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Jean-Paul Lachaud, Alain Dejean. Food Sharing in *Odontomachus troglodytes* (Santschi): A Behavioral Intermediate Stage in the Evolution of Social Food Exchange in Ants. *Anales de Biologia*, 1991, 17, pp.53-61. hal-02130970

HAL Id: hal-02130970

<https://hal.science/hal-02130970>

Submitted on 16 May 2019

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FOOD SHARING IN *ODONTOMACHUS TROGLODYTES* (SANTSCHI): A BEHAVIORAL INTERMEDIATE STAGE IN THE EVOLUTION OF SOCIAL FOOD EXCHANGE IN ANTS

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Recibido: 15 mayo 1991
Aceptado: 14 noviembre 1991

RESUMEN

Distribución de alimento líquido en *Odontomachus troglodytes* (Santschi): un nivel comportamental intermedio en la evolución del intercambio social de alimento en hormigas.

La hormiga ponerina *Odontomachus troglodytes*, bien conocida por su comportamiento de predación, es también capaz de explotar fuentes alimenticias azucaradas. La primera obrera que descubre una gota de miel puede rechazar a las siguientes en una «justa» ritualizada. Después de haber lamido la miel, las obreras elaboran pequeñas bolitas que traen al nido en donde las pueden almacenar. Estas bolitas de miel también pueden ser distribuidas por pseudotrofalaxia a las demás obreras de la sociedad por medio de una obrera «receptionista». La explotación de una fuente azucarada conduce, lo más frecuentemente, a dos tipos de reclutamiento: un reclutamiento de grupo por «tandem running» (reportado por primera vez en el género *Odontomachus*), o bien una forma primitiva de reclutamiento de masa por incitación a salir del nido y buscar el alimento. Se presenta un paralelo entre la complejidad y la flexibilidad del comportamiento de *O. troglodytes* y el nivel evolutivo que debe ocupar esta especie dentro de la subfamilia Ponerinae, en cuanto al comportamiento.

Palabras clave: *Formicidae*, *Ponerinae*, comportamiento ritualizado, reclutamiento, flexibilidad, evolución del comportamiento.

SUMMARY

The ponerine ant *Odontomachus troglodytes* is well known for its predominantly predatory behavior but it is equally able to exploit sugars as well. The first worker to discover a honey droplet sometimes repelled later arrivals in ritualized «joust». After licking the honey, the workers formed it into droplets. They then carried it to the nest where it was stored. The droplets were also frequently redistributed to other colony workers by pseudotrophallaxis. This took place through an intermediary «receptionist» worker. Exploitation of carbohydrates leads, most frequently, to two types of trail recruitment: group recruitment by tandem running (reported for the first time in the genus *Odontomachus*), or a primitive form of mass recruitment by incitement to leave the nest and search for food. We draw a parallel between the complexity and the flexibility of *O. troglodytes* behavior and the level of behavioral evolution occupied by this species among members of the Ponerinae subfamily.

Key words: *Formicidae*, *Ponerinae*, ritualized behavior, recruitment, flexibility, behavioral evolution.

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INTRODUCTION

Carbohydrate resources frequently constitute a very important part in the feeding of oligophagous ant species. The collection of sugary liquids of animal (e.g. honeydew excreted by aphids) or plant origin is one of the essential characteristics of provisioning in numerous species of *Formicinae*, *Dolichoderinae* and *Myrmicinae* (WHEELER, 1910; WAY, 1963; WILSON, 1971; LÉVIEUX & LOUIS, 1975; PASSERA, 1984). Collection of sugars is found equally often, however, among not a few primitive ant species which are usually considered essentially carnivorous. Various species in the genus *Myrmecia*, for example, have a partially nectar-feeding diet (HASKINS & HASKINS, 1950), and a similar diet exists in several ponerine species (HERMANN, 1975; VALENZUELA & LACHAUD, 1983; LACHAUD et al., 1984; BEATTIE, 1985). Even some of the terricolous ponerines will, under some conditions, forage for carbohydrates in trees (WEBER, 1946; WILSON, 1958; BENTLEY, 1976; SCHEMSKE, 1982; LACHAUD, 1990). Owing to the fact that the spatial distribution of carbohydrate sources is generally more stable than that of prey, the evolutionary importance of the ability to feed on carbohydrates shown by some Ponerinae has been frequently emphasized (FOWLER, 1980; YOUNG & HERMANN, 1980; HÖLLDOBLER, 1985; BREED & BENNETT, 1985; PRATT, 1989; LACHAUD, 1990). This ability to exploit carbohydrate foods should be equated with the utilization of homopteran honeydew and of nectar from floral and extrafloral sources by phylogenetically more advanced species, the use of these sources having been very important in their evolution allowing them to establish large and permanent populations (EVANS & LESTON, 1971; YOUNG, 1977).

This evolution inevitably leads to the question of the evolution of liquid food sharing among colony members and recruitment related behaviors which are two of the most distinctive aspects of social behavior. In the phylogenetically more advanced subfamilies (*Dolichoderinae*, *Myrmicinae* and *Formicinae*), the distribution of food collected by a small number of workers among a large number of nestmates is achieved by regurgitation, i.e. stomodeal trophallaxis (WILSON, 1971). This takes place after storage of the food for varying lengths of time in what is frequently termed the «social

stomach». A more elementary form of trophallaxis is found in very few species in the more primitive *Myrmeciinae* and *Ponerinae* subfamilies but, even in species where it does occur, its use is infrequent (LE MASNE, 1952; HASKINS & WHELDEN, 1954; HÖLLDOBLER, 1985). In these subfamilies, liquid food is usually transferred by pseudotrophallaxis, i.e. directly from the mandibles of one ant to those of another with no real regurgitation. This mechanism is known in various ponerine species (HERMANN, 1975; JAISSE & FRESNEAU, 1978; HÖLLDOBLER, 1985) from the most primitive (regarding to their social organization), like *Dinoponera quadriceps* (DANTAS DE ARAUJO et al., 1988 and unpublished observations), to the more socially structured like *Ectatomma tuberculatum* (FRESNEAU et al., 1982; DEJEAN et al., 1989; DEJEAN & LACHAUD, in press).

During food exchange between nestmates various types of tactile and chemical signals are used (see reviews in HÖLLDOBLER, 1977, 1978 and 1985 and in LENOIR & JAISSE, 1982). HÖLLDOBLER (1985) hypothesized that «... in the course of the evolution of social food exchange, signals used by many ponerine species in social greeting and the invitation behavior, became ritualized food solicitation signals ...». In such a context, however, invitation behavior is shown by the recruiting ant whereas it is the potential receiver ant which solicits food exchange. In order for Hölldobler's hypothesis to be valid, it would be necessary for the ants to have passed through a behavioral intermediate stage where invitation behavior no longer stimulated «nest leaving» but «food acceptance». Such behavior would, in a first stage, also have had to be initiated by the forager bringing food back to the nest. This appears to be what is observed in *Ectatomma tuberculatum* (DEJEAN et al., 1989; DEJEAN & LACHAUD, in press), at least in so far as the distribution of carbohydrates is concerned: in this species, the forager that discovered the source of carbohydrate initiates pseudo-trophallactic exchange. Nevertheless more information is needed on this type of invitation behavior and other examples would be of interest to support such an hypothesis.

In order to test this hypothesis, we studied social food exchange in a species of the genus *Odontomachus* which, on the basis of the existence of both highly developed behaviors related to carbohydrate exploitation strategies

(EVANS & LESTON, 1971) and evolutionary factors like increased colony size (COLOMBEL, 1969) and the existence of evolved forms of recruitment (FOWLER, 1980; OLIVEIRA & HÖLLDOBLER, 1989; CARLIN & GLADSTEIN, 1990), belongs with *Ectatomma* (BROWN, 1958; FRESNEAU et al., 1982; DEJEAN et al., 1989; DEJEAN & LACHAUD, in press) and *Brachyponera* (DEJEAN et al., 1987) to an evolutionary transitional group of ponerine ants regarding to their social behavior. We studied more particularly the behaviors associated with honey collection and the different patterns of food distribution behavior used by this ant and examined the behavioral mechanisms of recruitment to a source of sugars.

MATERIALS AND METHODS

Odontomachus troglodytes is an African species. Most colonies contain 400 to 500 workers on average and sometimes up to 1300 (COLOMBEL, 1969) approaching in size the colonies of the more socially advanced species of the subfamily: *Ectatomma tuberculatum* (200-800: COOK, 1905; WEBER, 1946; GARCIA PEREZ, 1979; CHAMPALBERT & LACHAUD, 1990; Lachaud, unpublished data), *Brachyponera senaarensis* (800-1400 workers: LÉVIEUX & DIOMANDÉ, 1978; Dejean & Lachaud, unpublished data) or *Megaponera foetens* (normally 400 to 700: LÉVIEUX, 1967, 1971 and 1976; LONGHURST, 1977; but sometimes up to 3000 in some regions: LEPAGE, 1981).

It is usually considered one of the major predators of the litter layer (STRICKLAND, 1951) and its hunting behavior has been well studied (COLOMBEL, 1969; DEJEAN & BASHINGWA, 1985; DEJEAN, 1988). However, several authors have recorded its feeding on sugars. In Ghana (EVANS & LESTON, 1971), this species tends coccids (*Stictococcus sjostedti*) and aphids (*Toxoptera aurentii*) on cacao trees and collects honeydew from them and, in some cases, the *O. troglodytes* workers are able to build earth and debris shelters for their Homoptera colonies.

Three colonies of *O. troglodytes*, each containing a queen, 200 or little more workers and abundant brood were collected in the Imbo region of Burundi. They were then placed in artificial nests consisting of a plastic box (120 x 90 x 50 mm.) containing a bed of plaster in which chambers had been hollowed out. The box was connected by a tube to a foraging arena (700 x 800 x 90 mm.). A trough was arranged along one side of the arena. Foraging workers were distinguished from those working inside the nest by

marking ants seen outside the nest with coloured dots.

The colonies were provided with insect prey (termite nymphs or *Tenebrio* larvae) every three days. Very limited supplies of sugar were provided weekly by placing a droplet of pure honey 600 mm. from the nest entrance.

RESULTS

DISCOVERY OF HONEY

Workers encountering the honey antennated it, then approached more closely and, keeping their mandibles open, licked it.

The honey was often discovered by several different workers. On many occasions (95 of 176 observations) we observed mutual antennation between the first arrival (or one of the first arrivals) and a worker arriving later. The later arrival would then leave the food source and recommence foraging (53,7%). Equally often (46,3%), however, the workers engaged in «jousting» during which hierarchical interactions were clearly involved. Moving slowly, the two workers grasped each other's mandibles and pushed against each other. Occasionally (in 19 of 44 cases), one or other of the workers retreated and took up the typical transport position with legs folded and body curved downward (see MÖGLICH & HÖLLDOBLER, 1974). The other ant then carried it away dropping it 30-80 mm from the honey. No further aggressive behavior was directed towards the transported ant and the transporting worker returned directly to the honey. The direction of adult transport away from the honey was random with respect to the direction of the nest.

These ritualized jousts can be compared with the submission rituals in the Mexican *Odontomachus* sp. (FRESNEAU, 1983 and personal communication) during agonistic interactions between workers from different colonies, although the behavioral acts are slightly different. Their precise function in our study remains unclear, however, because they involve foragers from the same nest. In other ponerines, such as *Ectatomma ruidum* (LACHAUD, 1990) or *Pachycondyla apicalis* (LACHAUD & FRESNEAU, unpublished data), adult transport or combat takes place between foraging workers from different colonies. In addition, in *O. troglodytes*, although most competing workers are driven

away, some may be tolerated and, a short time later, other workers even may be recruited.

FORMATION OF HONEY DROPLETS

After licking the honey, most *O. troglodytes* workers formed small honey droplets. The process had several stages. With the tips of their mandibles curved strongly inwards, each worker removed a series of tiny drops of honey from the mass. Each drop was added to those already collected and gradually built up into a viscous mass. The mass was moulded into a sphere and held in position using the forelegs.

DISTRIBUTION WITHIN THE NEST

The honey droplets were taken directly to the nest. We observed 67 different sequences of honey provisioning and were able to identify three main forms of disposal of the honey within the nest (fig.1):

- a) The honey droplet is deposited on the substrate in the nest entrance chamber (41,8% of cases) in the same way as the prey often

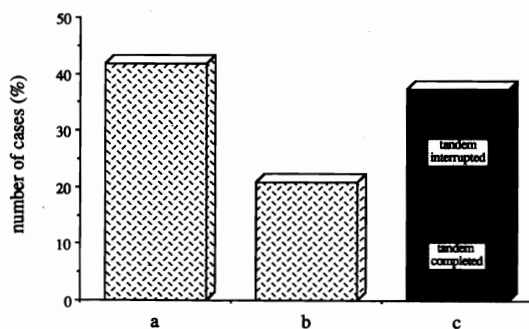


FIGURE 1. Representation of the main forms of honey distribution by *Odontomachus troglodytes* workers (67 cases studied).

- a) Honey droplet deposited in the entrance chamber of the nest.
 b) Honey droplet transferred to a receptionist worker.
 c) Recruitment.

Representación de los principales tipos de distribución de miel por las obreras de *Odontomachus troglodytes* (67 casos estudiados).
 a) Bolita de miel depositada en la recámara de entrada del nido.
 b) Bolita de miel transferida a una obrera recepcionista.
 c) Reclutamiento.

are. It is then either licked by workers passing nearby or taken by a non-forager acting as an intermediary «receptionist ant» (DEJEAN & LACHAUD, 1991). Indeed, this receptionist ant distributes the honey to the other colony members in the nest while the forager that brought the droplet returns to the source of the honey.

- b) After prolonged mutual antennation between the forager (which initiated it) and a non-forager, the honey is taken by the non-forager (20,9% of cases, see fig. 2a). The droplet is transferred directly from mandibles to mandibles or taken between the forelegs of the receptionist ant (fig. 2b) before being moved to its mandibles. During this process, the two ants continuously tap each other with their antennae and the droplet of honey is also frequently palpated. Subsequently, the forager returns to the source of the honey. After consuming some of the honey, the receptionist ant either deposits the droplet on the nest wall or distributes it to other workers. In the latter case, it is always the receptionist ant that initiates pseudotrophallaxis: all potential receivers are solicited by the receptionist ant antennating them. In response to this solicitation, workers quickly begin to touch the honey droplet with the tips of their antennae. They then open wide their mandibles (fig. 2c) and lick the honey droplet held between the receptionist's mandibles.

- c) The forager enters the nest in an excited state (37,3% of cases), with the honey droplet held in the mandibles. It displays dance-like behavior turning often and moving rapidly and jerkily. During this dancing behavior, the ant antennates rapidly in all directions and there are frequent antennal contacts with other ants in the entrance chamber. Surrounding ants also palpate the droplet of honey. Some of these workers become highly aroused and leave the nest. They search the foraging arena and find the honey source usually within a very short time. With colour-marking, it was determined that the workers that leave the nest under these circumstances appear always to be foragers familiar with the foraging arena for several days. After the invitation—or incitement to leave the nest—phase, the forager that discovered the honey is usually solicited by a non-

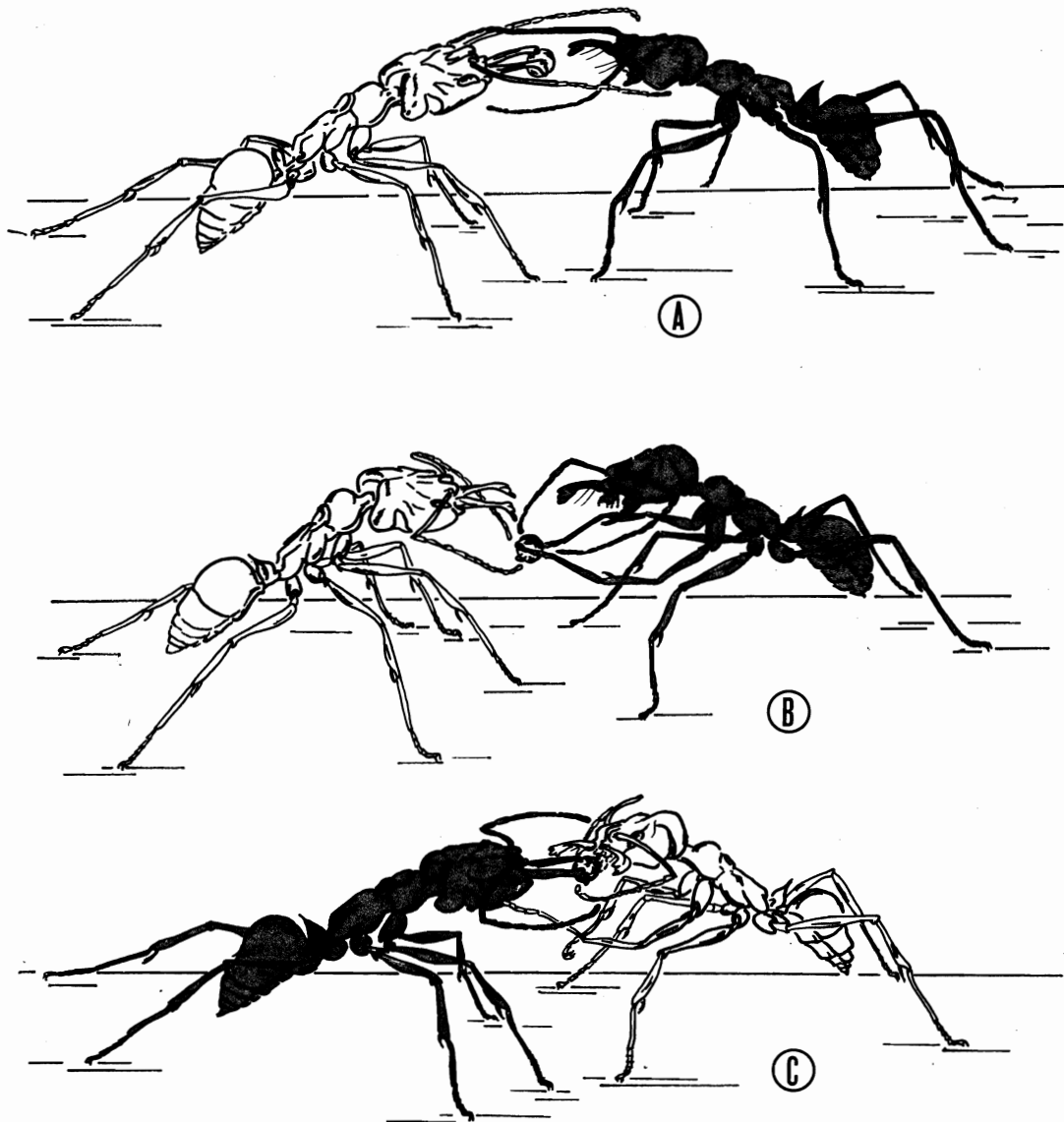


FIGURE 2. Food sharing behavior between *Odontomachus troglodytes* workers. Foragers form the honey into small droplets which they take back to the nest. After mutual antennation (a) a receptionist ant (shading) takes the droplet (b) using its front legs. The receptionist ant then distributes the honey to nest mates (c) by pseudotrophallaxis.

Distribución de alimento entre las obreras de *Odontomachus troglodytes*. Las forrajeras elaboran la miel en pequeñas bolitas que traen al nido. Después de un golpeteo de antenas mutuo (a), una obrera receptionista (en gris) toma la bolita en las mandíbulas utilizando sus patas protorácicas (b). La obrera receptionista, entonces, distribuye la miel a sus congéneres (c) por pseudotrofalaxia.

forager. This receptionist ant takes the honey droplet and redistributes it between nestmates. In all cases (n= 25), the original forager leaves the nest after 4-6 minutes followed in tandem by a forager recruited from among those at the nest entrance. Two patterns are then observed: a) in 10 cases, the recruiting ant guided the other forager until they were very close to the honey source (see fig. 1); b) in the remaining 15 cases, the two ants run in tandem for 150-350 mm after which the recruiting ant turned back to the nest and recruited another worker. In this second situation, the first recruited worker always managed to locate the honey even though it had been abandoned while merely headed in the direction of the source. Despite our very careful observation of the recruiting forager returning to the nest with honey we were never able to detect any trail-laying or scent marking that could have been used to find the honey source by subsequent recruits.

DISCUSSION

The sharing of sugar-rich liquid foods observed in *O. troglodytes* fulfills the same function as trophallaxis does in phylogenetically more advanced species. Food is transferred directly from forager to an intermediary receptionist ant or indirectly after the honey droplet is deposited on the wall or floor of the nest. In this case, the "social stomach" is «external» but the behavior involved is not fundamentally different from that shown by foragers returning with sugary liquids in *Iridomyrmex humilis* (MARKIN, 1970) or *Solenopsis invicta* (SORENSEN et al., 1981) and depositing it on the substrate inside the nest. Nevertheless, the structure of food distribution behavior in *O. troglodytes* is in fact very close to that seen in ants bringing prey, or even seeds, back to the nest. It retains primitive characteristics closely related to predatory behavior. The honey droplet is not licked slowly away from the forager by the receptionist as has been reported for other nectar-feeding ponerines (HÖLLDOBLER, 1985) like *Pachycondyla villosa* but is transferred complete, directly from the mandibles of the forager to those of the receptionist ant. Therefore, due to its almost

solid nature, the droplet is treated more like a prey item than as a liquid. It should be noted, however, that during transfer of honey the receptionist ant may use the forelegs which, as far as we know, has not been recorded for ponerines. The use of the forelegs during transfer of food can be equated with their role as ritualized food solicitation signals in phylogenetically more advanced species like *Myrmica scabrinodis* and *Lasius emarginatus* (LENOIR, 1973) and supports HÖLLDOBLER'S (1985) hypothesis concerning the evolution of the signals involved in social food exchange.

The second point of validation for Hölldobler's hypothesis shown by our results concerns the invitation behavior displayed by *O. troglodytes* foragers bringing food back to the nest. As in *Ectatomma tuberculatum* (DEJEAN et al., 1989; DEJEAN & LACHAUD, in press), the forager that discovered the honey source is capable of stimulating food acceptance instead of nest leaving. In *O. troglodytes*, however, there is a supplementary intermediate stage: firstly because food passes to a receptionist ant that forms an additional link in the distribution of food and is always the individual that initiates the subsequent pseudotrophallaxis; secondly because, unlike *E. tuberculatum*, the invitation behavior of *O. troglodytes* foragers remains able, in some cases, to elicit nest leaving through a transitional recruitment behavior.

Odontomachus troglodytes behavior thus appears remarkably flexible and can be compared with similar traits in *Ectatomma ruidum* (LACHAUD, 1985; PRATT, 1989). Several responses occur for the same species depending on circumstances and on the individuals involved (the real importance of these two factors has yet to be determined) while these responses are known to occur only in one or other of the *Odontomachus* species (see MÖGLICH & HÖLLDOBLER, 1974; FOWLER, 1980; OLIVEIRA & HÖLLDOBLER, 1989; CARLIN & GLADSTEIN, 1990). *Odontomachus troglodytes* may show no recruitment behavior (in around 60% of cases involving sugars and 100% of those involving prey) or a form of recruitment by incitement to leave the nest and search for food already known from other ponerines of the same (*O. bauri*: OLIVEIRA & HÖLLDOBLER, 1989) or different (*Ectatomma ruidum*: LACHAUD, 1985) genus. An intermediate form of recruitment, tandem running, occurred in about 40% of cases

involving provisioning with sugars and even transport of individuals occurred during nest moving (Dejean, unpublished data).

As reported during recruitment to dilute honey in *O. ruginodis* (CARLIN & GLADSTEIN, 1990), trail-laying was not observed in our experiments with *O. troglodytes*. Nevertheless, the ability to use trail-laying cannot be totally ruled out owing to the occurrence, in this species (VILLET et al., 1984) as well as in congeneric species (HÖLDOBLER & ENGEL, 1978), of a pygidial gland provided with reservoirs and known to be involved in trail-laying behavior in various ponerine species (MASCHWITZ & SCHÖNEGGE, 1977; HÖLDOBLER & TRANIello, 1980). Moreover, in *O. bauri* (OLIVEIRA & HÖLDOBLER, 1989), the secretions of the pygidial gland have been proved to serve as chemical recruitment signal though no trail-laying or tandem running has been demonstrated.

The fact that some aspects of carbohydrate-provisioning can produce in *O. troglodytes* extremely complex behavior like building shelters for the Homoptera whose honeydew they exploit (EVANS & LESTON, 1971) or ritualized competition for access to a food source (this work), together with the intermediate stage characteristics of the invitation behavior and recruitment they performed, can only strengthen the hypothesis that this species forms a transition stage in the evolution of behavior concerned with food exchange. In this respect and in so far as behavior is concerned, *O. troglodytes* would be placed as an intermediate stage between most ponerine species and *Ectatomma tuberculatum* (FRESNEAU et al., 1982; DEJEAN et al., 1989; DEJEAN & LACHAUD, in press) which introduces the behavioral patterns typical of the phylogenetically more advanced myrmicine ant species.

ACKNOWLEDGEMENTS

We are grateful to Dominique FRESNEAU for suggestions on an early draft of the manuscript, to Raymond CAMPAN for helpful comments on the manuscript and to Andrew DAVIS who improved english translation.

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