 3' 53" W), located at an altitude of 1450 m.a.s.l., with an average annual temperature of 23°C (Luna *et al.* 2006) and a bimodal precipitation regime showing rainfall peaks in May and October; (2) El Palmar, Dagua, Valle del Cauca Department (3° 38' 45" N; 76° 41' 30" W), located at 1390 m.a.s.l., with an average temperature of 22°C (Ramírez 2006) and two precipitation peaks in April-May and October-November. Both regions are similar in terms of the landscape appearance, and slopes, except that they are located at opposite sides of the same mountain range, the Western Mountain range of the Colombian Andes ("Cordillera Occidental").

Two plots per each type of pasture were haphazardly selected at each region (Cauca and Valle), that is, four plots at Pescador and four at El Palmar. Each sunny plot neighbored a shaded one. Each plot was sampled twice, during

the dry and wet periods. In order to determine the kind of distribution of *E. ruidum*, and according to Ludwig & Reynolds (1988), a linear (100 m x 5 m) transect was established at the center of each pasture area. Both ends of each transect were at least 20 m apart from the border of the pasture. Each transect was divided into twenty 25 m² parcels. Twenty tuna-in-oil baits (1 g each), separated 5 m from one another, were deposited on the topsoil at the center of each parcel. All *E. ruidum* workers attracted to the baits were followed to their nest entrances. Search intensity was of about 18 h per plot. The entrance of each nest was labeled with a pink flag.

Food preference trials

One of the nests of each parcel was chosen for food preference trials. If a parcel did not have *E. ruidum* nests, a nest was chosen from the immediate lateral surrounding (off the transect) until a minimum of 15 nests per pasture were completed. Three types of food items were offered at a distance of 30 cm from the nest entrance, equidistantly located in a semicircle fashion respective to the nest entrance: (1) five live and moving ticks consisting of a mixture of *Rhipicephalus* (formerly *Boophilus*) *microplus* and *R. sp.* engorged females and immature stages (average weight: 0.07 ± 0.04 g). These arachnids are common hematophagous ectoparasites of cattle and part of their life cycle occurs on the soil (Dale 2001); (2) five sweet granadilla seeds (*Passiflora ligularis* Juss., Passifloraceae, weight: 0.18 ± 0.02 g); and (3) five honey-bee droplets (average weight: 0.02 ± 0.0 g). All the food items were placed on 10 cm diameter paper disks. The position or sequence of each type of food was randomly chosen.

In total, for each one of the three food categories, 1200 items were provided. The number of food items removed was recorded at each "feeding" disk for 90 min. All trials were carried out between 08:00 and 12:00, on sunny days, alternating sunny with shaded pastures.

Each 25 m² parcel was sub-divided into fifteen equidistant quadrants, in each of which the percentage of canopy cover was measured using a densimeter (* Forestry Suppliers). This instrument provides a binary measure consisting of the presence or absence of canopy cover. For each 25 m² parcel, the percentage of canopy cover took into account corresponded to the mean of the fifteen measures performed.

Nest dispersion in each plot was determined by the Morisita index (Krebs 1999), which is a non-parametric dispersion estimator. A Chi-square test was used to statistically examine if the index was due to randomness, with $H_0: Id = 1$; $H_a: Id \neq 1$ (Krebs 1999).

The number of items removed for each of the three food categories and their global weight were organized in a 2x3 contingency table conformed by two variables: pasture type and food category. Independence of the data was tested (Zar 1999) for both dry and wet periods. The possible existence of differences was examined through a non parametric Kruskal-Wallis test, and through a Mann-Whitney test if differences were detected. For shaded pastures, a correlation test between the number of nests in each parcel (for each plot) and the canopy cover was performed using STATISTICA 7 and PAST ver. 1.73 programs.

RESULTS

Distribution and nest density

A total of 1005 *E. ruidum* nests were registered in all sites and regions. Sunny pastures had 778 nests (383 at El Palmar and 395 at Pescador) while 227 nests were detected in shaded pastures (130 and 97, respectively). With an average density of 1945 ± 399 nests/ha and 1945 ± 284 nests/ha during the dry and wet season, respectively, the presence of *E. ruidum* in sunny pastures was 3.4 times denser than in shaded pastures (average density of 565 ± 72 nests/ha and 570 ± 129 nests/ha, respectively; Fig. 1) and the difference was statistically significant ($t = -5.82$, $df = 1,7$, $P < 0.001$). The highest average value per parcel was 7.55 ± 3.69 nests in a sunny pasture, and the lowest was 0.9 ± 1.52 in a shaded one. Nest distribution in the four shaded pastures was mainly aggregated during both wet and dry seasons, with Morisita's index values of at least 1.5 and up to 2.8, except for one record. In contrast, whatever the season, nest distribution was more variable in the four sunny pastures (with five random distributions and three aggregated ones) but tended to be essentially random with a Morisita's index most often equal to 1 or very close to this value (no value surpassed 1.2; Table 1).

In shaded pastures 113 and 114 nests were recorded during the dry and wet season, respectively. An inverse linear relationship was detected between the number of nests per parcel and the percentage of canopy cover in these parcels

(Spearman's rho = - 0.398 for dry and -0.564 for wet season; Fig. 2A,B; N = 80 for each plot and $P < 0.001$ for both dry and wet seasons).

Considering the exact location of the nests in relation to the extension of soil surface under tree cover, *E. ruidum* colonies located their nest significantly outside the tree canopy projection (196 nests out of 227 nests registered in shaded pastures; 99 nests out 114 for the wet season and 97 out of 113 for the dry season) (Fig. 3), which partially explains the aggregation trend in shaded pastures (Wilcoxon Matched Pairs Test, $Z = 4.27$, $N = 80$, $P < 0.001$ and $Z = 3.86$, $N = 80$, $P = 0.001$ for the wet and dry season, respectively).

Food preferences

A total of 1614 food items (44.8% of all offered food items) were removed by *E. ruidum* workers, of which 896 corresponded to honey droplets, 521 to seeds and 197 to ticks. The total biomass removed was 125.5 g, from which 17.9 g (14.3%) corresponded to honey and 13.8 g (11.0%) to ticks. With a

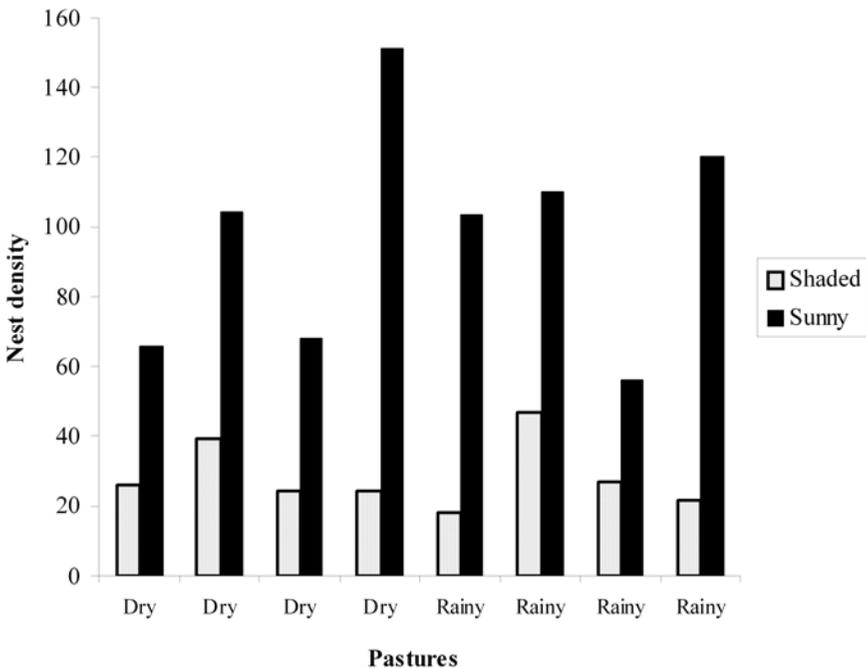


Fig. 1. Nest density for *E. ruidum* both in shaded (dark bars) and sunny (light bars) pastures. The first four pairs of bars correspond to the dry season, bars from five to eight correspond to the rainy (wet) season.

total weight of 93.8 g, seeds represented the highest biomass (74.7%) removed by *E. ruidum* (Table 2).

The accumulated total weight of the food items removed by the ants in sunny pastures was higher than that of the removed items in shaded pastures (73.0 g *vs.* 52.5 g, respectively). Differences in the weight of removed items were statistically significant between the three food categories ($H = 28.12$; $P < 0.0001$; $N = 48$): the weight of removed seeds was higher with respect to that of ticks ($U = 8$, $P < 0.0001$; $N = 16$) and honey ($U = 14$, $P < 0.0001$; $N = 16$). There was no statistical difference between the weight of removed honey and ticks.

Table 1. Nest distribution patterns according to Morisita's index. Values significantly > 1 indicate aggregation, those that do not differ significantly from 1 indicate a random distribution. No value significantly < 1 , corresponding to overdispersion, was found.

Morisita's Index	Type of Pasture	Spatial Distribution	Season	Municipality / Region	Chi-Square	<i>P</i>
1.1	Sunny	Random	Dry	El Palmar	23.69	0.21
1	Sunny	Random	Dry	El Palmar	15.6	0.68
1	Sunny	Random	Dry	Pescador	16.11	0.65
1.1	Sunny	Aggregated	Dry	Pescador	34.29	0.02
1.1	Sunny	Aggregated	Wet	El Palmar	31.82	0.03
1.2	Sunny	Aggregated	Wet	El Palmar	37.77	0.01
1	Sunny	Random	Wet	Pescador	19	0.46
1	Sunny	Random	Wet	Pescador	21.3	0.32
2.6	Shaded	Aggregated	Dry	El Palmar	58.62	$0.6 \cdot 10^{-5}$
1.2	Shaded	Random	Dry	El Palmar	26.13	0.13
2	Shaded	Aggregated	Dry	Pescador	42.66	0.001
2.4	Shaded	Aggregated	Dry	Pescador	51	$0.9 \cdot 10^{-4}$
1.5	Shaded	Aggregated	Wet	El Palmar	41.95	0.002
2.8	Shaded	Aggregated	Wet	El Palmar	48.66	$0.2 \cdot 10^{-3}$
2.1	Shaded	Aggregated	Wet	Pescador	46.3	$0.4 \cdot 10^{-3}$
1.6	Shaded	Aggregated	Wet	Pescador	30.7	0.04

Differences were also detected when the weights of removed items were compared within each type of pasture. For instance, significant differences were detected in the weight of the removed items for sunny pastures ($H = 13.99$; $N = 24$; $P = 0.0009$), the weight of the removed seeds being higher than that of ticks ($U = 3$; $N = 16$; $P = 0.0027$). No difference was detected between removed tick and honey weights in sunny pasture. A similar pattern of food preference was detected in shaded pastures with a clear difference

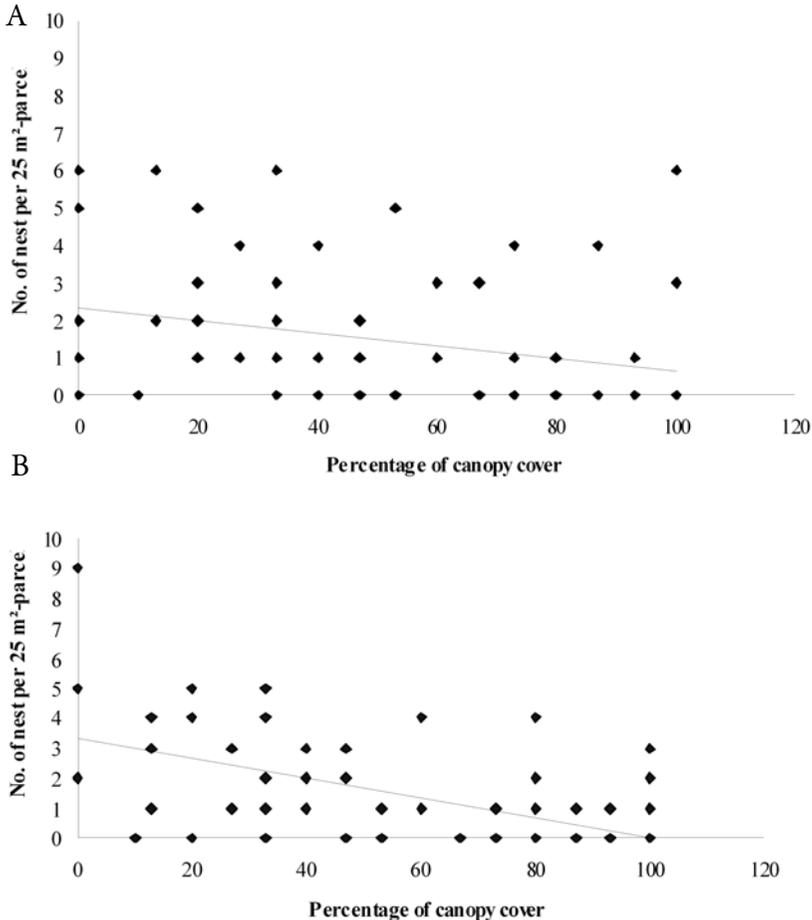


Fig. 2. Relationship between the number of nests per 25 m²-parcel and the percentage of canopy cover in the corresponding shaded parcels for the dry season (A) and the wet season (B); $n = 80$ in each case.

in the weight of the removed items ($H = 17.8$; $N = 24$; $P = 0.0001$). The weight of removed seeds was higher than that of honey ($U = 7$, $N = 18$; $P = 0.01$) and ticks ($U = 0$; $N = 16$; $P = 0.0008$), and the weight of removed honey was higher than that of ticks ($U = 2$, $P = 0.001$; Table 2). During the dry season there were also significant differences between the weight of the removed items ($H = 10$, $P = 0.0048$), and the difference was determined by the high weight of removed seeds with respect to the ticks and honey ($U = 5$, $P = 0.004$ and $U = 6$, $P = 0.006$, respectively; Table 2); there was no difference between the weight of removed honey items and ticks. During the wet season and the weight of removed seeds was higher than that of honey ($U = 0$, $P = 0.0008$) and ticks ($U = 0$, $P = 0.0007$), and the weight of removed honey was higher than that of ticks ($U = 10$, $P = 0.02$).

DISCUSSION

In ground-dwelling ants, both nest-site selection and, to a lesser extent, nest relocation have proved to be influenced by such diverse factors as soil characteristics (Carroll & Risch 1984, Elahi 2005), insolation (Harrison & Gentry 1981, Smallwood 1982, Sanada-Moriruma *et al.* 2006), vegetation structure (Briese 1982, Elmes & Wardlaw 1982, Díaz 1991, Schatz & Lachaud 2008), food availability (Reyes-López 1987, McGlynn *et al.* 2002) and intra- or interspecific competition (De Vita 1979, Ryti & Case 1988, Gordon 1991, McGlynn *et al.* 2004). According to both the species concerned and the characteristics of the microhabitat, some of these factors may have variable effects. This is particularly the case for the shading effect of vegetation which is known to either promote or limit the selection of the surface under tree or shrub cover for nesting. For example, location of starting nests under

Table 2. Number of food items and weight (g) removed by *E. ruidum* foragers in two types of pastures and two climatic seasons in 2007.

		No. Food items removed			Weight removed (g)		
		Honey	Seeds	Ticks	Honey	Seeds	Ticks
Sunny pasture	Wet	283	146	61	5.7	26.3	4.3
	Dry	189	147	93	3.8	26.5	6.5
Shaded pasture	Wet	248	150	17	5.0	27.0	1.2
	Dry	176	78	26	3.5	14.0	1.8
Total		896	521	197	17.9	93.8	13.8

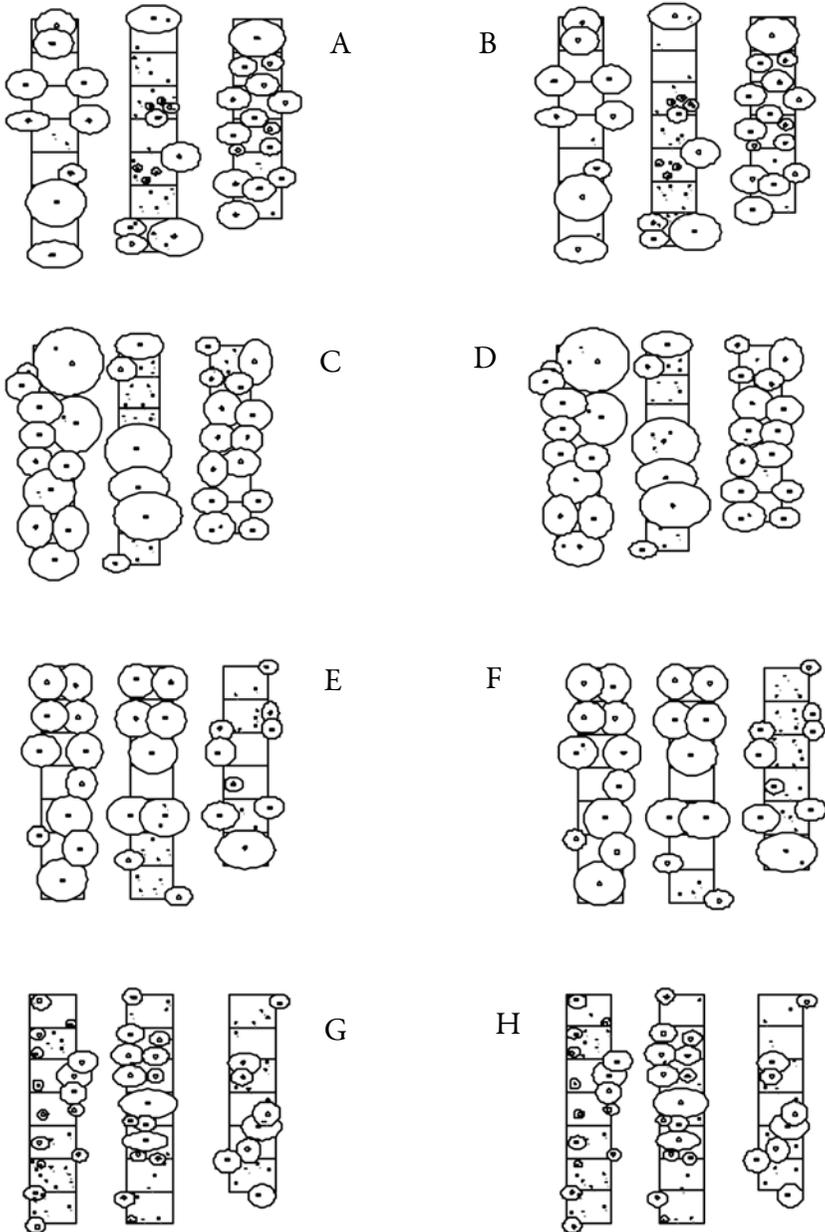


Fig. 3. Distribution of *E. ruidum* nests (dark dots) under the projection of the canopy of trees (represented by circles) in the transects (rectangles) of shaded pastures at Pescador and El Palmar. Pescador 1: wet (A), and dry (B), Pescador 2: wet (C), and dry (D), El Palmar 1: wet (E) and dry (F), El Palmar 2: wet (G) and dry (H).

tree canopies has been reported, in Arizona, for the founding queens of the fungus growing ant *Acromyrmex versicolor*, the shade allowing an easy and safe access to vegetation for initiation and growth of the fungus garden, shielded from potentially lethal temperatures (Rissing *et al.* 1986). In the same way, in cereal croplands of central Spain, the cold and wet winter climate is unfavorable to granivorous ants of the genus *Messor* and nests of *M. capitatus* located under shrub canopies may survive the winter weather conditions better than nests placed in more exposed microsites (Díaz 1991). On the other hand, always in central Spain but in grasslands and scrublands, two other *Messor* species, *M. barbarus* and *M. bowvieri*, reject the areas under the tree canopy for nesting, preferring subhumid and dry microsites (Azcárate & Peco 2003). Similarly, in our study, the clumped distribution of *E. ruidum* nests outside the tree canopy projection found in shaded pastures of both Colombian regions and during both dry and wet seasons showed a trend for this species to avoid being under the canopy of trees at this altitude and climate. However, the opposite distribution pattern (*i.e.*, uniform nest distribution in shaded ecosystems) has been measured by Santamaría *et al.* in sub-xerophytic zones of La Guajira, Northern Colombia in August 2008 (unpublished data). One possible explanation is that the immature stages of this ant species are very sensitive to high relative humidity inside the nests. Artificial colonies reared in shaded laboratory conditions at the Universidad del Valle (Cali) were quickly invaded by a pupae-attacking fungus (Santamaría & Herrera, pers. obs.). Interspecific interactions, such as competition, may also explain the aggregated distribution of nests in shaded pastures. These pastures were found to be the most diverse, in terms of ant species, among 16 pasture and coffee plots in both regions in an independent study using pitfall traps (Ramírez, Herrera & Armbrrecht, unpublished data) and other genera such as *Gnamptogenys*, *Pheidole*, *Solenopsis* and *Linepithema* were more abundant in shaded pastures. In this study, *Pachycondyla* sp. and *Odontomachus* sp. were frequently observed in shaded plots but not in sunny plots. Nevertheless, the location of their nests relative to those of *E. ruidum* was not measured. Shaded pastures offer a more stable microclimate and resources for the soil arthropod community; all these resources may determine foraging activity and nesting preferences for other ant species that may compete with *E. ruidum* (Levings 1983). In the study region, *E. ruidum* was present in open coffee agroecosystems but not in

shaded ones (Henaó 2008) and the explanation of interspecific competition determining nest distribution is still in the queue.

Random distribution dominated in sunny pastures during the dry and the wet seasons. More nests were present in sunny pastures than in shaded pastures, a fact that is consistent with the nesting behavior reported for Colombian open and disturbed ecosystems, but not so for lowland sub-xerophytic ecosystems with a relatively high arboreal component (Domínguez & Fontalvo 2005, Osorio García 2007). The negative correlation between the number of nests and the canopy cover during both dry and wet periods (Fig. 2A,B), as well as both the aggregated distribution in the shaded pastures and the location of the nests in open spaces, ratify that *E. ruidum* prefers open zones, as previously reported by Brown (1958) and Kugler & Brown (1982). For sunny pastures, the results of this study (*i.e.*, higher nest densities, random distribution, higher food removal) are also consistent with other studies performed in the Colombian eastern savanna plains (Medina 1994) and with the results obtained by Zelikova & Breed (2008) in four sites of Costa Rica that differed in land-use history and disturbance severity, showing that *E. ruidum* was the most abundant ant species collected in the open pasture habitat and the species responsible for the highest number of seed removals in this habitat. The above explanation proposed for shaded systems also applies for the distribution pattern in sunny pastures. If *E. ruidum* colonies were not limited by a high relative humidity (which is in turn related to pathogens) in open places, then its population density might increase along with a change in its distribution. Under open conditions, intraspecific competition may be important in the study region. *Ectatomma ruidum* showed to be a dominant species in open habitats in both regions (Ramírez, Herrera & Armbrecht, unpublished data), which indicates that this ant species might be influencing the behavior of neighboring ants (Perfecto 1990, Domínguez & Fontalvo 2005). Such an hypothesis is even more likely at the intraspecific competition level, considering the different evidences for colony territoriality reported for this species (Jaffé & Marquez 1987, Breed *et al.* 1990, Schatz *et al.* 1997a) and the resulting intraspecific competition between neighbors (De Carli *et al.* 1996, 1998, Jeral *et al.* 1997, Breed *et al.* 1999, Schatz & Lachaud 2008). Moreover, during the field stage of this study, inseminated queens of *E. ruidum* (without wings) were observed being chased by workers of other

colonies already established, suggesting intraspecific competition for nesting places. Although chasing fertilized females can be a reproductive strategy in *E. ruidum* (Lachaud *et al.* 1999), the evolution of this strategy may probably result from intraspecific competition to find proper nesting places.

However, the most plausible explanation for the nest distribution of *E. ruidum* found in this particular place in Colombia is that its nest density was very low as compared to that reported in Panama, Costa Rica or Mexico. Waloff & Blackith (1962) reported for *Lasius flavus*, in England, that the distribution of nests is uniform when the population density is high, but this distribution tends to be random when the nest density is low.

The high levels of honey droplets and seeds gathering performed by *E. ruidum* foragers reveal that these solitary workers use high quantities of energetic resources and rapidly take advantage of any available resources (Breed *et al.* 1990, Schatz *et al.* 1994, 1997b). The use of sugary resources is common in various *Ectatomma* species (Wood 1984, Del-Claro & Oliveira 1999, Blüthgen *et al.* 2000, Almeida & Figueiredo 2003, Richard *et al.* 2004) and has been repeatedly reported for *E. ruidum* (Weber 1946, Jaffé *et al.* 1989, Pratt 1989, Lachaud 1990, Passera *et al.* 1994, Altshuler 1999, Apple & Feener 2001). It is noteworthy that *P. ligularis* biomass represented 74.7% of the total biomass collected by ants in these experiments. However, the reason seems to be not only the energy content, but also the presence of other kinds of limiting nutrients (Aular *et al.* 2004, Peternelli *et al.* 2008), such as lipids, fatty acids and sugars, found in the elaiosome (the only edible part of the diaspore, the achene being rejected) which makes these seeds very attractive to the ants (Brew *et al.* 1989, Hughes *et al.* 1994, Mark & Olensen 1996). Although granivory in poneromorph ants is extremely scarce and limited to the single species *Pachycondyla sennaarensis* (Lévieux & Diomandé 1978, Dejean & Lachaud 1994), various species of large ponerine and ectatommine ants are known to depend largely on seeds and fruits to complement their diets (Berg 1975, Horvitz & Beattie 1980, Horvitz 1981, Andersen 1988, Pizo & Oliveira 1998, Fourcassié & Oliveira 2002). Myrmecochory is supposed to improve plant fitness reducing both predatory risks (Heithaus 1981, Turnbull & Culver 1983) and competition between sympatric congeneric plant species (Handel 1978), increasing seed germination (Leal *et al.* 2007) and enhancing seedling growth in nutrient-enriched or favorable microsites

(Beattie & Culver 1983, Horvitz & Schemske 1986, Andersen 1988, Leal *et al.* 2007; but see Bond & Stock 1989). As a consequence, myrmecochory by ants may affect the structure of plant communities (Davidson & Morton 1981, Beattie 1985). Among the poneromorph ants, several *Ectatomma* species have already been reported interacting with seeds: *E. brunneum* (Elias & McKey 2000), *E. edentatum* (Peternelli *et al.* 2004), *E. permagnum* (Peternelli *et al.* 2004), *E. muticum* (Leal *et al.* 2007). Some of them, like *E. brunneum*, *E. edentatum*, *E. muticum*, that carry diaspores to their nests and subsequently discard intact seeds on the ground, function as efficient high-quality dispersers *sensu* Giladi (2006). *Ectatomma ruidum*'s diet was already known to include an appreciable amount of vegetable items such as fruits and seeds (Weber 1946, Lachaud *et al.* 1984, Lachaud 1990, Kaspari 1993, Dalling *et al.* 1998, Zelikova & Breed 2008), a result confirmed by the present data. *Ectatomma ruidum* workers were strong enough to drag a seed individually, but the action could also be done by two or three ants. This fact opens the possibility that this ant could act, like various other *Ectatomma* species, as a good agent for seed dispersal in silvopastoral systems (Dalling *et al.* 1998, Escobar 2005, Escobar *et al.* 2007, Zelikova & Breed 2008).

Our results are consistent with other studies in that *E. ruidum* behaves as a multitrophic agent in these agroecosystems, involved in the exploitation of extrafloral nectaries and hemipterans, in seed dispersion and in predation (Wood 1984, Lachaud *et al.* 1984, Jaffé *et al.* 1989, 1990, Schatz *et al.* 1997b, Ibarra-Núñez *et al.* 2001, Escobar 2005). The generalist nature of its diet, its large size, along with the high flexibility of its foraging strategies (Lachaud 1985, Pratt 1989, Bestmann *et al.* 1995, Schatz *et al.* 1997b), would allow this ant to easily adapt to any drastic changes in its habitat and to unexpected variations in resource availability.

Apart from the amazing attraction of *E. ruidum* workers to myrmecochoric seeds, our results confirm that ticks can be actively attacked and retrieved by ants, a fact previously unreported in Colombia and seldom reported for different species of ants. Among poneromorph ants, predation on ticks has been reported essentially for ectatommine species (*E. brunneum* in Brazil, and *Rhytidoponera cristata*, *R. metallica* and *R. nudata* in Australia, review in Samish & Alekseev 2001) and for two ponerine species (*Pachycondyla striata* and *P. obscuricornis* in Brazil, Chagas *et al.* 2002). During our study, *E. ruidum*

was observed twice carrying live ticks which came from cattle and not from offered food items. In spite of this remarkable finding, the small number of ticks preyed by *E. ruidum* (by comparison with the quantities offered) could originate in the hardness of the immature's cuticle, which might interfere with the stinging behavior of the ant. There are several reports of arthropods attacking ticks, 41% of such reports are due to ants, and 30% to beetles (Coleoptera) (Samish & Alekseev 2001). Ants, and in particular dominant ants like *E. ruidum*, may be important in removing economically important pests of productive systems such as tick ectoparasites in cattle pastures. However, there are no studies that confirm that an ant species could be an effective natural enemy against these acarians. In a simultaneous study carried out in the same pastures on the same year, *E. ruidum* was one of the most effective ants preying on live fruit flies in sunny pastures and coffee plantations (Henao & Armbrrecht 2007) and this is consistent with Fernández (2003) and other previous works (Weber, 1946, Lachaud 1990, Perfecto 1991, Lachaud *et al.* 1996, Ibarra-Núñez *et al.* 2001) which stressed the likely importance of this species as a biocontrol agent in Neotropical agroecosystems.

In summary, this study showed that the nest distribution of a keystone generalist ant might change according to the conditions imposed by the management of the productive system, in this case, shaded pastures *vs.* unshaded neighboring pastures of the Colombian Andes. Learning how human actions affect the distribution of predatory ants may be important for further planning of agroecosystems, involving environmentally friendly practices directed to prevent pest outbreaks.

ACKNOWLEDGMENTS

We are grateful to C. Argote, F. Puentes and E. Álvarez for providing us permission for the use of their pastures and farms, G. Peñaranda and family for lodging, H. Henao, D. Pereira, R. Perea, O. Hidalgo, E. Álvarez and family for helping in the field work, and L. Rivera, H. Henao, S. Escobar, C. Cultid, M. Ramírez and Y. Domínguez for statistical and literature advisory. This research was financed by Colciencias 1106-07-17808 (Do trees stimulate biological control? The role of predator ants in Colombian coffee plantations and pastures, I. Armbrrecht; IP) and partially by the Colombian Entomological Society (SOCOLEN Becas estudiantiles).

REFERENCES

- Alinvi, O., J. Bohlin & J.P. Ball. 2008. Interspecific competition among ants in the boreal forest: Testing predictions from a linear hierarchical competition model. *Insectes Sociaux* 55: 1-11.
- Almeida, A.M. & R.A. Figueiredo. 2003. Ants visit nectaries of *Epidendrum denticulatum* (Orchidaceae) in a Brazilian rainforest : effects on herbivory and pollination. *Brazilian Journal of Biology* 63: 551-558.
- Altshuler, D.L. 1999. Novel interactions of non-pollinating ants with pollinators and fruit consumers in a tropical forest. *Oecologia* 119: 600-606.
- Andersen, A. 1988. Dispersal distance as a benefit of myrmecochory. *Oecologia* 75: 507-511.
- Apple, J.L. & D.H. Feener. 2001. Ant visitation of extrafloral nectaries of *Passiflora*: the effects of nectary attributes and ant behavior on patterns in facultative ant-plant mutualisms. *Oecologia* 127: 409-416.
- Aular, J., Y. Rodríguez, S. Roa, P. Iade & M. Antolínez. 2004. Características del fruto de cuatro pasifloras de la zona andina venezolana. *Bioagro* 16: 137-142.
- Azcárate, F.M. & B. Peco. 2003. Spatial patterns of seed predation by harvester ants (*Messor Forel*) in Mediterranean grassland and scrubland. *Insectes Sociaux* 50: 120126.
- Beattie, A.J. 1985. The evolutionary ecology of ant-plant mutualisms. Cambridge University Press, Cambridge. 196 pp.
- Beattie, A.J. & D.C. Culver. 1983. The nest chemistry of two seed-dispersing ant species. *Oecologia* 56: 99-103.
- Ber, J., R. Muschler, D. Kass & E. Somarriba. 1998. Shade management in coffee and cacao plantations. *Agroforestry Systems* 38: 139-164.
- Berg, R.Y. 1975. Myrmecochorous plants in Australia and their dispersal by ants. *Australian Journal of Botany* 62: 714-722.
- Bernstein, R.A. 1975. Foraging strategies of ants in response to variable food density. *Ecology* 56: 213-219.
- Bernstein, R.A. & M. Gobbel. 1979. Partitioning of space in communities of ants. *Journal of Animal Ecology* 48: 931-942.
- Bestmann, H.J., E. Janssen, F. Kern, B. Liepold & B. Hölldobler. 1995. All-*trans* geranylgeranyl acetate and geranylgeraniol, recruitment pheromone components in the Dufour gland of the ponerine ant *Ectatomma ruidum*. *Naturwissenschaften* 82: 334-336.
- Blüthgen, N., M. Verhaagh, W. Goitía, K. Jaffé, W. Morawet & W. Barthlott. 2000. How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. *Oecologia* 125: 229-240.
- Bolaños, F. 1999. Distribución Espacial. Guía laboratorio de ecología general. Escuela de Biología, Universidad de Costa Rica. 85 pp.
- Bond, W.J. & W.D. Stock. 1989. The cost of leaving home: ants disperse myrmecochorous seeds to low-nutrient sites. *Oecologia* 81: 412-417.

- Braschler, B. & B. Baur. 2003. Effects of experimental small-scale grassland fragmentation on spatial distribution, density, and persistence of ant nests. *Ecological Entomology* 28: 651-658.
- Breed, M.D., P. Abel, T.J. Bleuze & S.E. Denton. 1990. Thievery, home ranges, and nestmate recognition in *Ectatomma ruidum*. *Oecologia* 84: 117-121.
- Breed, M.D., T.P. McGlynn, E.M. Stocker & A.N. Klein. 1999. Thief workers and variation in nestmate recognition behavior in a ponerine ant, *Ectatomma ruidum*. *Insectes Sociaux* 46: 327-331.
- Brew, C.R., D.J. O'Dowd & I.D. Rae. 1989. Seed dispersal by ants: behaviour-releasing compounds in elaiosomes. *Oecologia* 80: 490-497.
- Briese D.T. 1982. Relationship between the seed-harvesting ants and the plant community in a semi-arid environment. In: *Ant-Plant Interactions in Australia* (R.C. Buckley, Ed.), Junk, The Hague. pp. 11-24.
- Brown, W.L. Jr. 1958. Contributions toward a reclassification of the Formicidae. II. Tribe Ectatommini (Hymenoptera). *Bulletin of the Museum of Comparative Zoology, Harvard* 118: 175-362.
- Carroll, C.R. & S.J. Risch. 1984. The dynamics of seed harvesting in early successional communities by a tropical ant, *Solenopsis geminata*. *Oecologia* 61: 388-392.
- Chagas, A.C.S., J. Furlong & C.B. Nascimento. 2002. Predation of *Boophilus microplus* (Canestrini, 1887) (Acari: Ixodidae) tick engorged female by the ant *Pachycondyla striata* (Smith, 1858) (Hymenoptera: Formicidae) in pastures. *Bioscience Journal* 18: 77-81.
- Crist, T.O., 1998. The spatial distribution of termites in shortgrass steppe: a geostatistical approach. *Oecologia* 114: 410-416.
- Dale, W.E. 2001. Plagas pests médicas veterinarias. *Garrapatas neotropicales* 1: 1-9.
- Dalling, J.W., M.D. Swaine & N.C. Garwood. 1998. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology* 79: 564-578.
- Davidson, D.W. & S.R. Morton. 1981. Competition for dispersal in ant-dispersed plants. *Science* 213: 1259-1261.
- De Carli, P., J.-P. Lachaud & G. Beugnon. 1996. Behavioural plasticity in *Ectatomma ruidum* Roger (Hymenoptera, Ponerinae), in a homospecific interactive situation. *Insect Social Life* 1: 137-143.
- De Carli, P., J.-P. Lachaud, G. Beugnon & J.A. López Méndez. 1998. Études en milieu naturel du comportement de leptobiose chez la fourmi néotropical *Ectatomma ruidum* (Hymenoptera, Ponerinae). *Actes des Colloques Insectes Sociaux* 11: 29-32.
- De la Fuente, M.A.S. & R.J. Marquis. 1999. The role of ant-tended extrafloral nectaries in the protection and benefit of a neotropical rainforest tree. *Oecologia* 118: 192-202.
- De Vita, J. 1979. Mechanisms of interference and foraging among colonies of the harvester ant, *Pogonomyrmex californicus* in the Mojave Desert. *Ecology* 60: 729-737.
- Dejean A. & J.-P. Lachaud. 1994. Ecology and behavior of a seed-eating ponerine ant: *Brachyponera senaarensis* (Mayr). *Insectes Sociaux* 41: 191-210.

- Del-Claro, K. & P.S. Oliveira. 1999. Ant-Homoptera interactions in a Neotropical savanna: the honeydew-producing treehopper, *Guayaquila xiphias* (Membracidae), and its associated ant fauna on *Didymopanax vinosum* (Araliaceae). *Biotropica* 31: 135-144.
- Díaz, M. 1991. Spatial patterns of granivorous ant nest abundance and nest site selection in agricultural landscapes of Central Spain. *Insectes Sociaux* 38: 351-363.
- Domínguez, Y. & L. Fontalvo. 2005. Composición y distribución de las comunidades de hormigas cazadoras (Hymenoptera: Formicidae, subfamilias poneromorfas) en remanentes de bosque seco tropical en el departamento del Atlántico, Colombia. Trabajo de Grado. Barranquilla-Colombia, Universidad del Atlántico, Facultad de Ciencias Básicas, Programa de Biología. 91 pp.
- Elahi, R. 2005. The effect of water on the ground nesting habits of the giant tropical ant, *Paraponera clavata*, 7 pp. *Journal of Insect Science*, 5:34, available online: insectscience.org/5.34.
- Elias, M. & D. McKey. 2000. The unmanaged reproductive ecology of domesticated plants in traditional agroecosystems: An example involving cassava and a call for data. *Acta Oecologica* 21: 223-230.
- Elmes, G.W. & J.C. Wardlaw. 1982. A population study of the ants *Myrmica sabuleti* and *M. scabrinodis* living at two sites in the South England. II. Effects of above-nest vegetation. *Journal of Animal Ecology* 51: 665-680.
- Escobar, S. 2005. Transporte de semillas por hormigas en agroecosistemas de la cuenca del Río La Vieja, Quindío y Valle del Cauca. Trabajo de Grado. Cali-Colombia, Universidad del Valle, Facultad de Ciencias. 66 pp.
- Escobar, S., I. Armbrecht & Z. Calle. 2007. Transporte de semillas por hormigas en bosques y agroecosistemas ganaderos de los Andes Colombianos. *Agroecología* 2: 65-74.
- Fernández, F. 2003. Introducción a las hormigas de la región Neotropical. Instituto de Investigación de Recursos Biológicos Alexander von Humboldt. 424 pp.
- Fourcassié, V. & P.S. Oliveira. 2002. Foraging ecology of the giant Amazonian ant *Dinoponera gigantea* (Hymenoptera, Formicidae, Ponerinae): activity schedule, diet and spatial foraging patterns. *Journal of Natural History* 36: 2211-2227.
- Galindo-González, J., S. Guevara & V.J. Sosa. 2000. Bat- and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. *Conservation Biology* 14: 1693-1703.
- Giladi, I. 2006. Choosing benefits or partners: a review of the evidence for the evolution of myrmecochory. *Oikos* 112: 481-492.
- Gómez, M.E. 2007. Uso de los árboles en sistemas de producción. CIPAV. http://www.cipav.org.co/index.php?option=com_content&task=view&id=129&Itemid=182
- Gordon, D.M. 1991. Behavioral flexibility and the foraging ecology of seed-eating ants. *American Naturalist* 138: 379-411.
- Handel, S.N. 1978. The competitive relationship of three woodland sedges and its bearing on the evolution of ant-dispersal of *Carex pedunculata*. *Evolution* 32: 151-163.
- Harrison J.S. & J.B. Gentry. 1981. Foraging pattern, colony distribution, and foraging range of the Florida harvester ant, *Pogonomyrmex badius*. *Ecology* 62: 1467-1473.

- Heithaus, E.R. 1981. Seed predation by rodents on three ant-dispersal plant species. *Ecology* 62: 136-145.
- Henaó, H. 2008. Análisis de la actividad depredadora por hormigas en cafetales con y sin sombra de árboles de cauca y Valle. Tesis Ms-C Universidad del Valle, Facultad de Ciencias Naturales y Exactas, Departamento de Biología. Cali, Colombia. 78 pp.
- Henaó, H. & I. Armbrecht. 2007. Depredación por hormigas en cafetales y potreros (con y sin árboles) del suroccidente Colombiano. I Congreso Científico Latinoamericano de Agroecología, SOCLA Agosto 13–15 de 2007, Antioquía, Colombia.
- Herbers, J.M. 1985. Seasonal structuring of a north temperate ant community. *Insectes Sociaux* 32: 224–240.
- Hölldobler, B. & C.J. Lumsden. 1980. Territorial strategies in ants. *Science* 210: 732-739.
- Hölldobler, B. & E.O. Wilson. 1990. *The Ants*. Harvard University Press/Springer. Berlin/Heidelberg. 732 pp.
- Horvitz, C.C. 1981. Analysis of how ant behaviors affect germination in a tropical myrmecochore *Calathea microcephala* (P. & E.) Koernicke (Marantaceae): microsite selection and aril removal by neotropical ants, *Odontomachus*, *Pachycondyla*, and *Solenopsis* (Formicidae). *Oecologia* 51: 47-52.
- Horvitz, C.C. & A.J. Beattie. 1980. Ant dispersal of *Calathea* (Maranthaceae) seeds by carnivorous ponerines (Formicidae) in a tropical rain forest. *American Journal of Botany* 67: 321-326.
- Horvitz, C.C. & D.W. Schemske. 1986. Ant-nest soil and seedling growth in a neotropical ant-dispersed herb. *Oecologia* 70: 318-320.
- Hughes L., M. Westoby & E. Jurado. 1994. Convergence of elaiosomes and insect prey: evidence from ant foraging behaviour and fatty acid composition. *Functional Ecology* 8: 358-365.
- Ibrahim, M., A. Camero, J.C. Camargo & H.J. Andrade. 1999. Sistemas silvopastoriles en América Central: Experiencias de CATIE. Primer Congreso Latinoamericano de Agroforestería para la Producción Animal Sostenible. Cali, Colombia, 25-27 de Octubre de 1999. <http://www.cipav.org.co/redagrofor/memorias99/Memorias.htm>
- Ibarra-Núñez, G., J.A. García., J.A. López & J.-P. Lachaud. 2001. Prey analysis in the diet of some ponerine ants (Hymenoptera: Formicidae) and web-building spiders (Araneae) in coffee plantations in Chiapas, Mexico. *Sociobiology* 37: 723-755.
- Jaffé, K. & M. Marquez. 1987. On agonistic behaviour among workers of the ponerine ant *Ectatomma ruidum* (Hymenoptera: Formicidae). *Insectes Sociaux* 34: 87-95.
- Jaffé, K., C. Pavis, G. Vansuyt & A. Kermarrec. 1989. Ants visit extrafloral nectaries of the orchid *Spathoglottis plicata* Blume. *Biotropica* 21: 278-279.
- Jaffé, K., H. Mauléon & A. Kermarrec. 1990. Qualitative evaluation of ants as biological control agents with special reference to predators on *Diaprepes* spp. (Coleoptera: Curculinidae) on citrus groves in Martinique and Guadeloupe. *Les Colloques de l'INRA* 58: 405-416.

- Jeral, J.M., M.D. Breed & B.E. Hibbard. 1997. Thief ants have reduced quantities of cuticular compounds in a ponerine ant, *Ectatomma ruidum*. *Physiological Entomology* 22: 207-211.
- Jouquet, P., N. Boulain, J. Gignoux & M. Lepage. 2004. Association between subterranean termites and grasses in a West African savanna: spatial pattern analysis shows a significant role for *Odontotermes n. pauperans*. *Applied Soil Ecology* 27: 99-107.
- Kang, B.T & F.K. Akinnifesi. 2000. Agroforestry as alternative land-use production systems for the tropics. *Natural Resources Forum* 24: 137-151.
- Kaspari, M. 1993. Body size and microclimate use in Neotropical granivorous ants. *Oecologia* 96: 500-507.
- Krebs, C.J. 1999. *Ecological Methodology*. 2nd ed., N.Y., USA. Addison-Wesley Logman. 620 pp.
- Kugler, C. & W.L. Jr. Brown. 1982. Revisionary and other studies on the ant genus *Ectatomma*, including the descriptions of two new species. *Search: Agriculture, Ithaca* 24: 1-7.
- Lachaud, J.-P. 1985. Recruitment by selective activation: an archaic type of mass recruitment in a ponerine ant (*Ectatomma ruidum*). *Sociobiology* 11: 133-142.
- Lachaud, J.-P. 1990. Foraging activity and diet in some neotropical ponerine ants. I. *Ectatomma ruidum* Roger (Hymenoptera, Formicidae). *Folia Entomológica Mexicana* 78: 241-256.
- Lachaud, J.-P., A. Cadena, B. Schatz, G. Pérez-Lachaud & G. Ibarra-Núñez. 1999. Queen dimorphism and reproductive capacity in the ponerine ant, *Ectatomma ruidum* Roger. *Oecologia* 120: 515-523.
- Lachaud, J.-P., D. Fresneau & J. García-Pérez. 1984. Étude des stratégies d'approvisionnement chez 3 espèces de fourmis ponérines. *Folia Entomológica Mexicana* 61: 159-177.
- Lachaud, J.-P., J.A. López-Méndez, B. Schatz, P. De Carli & G. Beugnon. 1996. Comparaison de l'impact de prédation de deux ponérines du genre *Ectatomma* dans un agroécosystème néotropical. *Actes des Colloques Insectes Sociaux* 10: 67-74.
- Lachaud, J.-P. & G. Pérez-Lachaud. 2009. Impact of natural parasitism by two eucharitid wasps on a potential biocontrol agent ant in southeastern Mexico. *Biological Control* 48: 92-99
- Lavelle, P., T. Decaëns, M. Aubert, S. Barot, M. Blouin, F. Bureau, P. Margerie, P. Mora & J.-P. Rossi. 2006. Soil invertebrates and ecosystem services. *European Journal of Soil Biology* 42: S3-S15.
- Leal, I.R., R. Wirth & M.C. Tabarelli. 2007. Seed dispersal by ants in the semi-arid Caatinga of North-east Brazil. *Annals of Botany* 99: 885-894.
- Lévieux, J. & T. Diomandé, 1978. La nutrition des fourmis granivores. II. Cycle d'activité et régime alimentaire de *Brachyponera senaarensis* (Mayr) (Hymenoptera: Formicidae). *Insectes Sociaux* 25: 187-196.
- Levings, S.C. 1983. Seasonal, annual, and among-site variation in the ground ant community of a deciduous tropical forest: some causes of patchy species distributions. *Ecological Monographs* 53: 435-455.

- Levings, S.C. & N.R. Franks. 1982. Patterns of nest dispersion in a tropical ground ant community. *Ecology* 63: 338-344.
- Levings, S.C. & J.F.A. Traniello. 1981. Territoriality, nest dispersion, and community structure in ants. *Psyche* 88: 265-319.
- Ludwig, J.A. & J.F. Reynolds. 1988. *Statistical Ecology. A primer on methods and computing*. N.Y., USA. A Wiley-Interscience Publication. 337 pp.
- Luna, W.A., J.A. Mera & J.A. Gallvis. 2006. Producción de dextrinas de yuca a partir de almidón nativo en la rallandería Todoyuca ubicada en el corregimiento Pescador (municipio de Caldonó, Cauca). http://www.clayuca.org/clayucanet/edicion09/articulo_rallanderia.pdf
- Mark, S. & J.M. Olesen. 1996. Importance of elaiosome size to removal of ant-dispersed seeds. *Oecologia* 107: 95-101.
- Medina U., C.A. 1994. Nidificación y patrones de distribución espacial de nidos de hormigas en una sabana tropical, Carimagua: Llanos Orientales de Colombia. *Boletín del Museo de Entomología de la Universidad del Valle* 2: 31-42.
- Medina U., C.A. 1995. Hormigas depredadoras de huevos de salivazo de los pastos *Aeneolamia varia* (Hemiptera: Cercopidae) en pasturas de *Brachiaria*, en los Llanos Orientales de Colombia. *Boletín del Museo de Entomología de la Universidad del Valle* 3: 1-13.
- McGlynn, T.P., R.A. Carr, J.H. Carson & J. Buma. 2004. Frequent nest relocation in the ant *Aphaenogaster araneoides*: resources, competition, and natural enemies. *Oikos* 106: 611-621.
- McGlynn, T.P., J.R. Hoovort, G.S. Jasper, M.S. Kelly, A.M. Polis, C.M. Spangler & B.J. Watson. 2002. Environmental heterogeneity affects demography of the Central American ant *Aphaenogaster araneoides*. *Journal of Tropical Ecology* 18: 231-244.
- Osorio García, A.M. 2007. Diversidad de hormigas poneromorfas en el paisaje fragmentado del bosque seco en el valle geográfico del Río Cauca. Trabajo de Grado. Cali-Colombia, Universidad del Valle, Facultad de Ciencias. 58 pp.
- Passera, L., J.-P. Lachaud & L. Gomel 1994. Individual food source fidelity in the neotropical ponerine ant *Ectatomma ruidum* Roger (Hymenoptera Formicidae). *Ethology Ecology & Evolution* 6: 13-21.
- Perfecto, I. 1990. Indirect and direct effects in a tropical agroecosystem: the maize-pest-ant system in Nicaragua. *Ecology* 71: 2125-2134.
- Perfecto, I. 1991. Ants (Hymenoptera: Formicidae) as natural control agents of pests in irrigated maize in Nicaragua. *Journal of Economic Entomology* 84: 65-70.
- Pternelli, E.F.O., L.C.A. Barbosa & T.M.C. Della Lucia. 2008. Isolation of compounds attractive to the leaf-cutting ant *Atta sexdens rubropilosa* Forel (Hymenoptera: Formicidae) from *Mabea fistulifera* elaiosome. *Química Nova* 31: 475-478.
- Pternelli, E.F.O., T.M.C. Della Lucia & S.V. Martins. 2004. Espécies de formigas que interagem com as sementes de *Mabea fistulifera* Mart. (Euphorbiaceae). *Revista Árvore* 28: 733-737.
- Philpott, S.M. & I. Armbrrecht. 2006. Biodiversity in tropical agroforests and the ecological role of ants and ant diversity in predatory function. *Ecological Entomology* 31: 369-377.

- Pizo, M.A. & P.S. Oliveira. 1998. Interactions between ants and seeds of a non-myrmecophilous neotropical tree, *Cabralea canjerana* (Meliaceae), in the Atlantic forest of southeast Brazil. *American Journal of Botany* 85: 669-674.
- Pratt, S.C. 1989. Recruitment and other communication behavior in the ponerine ant *Ectatomma ruidum*. *Ethology* 81: 313-331.
- Ramírez, M. 2006. Estudio del impacto del manejo en banco de forraje sobre las comunidades de hormigas (Hymenoptera - Formicidae) en el Valle del Cauca. Tesis Ms-C Universidad del Valle, Cali, Colombia.
- Reyes-López, J.L., 1987. Optimal foraging in seed-harvester ants: computer-aided simulation. *Ecology* 68: 1630-1633.
- Richard, F.-J., A. Dejean & J.-P. Lachaud. 2004. Sugary food robbing in ants: a case of temporal kleptobiosis. *Comptes Rendus Biologies* 327: 509-517.
- Rissing, S.W., R.A. Johnson & G.B. Pollock. 1986. Natal nest distribution and pleometrosis in the desert leaf-cutting ant *Acromyrmex versicolor* (Pergande) (Hymenoptera: Formicidae). *Psyche* 93: 177-186.
- Rivera, L. 2003. Diversidad de tres gremios de hormigas en cafetales bajo diferentes manejos de sombra. Trabajo de grado. Cali-Colombia, Universidad del Valle, Facultad de Ciencias. 56 pp.
- Ryti, R.T. & T.J. Case. 1984. Spatial arrangement and diet overlap between colonies of desert ants. *Oecologia* 62: 401-404.
- Ryti, R.Y. & T.J. Case. 1988. Field experiments on desert ants: testing for competition between colonies. *Ecology* 69: 1993-2003.
- Samish, M. & E. Alekseev. 2001. Arthropods as predators of ticks (Ixodoidea). *Journal of Medical Entomology* 38: 1-11.
- Sanada-Moriruma S., T. Satoh & Y. Obara. 2006. Territorial behavior and temperature preference for nesting sites in a pavement ant *Tetramorium tsushimae*. *Insectes Sociaux* 53: 141-148.
- Schatz, B., G. Beugnon & J.-P. Lachaud. 1994. Time-place learning by an invertebrate, the ant *Ectatomma ruidum* Roger. *Animal Behaviour* 48: 236-238.
- Schatz, B. & J.-P. Lachaud. 2008. Effect of high nest density on spatial relationships in two dominant Ectatommine ants (Hymenoptera: Formicidae). *Sociobiology* 51: 623-643.
- Schatz, B., J.-P. Lachaud & G. Beugnon. 1997a. Dynamics and flexibility of the foraging area in the ant *Ectatomma ruidum* Roger (Hymenoptera; Formicidae; Ponerinae). *Advances in Ethology (Supplement Ethology)* 32: 170.
- Schatz, B., J.-P. Lachaud & G. Beugnon. 1997b. Graded recruitment and hunting strategies linked to prey weight and size in the ponerine ant *Ectatomma ruidum*. *Behavioral Ecology and Sociobiology* 40: 337-349.
- Schatz, B., J.-P. Lachaud, V. Fourcassié & G. Beugnon. 1998. Densité et distribution des nids chez la fourmi *Ectatomma ruidum* Roger (Hymenoptera; Formicidae; Ponerinae). *Actes des Colloques Insectes Sociaux* 11: 103-107.

- Smallwood, J. 1982. The effect of shade and competition on emigration rate in the ant *Aphaenogaster rudis*. *Ecology* 63: 124-134.
- Soares, S.M. & J.H. Schoeder. 2001. Ant-nest distribution in a remnant of tropical rainforest in southeastern Brazil. *Insectes Sociaux* 48: 280-286.
- Turnbull, C.L. & D.C. Culver. 1983. The timing of seed dispersal in *Viola nuttallii*: attraction of dispersers and avoidance of predators. *Oecologia* 59: 360-365.
- Waloff, N. & R.E. Blackith. 1962. The growth and distribution of the mounds of *Lasius flavus* (Fabricius) (Hym: Formicidae) in Silwood Park, Berkshire. *Journal of Animal Ecology* 31: 421-437.
- Way, M.J. & K.C. Khoo. 1992. Role of ants in pest management. *Annual Review of Entomology* 37: 479-503.
- Weber, N.A. 1946. Two common ponerine ants of possible economic significance, *Ectatomma tuberculatum* (Olivier) and *E. ruidum* Roger. *Proceedings of the Entomological Society of Washington* 48: 1-16.
- Wilson, L.T. 1985. Estimating the abundance and impact of arthropod natural enemies in IPM systems. *Biological control in agricultural IPM systems*. Academic Press, Inc. 321 pp.
- Windsor, D.M., D.W. Trapnell & G. Amat. 1996. The egg capitulum of a Neotropical walkingstick, *Calynda bicuspis*, induces aboveground egg dispersal by the ponerine ant, *Ectatomma ruidum*. *Journal of Insect Behavior* 9: 353-367.
- Wood, T.K. 1984. Life history patterns of tropical membracids (Homoptera: Membracidae). *Sociobiology* 8: 299-344.
- Zar, J.H. 1999. *Bioestadistical Analysis*. 4th Edition Prentice Hall. 663 pp.
- Zelikova, T.J. & M.D. Breed. 2008. Effects of habitat disturbance on ant community composition and seed dispersal by ants in a tropical dry forest in Costa Rica. *Journal of Tropical Ecology* 24: 309-316.



