ENTOMOTROPICA
Vol. 21(2): 117-123. Agosto 2006.

ISSN 1317-5262

On foraging behavior of the polymorphic tree dwelling ant *Daceton armigerum* (Hymenoptera: Formicidae)

Yamil Madi y Klaus Jaffe
Universidad Simón Bolívar, Apdo. 89000. Caracas 1080-A. Venezuela. Tel-Fax: 0212-9063624

Abstract

Madi Y, Jaffe K. 2006. On foraging behavior of the polymorphic tree dwelling ant *Daceton armigerum* (Hymenoptera: Formicidae). Entomotropica 21(2): 117-123.

The exclusively arboreal ant *Daceton armigerum* is unusual in that it has highly polymorphic workers. We studied the foraging behavior and chemical recruitment to food by workers of *Daceton armigerum* in the laboratory and in the field. Workers hunt by ambush and use two strategies for recruiting nestmates aided by chemicals. One consists in placing chemical marks around food that recruits nestmates at distances of up to 15 cm. Another consists of trails, laid with chemicals originated from the abdomen, that can be several meters long. The chemical mark on the trail has two effects: one of attraction and other of orientation. These ants also use long lasting chemical trails to connect nest chambers distributed along diverse branches or trees. Polymorphism in this ant correlates somewhat with polyethism, as the smallest workers were never seen outside their nest.

Additional key words: Chemical communication, recruiting, social insects.

Resumen

Madi Y, Jaffe K. 2006. Sobre el comportamiento de forrajeo de la hormiga arbórea polimórfica *Daceton armigerum* (Hymenoptera: Formicidae). Entomotropica 21(2): 117-123.

La hormiga arbórea *Daceton armigerum* es excepcional en su tribu en cuanto que posee obreras altamente polimórficas. Aquí reportamos los resultados de estudios, tanto en el campo como en el laboratorio, de sus conductas de forrajeo y de reclutamiento utilizando señales químicas. Las obreras cazan por acecho y utilizan dos estrategias diferentes para reclutar compañeras de nido a fuentes de alimento. Una de estas estrategias consiste en colocar marcas de olor alrededor de la fuente de alimento para alertar y atraer a sus compañeras a distancias de hasta 15 cm. Otra estrategia consiste en colocar trillas de olor de hasta varios metros, colocando una secreción de una glándula abdominal sobre el sustrato. Esta marca química tiene dos efectos sobre las compañeras de nido: las atrae hacia la trilla y las orienta hacia la fuente de alimento. Estas hormigas también utilizan trillas químicas para conectar diferentes partes de sus nidos ubicados en cavidades diferentes en diferentes ramas de un árbol. El polimorfismo de esta hormiga correlaciona con un débil politeísmo de las obreras, donde las obreras más pequeñas nunca salen del nido.

Palabras clave adicionales: Comunicación química, forrajeo, insectos sociales, reclutamiento.

Introduction

The ant *Daceton armigerum* is one of the few ant species that lives and forages practically exclusively on trees and has highly polymorphic workers. Another such ant species is *Cephalotes atratus*. We lack knowledge of the foraging habits of any of those species. Yet a more detailed knowledge of the tasks workers have to fulfill in their daily lives will guide our understanding into the adaptive value of worker polymorphism in these ants and understand better their ecological role in tropical tree canopies. Preliminary studies indicated that in *D. armigerum*, individuals forage independently from each other, and recruiting for food is based on visual signals only (Wilson 1962a).

Miscellaneous information in the literature tells us that *D. armigerum* does not follow trails (Blum and Portocarrero 1966), but that *Solenopsis invicta* and other species follow the trails made with the contents the Dufor´s gland (Wilson 1962a) or poison gland (Blum and Portocarrero 1966) of *D. armigerum*. Recent studies reported that these ants use three types of chemical communication: Trail following mediated by sternal gland secretion; alarm mediated by the secretions of the mandibular glands; and attraction mediated by pygidial gland secretions (Holldöbler et al. 1990, Morgan et al. 1992).

Here we provide more detailed ethological information about the foraging behavior of workers of this species, the most polymorphic species of the tribe Dacetini, a very distinct group of poorly known Myrmicinae.

Methods

Two *D. armigerum* colonies were brought into the laboratory in December 1992, where we studied them from January to October 1993. They were collected at Uracoa, Venezuela (lat 8º45' long 62º47'), by cutting the trunk of the tree were the nest was located. The colonies contained 201 and 226 workers respectively. The larger colony died shortly after the end of this study and thus we found out that it included 69 males, 7 females and one queen. Both colonies were kept on the same trunks where they were found. Each nest was placed inside a plastic box (2x2 m) impregnated with oil in its internal walls to stop workers from escaping. A wooden framework was placed around each nest with four platforms (p). Food was regularly placed on p1 and p2 while p3 and p4 were kept empty. Food consisted of insects captured with light traps, crickets, fly larvae and adult *Drosophila*. Experiments in the field were carried out form September to October 1993, using five colonies living at Uracoa.

Ethograms: We made a descriptive list of behaviors of *D. armigerum* based on direct observations and videos made in the laboratory and in the field. Because these animals are diurnal, observation periods of thirty minutes, programmed at random, were made in the morning (6-11am), at noon (11am-1pm) and in the afternoon (1-6pm), during 16 days in the field and 90 days in laboratory. Castes were recorded according to the maximum length of the head of the worker.

Recruiting system in the field: Each of the five nests was tested twice starting at 10 am. The test consisted in offering two live butterflies, 4-5 cm long, pinned to the trunk near an active trail of *D. armigerum*. The site was filmed for ninety minutes with a Sony Handycam CCD-F55. Each 10 minutes we counted: the number of individuals in the area; the number of workers per minute that arrived and left the foraging area; the number of workers per minute that displayed chemical marking behavior as defined by Hölldobler et al. (1990). Counting started thirty minutes before positioning of the food in order to obtain an estimate of base activity for each area. Recruiting times were estimated by counting the ants recruited starting at the moment an explorer found the food.

Types of behavior: In another video, the behavior of the first individuals finding the food was registered. We marked with fluorescent paint or white corrector fluid (Typex) a spot on the abdomen of the first five workers who dragged the abdomen from the food to the nest, and with a different mark five additional workers chosen at random among at the food source. The relative size of the workers was estimated by visual comparison with a reference collection.

Laboratory tests: We used the same methodology as described above but increased observations of the basal level to two hours. Food consisted of four adult crickets for each test. The water source was used as a control. Specific points were marked on the routes followed by workers when they moved on the foraging areas in order to register the frequency and fidelity with which these routes were used. In addition, thirty ants were marked with individualized colour coded spots painted on their abdomen. The maximum width of the head of workers was determined with a Vernier. Each experiment was repeated 11 times in each nest, except when counting the total number of ants on the foraging area, where we made 15 repetitions.

Results

A series of behaviors was seen repeatedly, both in the laboratory and in the field, the most common of which were:

Hunting in ambush: This behavior was displayed by ants foraging alone. The ant opens the mandibles at 180º and introduces the head into cavities or tunnels or rested on the trunks surface, remaining static in that position for 30-90 min, or until a prey touched the jaws which triggered an immediate violent closing of the jaws (Gronenberg 1996, Gronenberg et al. 1998, Bolton 1999) and a characteristic snapping sound. Once the prey was captured, the ant carried the prey to the nest.

Chemical trail following: workers, after encountering a large food item, returned to the nest, bending their abdomen and dragging the tip of the gaster upon the substrate, as described by Hölldobler et al. (1990). Nestmates responded by walking quickly towards the trail, following it towards the food. We often observed workers, in groups of two to nine, exiting the nest and following the recruiting worker or its trail to the food. (Fig 1-4).

Short range chemical recruitment: workers place chemical marks around the food. The ant ran around the prey following irregular paths at a distance of maximum 15 cm from it, with the abdomen bent down and dragging the tip of the gaster on the substrate. Up to 45 workers were recruited to the prey. Foraging ants passing over these marks modified their trajectory and speed, quickly reaching the prey without any sign of trail following. The stimulus was strong enough to make some exploring workers that carried small preys abandon them and engage in this new recruitment.

Short range visual recruitment We observed short range recruiting by means of visual signals as reported by Wilson (1962a). This recruitment consists of short circular runs around a prey hold by another nestmate. Often the recruiting workers moves its abdomen up and down. Nestmates in the surroundings are alerted, making fast circular runs, eventually finding the prey. Workers attracted to the moving abdomen of the recruiting ant always touched it with their antennae, but not necessarily cooperated later in the recruitment process.

Long range chemical recruitment: The recruiting ant, after finding food, walks to the nest laying an odour trail. Other ants stumbling on the trail follow it with great excitation to the food. Trail following is achieved with great fidelity. Soon after the recruiting ant arrives at the nest, marking a trail, several individual workers or in small groups follow the trail to the prey. Some minutes later the recruiting ants return to the food showing trail marking behavior, often closely followed by several nestmates. Recruiting ants rarely stop when walking on the trail, often to antennate with a nestmate. The role of recruiting ants can shift to other workers during a recruitment process. The role of chemical recruitment is not restricted to a specific worker's size. The maximum head width of recruiters varied between 2,3 and 4,2 mm. The recruitment process included stereotyped behaviors such as: chemical remarking of the trail, trophallaxis and the touching of nestmates with their antennae. Many workers that return to the nest did not marked the trail nor carried any visible fragments of food, but engaged in trophallaxis with several nestmates encountered on the trail.

After the recruitment process was initiated, ants accumulate at the food source (**Figure 2)**. While some workers engaged in cutting the prey into smaller pieces, others walk circularly in the surroundings. Sometimes ants from other species start arriving at the prey triggering acts of aggression from *D. armigerum* workers at the surroundings. Recruitment continues until the prey is completely transported to the nest, often using cooperative transportation. Ants used to explore more the areas were they had received food than areas were they never were fed (Figure 1).

In several occasions we saw ants dragging the tip of their abdomen on the ground while walking to the nest without causing any reaction on nestmates walking nearby (Fig 2). Nevertheless, once a food source was found, activity of recruiting ants increase, and a flux of 2.5 workers /min could be maintained during the following 60 min. We never observed recruitment triggered by a source of water. Offering water to thirty colonies increased the flux of workers between the nest and the foraging area (Figures 3 and 4), but not specifically to the area were water was offered.

Caste polymorphism:

These ants showed to be polymorphic but the sizes were distributed normally around a single mode, as can be seen from the frequency distribution in

Figure 1. Number of workers on the foraging area before and after food was discovered. Each point represents the average for 10 minutes intervals with its standard deviation for experiments in the field, the laboratory and for the control in the laboratory.

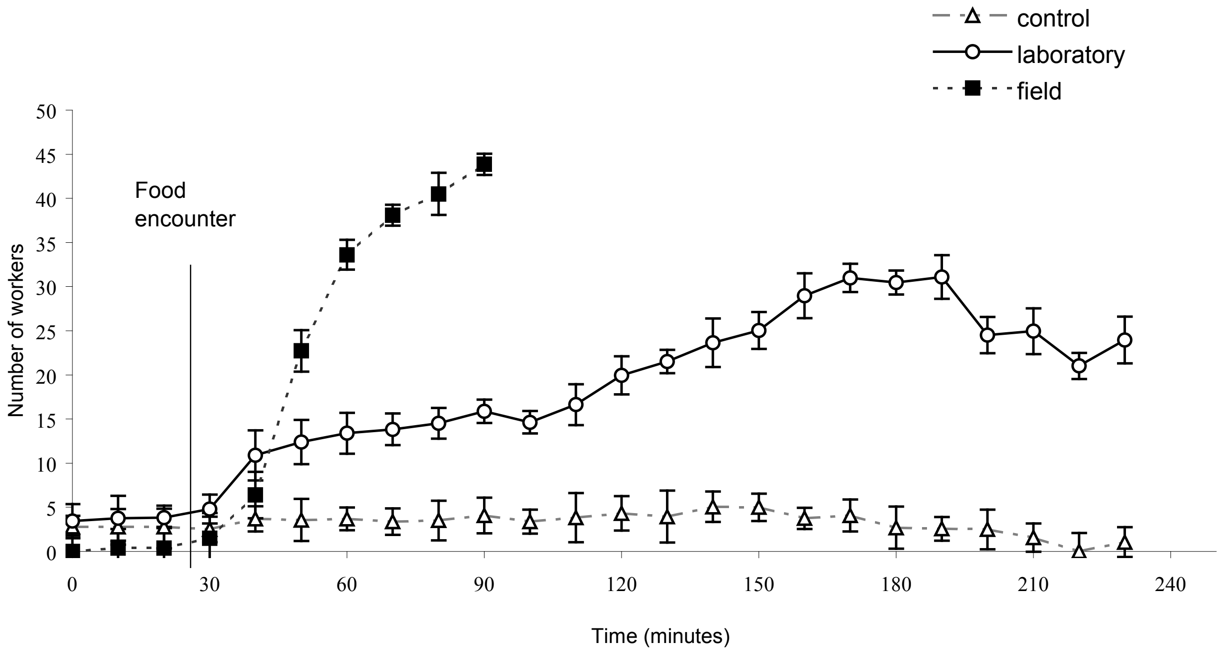

Figure 2. Number of ants showing marking behavior when walking to or from the nest, before and after discovering the food. Points are averages as explained in Figure 1

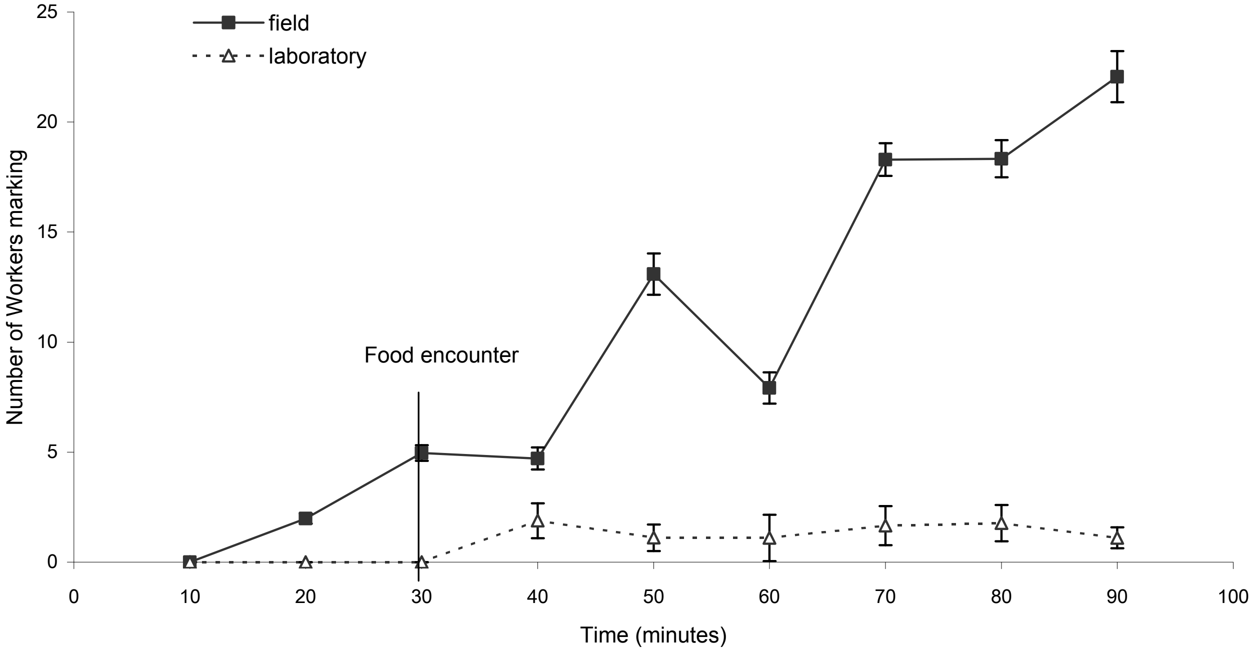

Figure 3. Number of ants walking to or from the nest, before and after discovering the food. Points are averages as explained in Figure 1

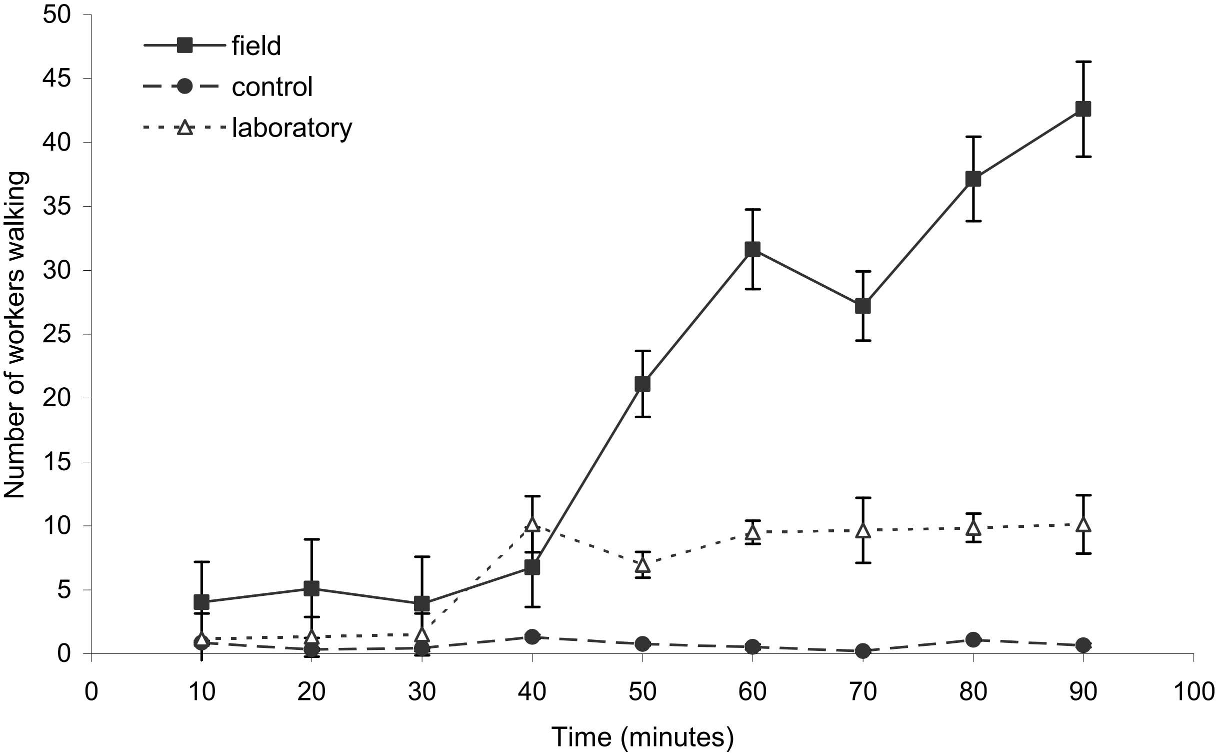

Figure 4. Number of workers walking to the nest from the foraging area before and after encountering food. Points are averages as explained in Figure 1

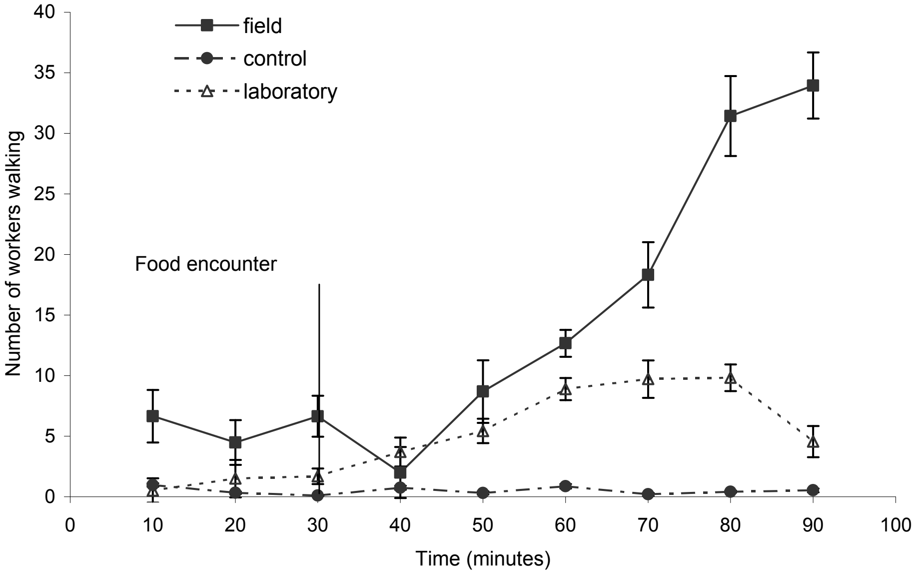

Figure 5: Frequency distribution of workers in the different size categories. Vertical axis gives the number of workers with maximum head with as indicated in the horizontal axis. Data are from two different colonies.

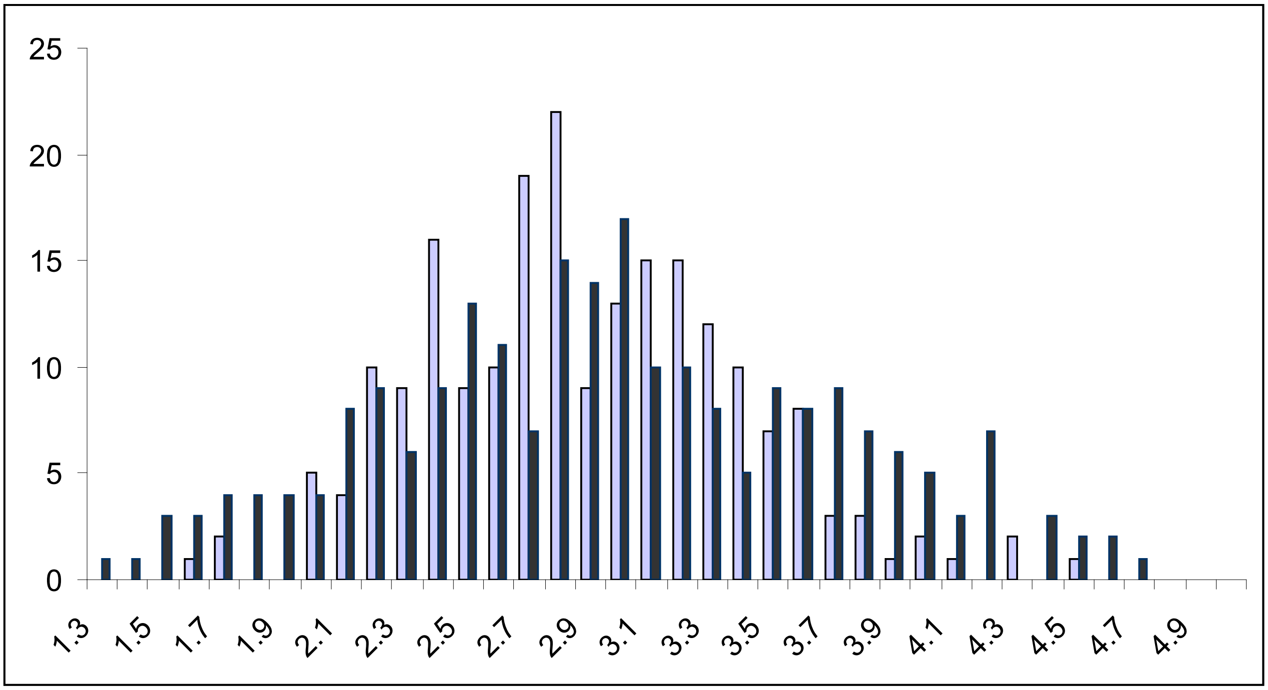

Figure 5. One striking observation was that we never saw a single ant with headwith (HW) below 2 mm walking outside the nest. Only larger workers were seen foraging. Among them, the largest (HW 4.0 - 4.9; 60 ants) were seen 33% of their time sitting still probably waiting for a prey, whereas small workers (HW 2.0 – 2.9; 34 ants) spend only 14% of their time in this behavior. These smaller workers were seen feeding in 17% of their time, whereas the larger one were never seen feeding, though they engaged in trophalaxis slightly more than the smaller ones (3.3% vs 0%)

Discussion

Surprisingly, *D. armigerum* workers recruit with and without chemical means, with and without trails. That is, they use a mix of recruitment strategies that have formerly been cataloged both as "primitive" and "derived" behaviors. Thus, these ants have a large set of foraging strategies on which they can relay, depending on their needs.

The fact that they hunt and ambush is very surprising. This behavior has rarely been described by ants and should be much more common than actually recognized. Other members of the tribe are terrestrial, foraging between dead leaves on the ground, using techniques of hunting in ambush with little or none visual input (Hölldobler et al. 1990, Hölldobler and Wilson 1990). Thus, our results show that even the most derived species in this group (Bolton B. 1999), that is even capable of chemical mass recruitment, the most advanced recruiting technique known among ants (Jaffe 1980), continues to show this behavior.

The movements of the gaster displayed by the workers when holding a prey is clearly a recruiting signal, which remembers similar behavior in other ants, which produce ultrasound as additional attractive stimulus (Wilson 1980, Holldobler and Wilson 1990). Nevertheless the stridulatory organ (Hölldobler and Wilson 1990) that would capacitate *D. armigerum* to produce sounds with this movement was not found. Despite this, we cannot exclude production of sounds or ultrasounds associated to this movement.

The short range chemical recruiting here described appears to be equivalent to the laying of signal posts mentioned by Hölldobler and Wilson (1978) for *Oecophylla longinoda* and is very similar to the one reported for *Novomesor* sp. (Hölldobler et al. 1978), where the explorers that discover food lay odor marks or elaborate odor trails around it. The long range recruiting behavior observed in *D. armigerum* is congruent with trail marking behavior described for many ant species (Jaffe et al. 1980). In the case of *D. armigerum*, chemical recruitment is reinforced by visual display and tactile stimuli, such as reported for *O. longinoda* (Hölldobler and Wilson 1978), *Tapinoma* sp., *Monomorium* sp. (Szlep and Jacobi 1967) and other species.

The main result of these observations is that this arboreal ant has a large repertoire of hunting and foraging strategies and that visual and chemical recruitment systems are not incompatible. Polymorphism in these ants is slightly related to their polyethism and probably helps them to recruit on a wide range of prey (Jaffe and Denebourg 1988) whereas chemical recruitment allows to retrieve very large prey items, allowing to maintain large colonies.

Acknowledgements

We thank: A. Osío, C. Bosques, C. Bertsh, C. Sainz and L. Galindo, for comments to the manuscript, P. Borges, P Tojeiro de Madi, R. Gajardo and T. Oliveira, for technical assistance, C. Ramos and CVG-Proforca for hospitality during the field work.

References

Bolton B. 1999. Ant genera of the tribe Dacetonini (Hymenoptera: Formicidae) J Nat Hist 33:1639-1689.

Blum M, Portocarrero C. 1966. Chemical releasers of social behavior, X: An attine trail substance in the venom of non-trail laying myrmicine, *D.armigerum* (Latreille). Psyche. 73: 150-156.

Gronenberg W, Brandao CRF, Hasso DB, Just S. 1998. Trap-jaws revisited: the mandible mechanism of the ant *Acanthognathus*. Physiol Entomol, London, 23: 227-240.

Gronenberg G. 1996. The trap-jaw mecanism in the Dacetine ants *Daceton armigerum* and *Strumigenys* sp. J Exp Biol 199: 2021-2033.

Hölldobler B, Palmer M, Moffett W. 1990. Chemical communication in the dacetine Ant *D. armigerum* (Hymenoptera: Formicidae). J Chem Ecol 16(4): 1207-1218.

Hölldobler B, Stanton R, Markl H. 1978. Recruitment and food-retrieving behavior in *Novomessor* (Formicidae, Hymenoptera). Behav Ecol Sociobiol 4:163-181.

Hölldobler B, Wilson E. 1978.The multiple recruiment systems of the african weaver ant *Oecophylla longinoda* (Latreille) (Hymenoptera: Formicidae). Behav Ecol Sociobiol 3: 19-60.

Hölldobler B, Wilson E. 1990. The Ants. The Belknap Press Harvard University Press Cambridge, Massachusetts. VII + 732p.

Jaffe K. 1980. Theorical analisis of communication systems for chemical mass recruitment in ants. J theor Biol 84: 589-609.

Jaffe K. 1984. Negentropy and the Evolution of Chemical Recruitment in Ants (Hymenoptera: Formicidae). J theor Biol. 106: 587-604.

Jaffe K, Denebourg JL. 1992. On foraging, recruitment systems and optimum number of scouts in ants. Insect Sociaux 39: 201-213.

Morgan E, Hölldobler B, Vaisar T, Jackson B. 1992. Contents of poison apparatus and their relation to trail-followig in the ant *D. armigerum*. J Chem Ecol 18(12): 2161-2168.

Szlep E, Jacobi M. 1967. The mechanism of recruitment to mass foraging in colonies of *Monomorium venustum* Smith, *M. subopacum* ssp. *phœnicium* Em.,*Tapinoma israelis* For. and *T. simothi* v. *phœnicium* Em. Ins Soc 14: 25-40.

Wilson E. 1962a. Behavior of *Daceton armigerum* (Latreille), with a classification of self-grooming movements in Ants. Bull MZC 127(7): 402-421.

Wilson E. 1980. Sociobiología la nueva síntesis. Ediciones Omega, S. A. Barcelona, España. X + 701pp.