

LIQUID FOOD TRANSMISSION AND ANTENNATION SIGNALS IN PONERINE ANTS

BERT HOLLOBLER

*Department of Organismic and Evolutionary Biology,
MCZ-Laboratories, Harvard University, Cambridge,
Massachusetts 02138 USA*

ABSTRACT

As previously reported for other ponerine ants (*Odontomachus*, sp., *Paraponera clavata*, *Ectatomma tuberculatum*), *Pachycondyla villosa* and *Pachycondyla obscuri-cornis* also transport liquids between their mandibles. This behavior is considered a primitive behavioral character in ants. The present paper describes for the first time how this externally transported liquid food is distributed among colony members. It is shown that ponerines employ an external social bucket, which functions in the same capacity in social food exchange as the internal social crop in phylogenetically more advanced species. It is suggested that antennation signals involved in social food exchange evolved from antennation signals used in social greeting and recruitment invitation behavior.

KEY WORDS: Formicidae, Ponerinae, trophallaxis, communication, antennation signals.

INTRODUCTION

One of the most remarkable features of many social insect species is the sharing of food among members within the society. Prey objects brought into the nest by a few individuals are usually consumed by many other individuals. Liquid food, stored in the foragers' crop (or "social stomach") is regurgitated to nestmates and thus distributed over large portions of the colony. This latter form of food transmission is called stomodeal (or oral) trophallaxis. Typically, a soliciting ant evokes regurgitation in a nestmate by stimulating it with stereotyped tactile signals with the antennae and forelegs (Wallis, 1969; Lenoir, 1973a, b; Holldobler, 1973), whereby the mechanical stimulation of the donor's mouthparts (especially the labium) appears to be an important releaser of the regurgitation reflex (Holldobler, 1970, 1973).

Liquid food exchange by regurgitation is a highly evolved form of food sharing in ants. It is much more common among species belonging to phylogenetically advanced subfamilies than in the more primitive subfamilies Myrmeciinae and Ponerinae (see Wilson, 1971). In the present paper I describe a mode of liquid food transmission in ponerine ants that appears to represent an evolutionary precursor of the advanced stomodeal trophallaxis in ants.

Most ponerine ants are primarily predators and scavengers, but some species have been observed collecting liquid material as well. Evans and Leston (1971) discovered that a West African species of *Odontomachus* gathers honeydew from aphids and coccids. The ants carry the liquid in small droplets between their mandibles. Other ponerines have been observed transporting liquid in a similar fashion, for example *Ectatomma tuberculatum* (Weber, 1946; Hölldobler, unpublished observations), and *Paraponera clavata* (McCluskey and Brown, 1972; Hermann, 1975; Young and Herman, 1980). In the case of *Paraponera* most of the liquid presumably originates from extrafloral nectaries, water and fruits, and can comprise a substantial amount of the forage (Hermann, 1975; Young, 1977). However, nothing is known concerning the processing of this liquid inside the nest.

Based on our recent observations with *Pachycondyla villosa* and *Pachycondyla obscuricornis*, I am now able to add new records of mandibular liquid food transport and provide the first information concerning the mode of liquid food transmission in ponerines.

Antennation signals are employed by ants in many different behavioral contexts (see Lenoir and Jaisson, 1982), including food exchange, recruitment invitation behavior, social greeting, and ritualized aggressive displays (Hölldobler, 1976, 1982; Hölldobler and Carlin, 1985; Ettershank and Ettershank, 1982). In this paper I will also discuss some examples of antennal communication in ponerine ants that closely resemble the antennation behavior employed by phylogenetically more advanced ants when soliciting regurgitation.

This article is dedicated to Professor Jehosua Kugler on the occasion of his seventieth birthday.

MATERIALS AND METHODS

Pachycondyla villosa and *Pachycondyla obscuricornis* were collected in primary rain forest of the La Selva Biological Station operated by the Organization of Tropical Studies, Heredia Province, Costa Rica. *P. villosa* was found inside an almost abandoned *Nasutitermes* nest approximately 250 cm above the ground. Forty three workers and five pupae, but no queens were collected. A colony of *P. obscuricornis* consisting of eighteen workers, six larvae, two pupae and one queen was extracted from a partially hollow, dry branch lying on the ground. Single workers of both species were observed moving up tree trunks, and in one case I observed a *P. obscuricornis* carrying liquid between its mandibles.

At Harvard University the colonies were housed in test tubes with 2.5 cm inner diameter, in the bottom of which water had been trapped by a tight cotton wad, leaving a chamber 8 cm long for the ants to occupy. The ants were allowed access to a 30 x 22 cm foraging chamber, where they were fed mealworms (*Tenebrio molitor* larvae), cockroaches (*Nauphoeta cinera*), and honeywater. Both species readily accepted the insect prey, but they also eagerly collected huge droplets of honeywater between their mandibles and carried the liquid into the nest (Fig. 1). Most of the more detailed observations on liquid food transmission to be reported below were conducted with *P. villosa*.



Fig. 1. *Pachycondyla* worker loading liquid between its mandibles from a cellulose wad soaked in honeywater.

RESULTS

Food Transmission

When a forager enters the nest laden with liquid food, it either stands still for a while, slightly swinging its head to the right and left side, apparently waiting for a nestmate to approach, or it moves directly toward nestmates while actively presenting them with the food droplet held between its widely opened mandibles. If a colony is well fed a forager may have to wait as long as 30 minutes before a nestmate responds. Sometimes it is wholly ignored and is not able at all to share its booty. In this case it imbibes a portion of the droplet itself and wipes off the rest of it on the floor and walls of the nest.

Most of the time, however, nestmates readily accept the liquid food and even actively solicit it from the forager. Employing rapid vertical jerking movements that last about 1-2 seconds (with 1-3 jerks per second), the solicitor approaches the food carrier head on and intensely antennates the front of its head and mandibles (Fig. 2). In response, the food-carrying ant folds back its antennae and presents the food droplet that it holds between its widely opened mandibles. Under the stereo-microscope (10-20x magnification) one can clearly see the licking or "spooning" motions of the labium. Slowly a droplet accumulates between the mandibles of the begging ant. During this process the solicitor continues to antennate the head of the donor ant, while the latter keeps its antennae pulled back most of the time. From approximately 1/4 to more than 3/4 of the droplet often passes from the donor to the solicitor (Fig. 2c).

After the solicitor has accumulated a droplet between its mandibles and has separated from the donor, it apparently imbibes portions of the liquid (one can see the

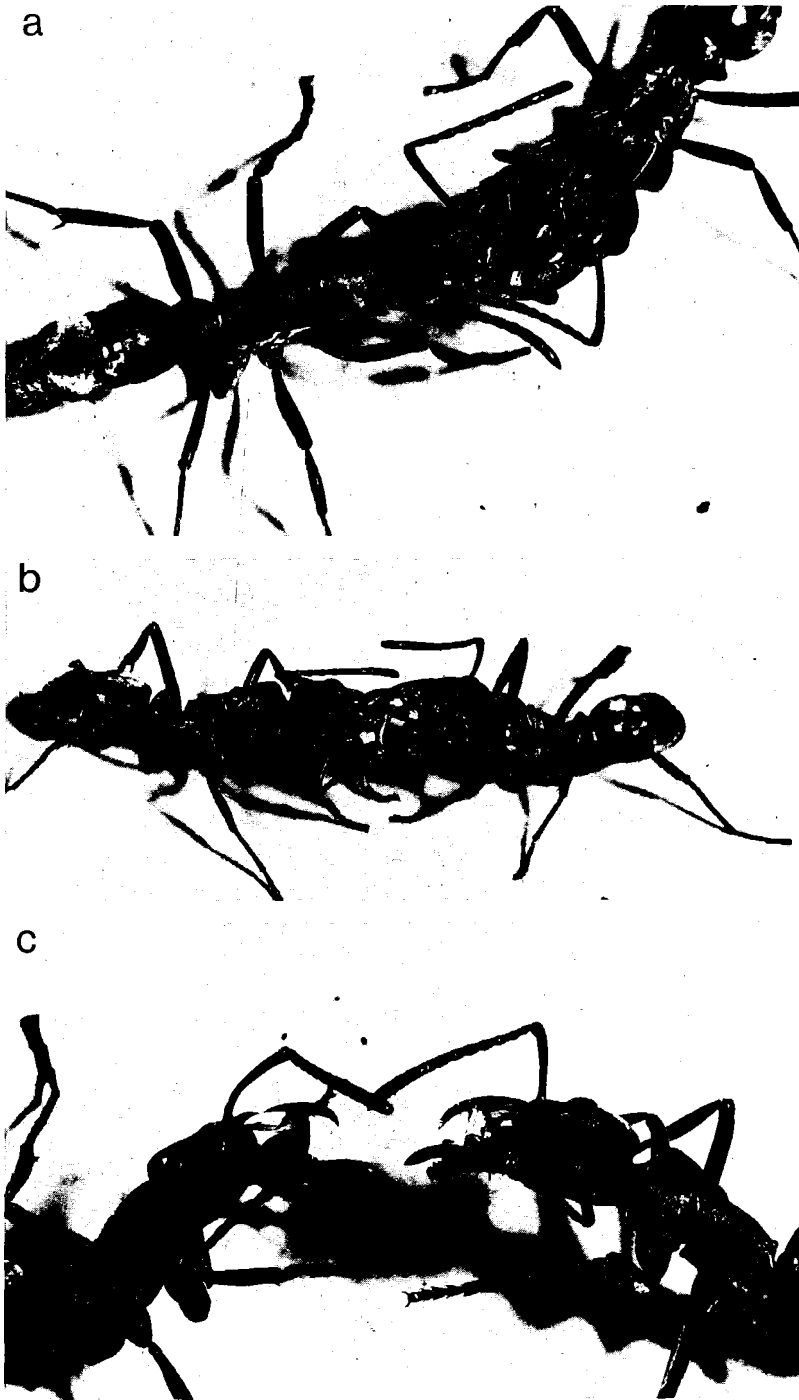


Fig. 2. a. The soliciting ant (right) approaches the food carrier (left) head on and intensely antennates its front head and mandibles. b. Food exchange between donor ant (left) and solicitor (right). c. Approximately 1/2 of the liquid carried by the donor has been loaded between the mandibles of the solicitor.



Fig. 3. a. SEM micrograph of the mouthparts of a *Pachycondyla* worker. Note the inwardly curved heavy setae on the mandibles. b. The "social bucket" of *Pachycondyla*. The liquid is held in place by surface tension.

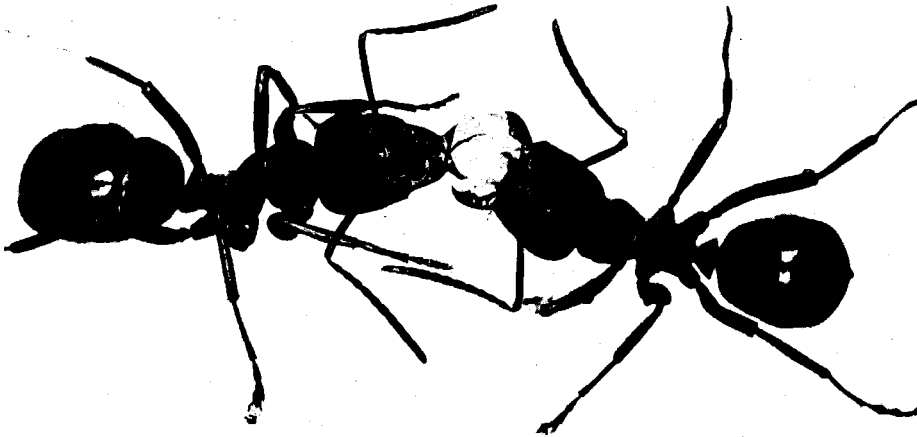


Fig. 4. Food exchange between two *Formica* workers. The ant on the right has regurgitated a large droplet which is now held between the mandibles while it is slowly imbibed by the ant on the left. (From Hölldobler 1973).

droplet becoming smaller). However, when approached by another begging nestmate, this secondary food carrier surrenders a major portion of the droplet to the nestmate, which in turn shares it with other soliciting members of the colony. Two experiments were conducted in which one primary food carrier was combined with a group of 15 nestmates. In one case 8 ants and in the other case 11 ants had received a share of the droplet within a 40 minute period. In a third experiment I kept 5 workers without food for a period of 5 days, then joined them with a group of 10 workers which had been fed a day before. The starved workers approached the nestmates and performed a vigorous jerking display with rapid antennation directed at the nestmates' heads. Nestmates often responded by opening the mandibles widely, extruding the labium and folding the antennae backwards. This is precisely the position of an ant offering a food droplet, but in this case no droplet was present, and furthermore no droplet was regurgitated. Nevertheless, the solicited ant responded to the begging signals with the stereotyped food-offering behavior.

These and similar observations suggest that *Pachycondyla villosa*, *P. obscuricornis* do not share liquid food by regurgitating (stomodeal trophallaxis), but rather employ an external "social bucket" system in which they collect liquid food, and from which portions of the food are "spooned" into the "social buckets" of nestmates. The bucket is formed by the mandibles with inwardly curved heavy setae and extruded labium (Fig. 3a). The liquid is held in place by surface tensions (Fig. 3b). Each food carrier imbibes only small amounts for its own use, unloading the major portions into the "social buckets" of its nestmates. The similarity to the liquid food exchange by regurgitation in more advanced ants, for example certain formicine species (Hölldobler, 1973), is striking. In the latter case the food is collected in the crop. In response to very similar antennal signals and mechanical stimulation of the labium, the food carrier regurgitates a droplet of liquid from its crop. The donor ant opens its mandibles widely, extrudes the labium and folds the antennae backwards. Occasionally, when a large droplet is regurgitated all at once, it is held between the mandibles in very much the same manner as described for ponerine ants (Fig. 4). In contrast to the typical

response by ponerines, the receiving ant imbibes all the food it receives and stores it in the crop. Small amounts of this food pass through the proventriculus into the midgut, where it is digested. The major portions, however, are distributed by regurgitation to other nestmates.

Antennation Behavior

A comparative study of the antennation signals in ponerine ants has disclosed a striking similarity across the categories of social greeting, recruitment invitation, and food solicitation. For example, when a patrolling worker of the African ponerine species *Paltothyreus tarsatus* meets a stray nestmate both ants first engage in mutual antennation. This behavior closely resembles the antennation pattern preceding trophallactic food exchange in many other ant species, yet no trophallaxis was found in *P. tarsatus*. In this species the stereotyped antennation is part of a greeting and invitation behavior, by which the nestmate is solicited to follow in tandem to the nest (Hölldober, 1984). The stereotyped invitation behavior is even more striking in an Australian *Hypoponera* species (Fig. 5a). The ants approach each other head on. The recruiting ant tilts its head sideways almost 90° and strikes the upper and underside of the nestmate's head intensely with its antennae (Fig. 5b). Often the solicited ant responds with a similar antennation behavior. The recruiting ant then turns around and tandem running starts (Fig. 5c). This antennation behavior also occurs inside the nest, but it was never observed to elicit food exchange, only the enticement of nestmates from one nest area to another. Le Masne (1952) describes a similar antennation behavior for the European species *Hypoponera eduardi*. He suggests that in this species the behavior results in regurgitated food exchange. I could not confirm this for two Australian *Hypoponera* species, and Carlin (pers. communication), who studied very similar behavior in *Ponera coarctata*, also failed to observe unequivocally food exchange by regurgitation in this species. Moreover, the jerking movements, often associated with food solicitation in *Pachycondyla villosa*, have also been found to be part of the invitation behavior in other *Pachycondyla* species (Hölldobler et al., 1973; Maschwitz et al., 1974; Traniello and Hölldobler, 1984).

Thus, in these ponerine ants, behavioral solicitation signals, employed in social food exchange and recruitment appear to be identical. Since these signals are used by many ponerine species which apparently do not exchange liquid food, but employ them in social greeting and invitation behavior, it is suggested that in the course of the evolution of social food exchange, they became ritualized food solicitation signals.

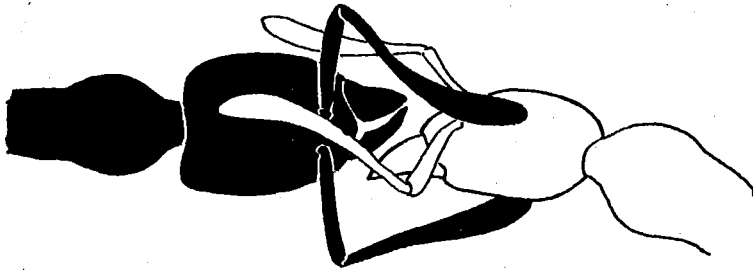
DISCUSSION

The ability to regurgitate food from the crop and surrender it to begging nestmates is common among ant species belonging to the phylogenetically more advanced subfamilies Aneuretinae, Dolichoderinae, Formicinae, and Myrmicinae (see review in Wilson, 1971). Some of these species may have lost this capacity secondarily in the course of evolving more specialized food habits, as for example in seed eating harvester ants of the genus *Pogonomyrmex* (Wilson and Eisner, 1957). The frequency of liquid food exchange in a given species appears to increase with the relative amount of liquid in the natural diet (Gösswald and Kloft, 1960). All adult castes, including the

a



b



c



Fig. 5. a. A worker of *Hypoponera* (right) invites a nestmate to follow in tandem. b. Schematic illustration of the antennation behavior employed during invitation for tandem running recruitment. c. Tandem running in *Hypoponera*.

males, can participate in the oral trophallaxis, and there is no substantial variation in the basic pattern of the underlying tactile soliciting signals (Hölldobler, 1966). In fact, there seems to be very little variation in these signals even among different species (Wallis, 1961; Lenoir, 1973a, b; Hölldobler, 1973). Many myrmecophiles crudely imitate these signals and are thereby able to parasitize the social food flow in an ant society (Hölldobler, 1970, 1971).

In the phylogenetically more primitive subfamilies Nothomyrmecinae, Myrmeciinae and Ponerinae the existence of oral trophallaxis is less certain. There are reports that occasional trophallaxis has been observed in the most primitive living ant *Nothomyrmecia macrops* (Taylor, 1978), and in some species of the Myrmeciinae and Ponerinae (Le Masne, 1952; Haskins and Whelden, 1954).

The findings presented in this paper provide a clue as to how oral trophallaxis evolved in ants. Like some bees and wasps, including the tephritid wasps (Krombein, 1939), a group considered phylogenetically close to the ants' ancestors, ponerine ants can transport liquid between their mandibles. This is obviously a primitive behavioral character. From our findings we now have proof that ponerine ants are able to distribute the liquid among nestmates by employing an external social bucket, which serves in the same capacity as the internal social crop in the more advanced ant species. In both cases very similar antennal solicitation signals are used to elicit food transmission. Also, as in the case of oral trophallaxis, the recipient ponerine ants usually load more liquid into their carrying container than they can use for their own consumption. They next participate in the rapid social distribution of this liquid resource. Thus, the ability to transport liquids externally led to the development of the social bucket-behavior. Simple tactile solicitation signals, already available for communication in other social contexts, became ritualized into food begging signals. With the shift to more extensive liquid food utilization, such as the tending of herds of homopterans, a more efficient means of liquid food transportation and storage evolved. The social bucket became "internalized" in the form of the social crop, and the ants developed the ability to transmit food by regurgitation; (the mandibles were also freed for other functions). Eisner (1957) has demonstrated that the proventriculus evolved in the ants to facilitate this particular social function. The antennal solicitation signals remained mostly unchanged, but in most cases the forelegs became increasingly involved in stimulating the labium to elicit the regurgitation reflex.

ACKNOWLEDGEMENTS

I would like to thank E.O. Wilson for his companionship, help and advice during the field work in Costa Rica, and W.L. Brown for identifying the ants. This work was supported by SNF grant BNS 82-19060.

REFERENCES

- Eisner, T. 1957. A comparative morphological study of the proventriculus of ants (Hymenoptera; Formicidae). *Bulletin of the Museum of Comparative Zoology, Harvard* 116:439-490.
- Ettershank, G. and J.A. Ettershank. 1982. Ritualized fighting in the meat ant *Iridomyrmex pupureus* (Smith) (Hymenoptera: Formicidae). *Journal of the Australian Entomological Society* 21:97-102.
- Evans, H.C. and D. Leston 1971. A ponerine ant (Hym., Formicidae) associated with Homoptera on cocoa in Ghana. *Bulletin of Entomological Research* 61:357-362.

- Gösswald, K. and W. Kloft 1960. Neuere Untersuchungen über die sozialen Wechselbeziehungen im Ameisenvolk, durchgeführt mit Radio-Isotopen. *Zoologische Beiträge* 5:519-556.
- Haskins and Whelden 1954. Note on the exchange of ingluvial food in the genus *Myrmecia*. *Insectes Sociaux* 1:33-37.
- Hermann, H.R. 1975. Crepuscular and nocturnal activities of *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). *Entomological News* 86:94-98.
- Hölldobler, B. 1966. Futterverteilung durch Männchen im Ameisenstaat. *Zeitschrift für vergleichende Physiologie* 52:430-455.
- Hölldobler, B. 1970. Zur Physiologie der Gast-Wirt-Beziehungen (Myrmecophilie) bei Ameisen: II. Das Gastverhältnis des imaginalen *Atemeles pubicollis* Bris. (Col. Staphylinidae) zu *Myrmica* und *Formica* (Hym. Formicidae). *Zeitschrift für vergleichende Physiologie* 66:215-250.
- Hölldobler, B. 1971. Communication between ants and their guests. *Scientific American* 224:86-93.
- Hölldobler, B. 1973. *Formica sanguinea* (Formicidae): Futterbetteln. *Encyclopaedia Cinematographica*, E 2013, pp. 3-11, Göttingen, 1973.
- Hölldobler, B. 1976. Tournaments and slavery in a desert ant. *Science* 192:912-914.
- Hölldobler, B. 1982. Foraging and spatiotemporal territories in the honey ant *Myrmecocystus mimicus* Wheeler (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* 9:301-314.
- Hölldobler, B. 1984. Communication during foraging and nest-relocation in the African stink ant, *Paltothyreus tarsatus* Fabr. (Hymenoptera, Formicidae, Ponerinae). *Zeitschrift für Tierpsychologie* 65:40-52.
- Hölldobler, B. and N.F. Carlin. 1985. Colony founding, queen dominance and oligogyny in the Australian meat and *Iridomyrmex purpureus*. *Behavioral Ecology and Sociology* 18:45-58.
- Hölldobler B., M. Möglich, I. Maschwitz 1973. *Bothroponera tesserinoda* (Formicidae): Tandemlauf beim Nestumzug. *Encyclopaedia Cinematographica*, Film E. 2040, pp. 3-14, Göttingen.
- Krombein, K.V. 1939. Habits of Tiphidae. *Transactions of the Entomological Society of America* 65:415-466.
- Le Masne, G. 1952. Les échanges alimentaires entre adultes chez la fourmi *Ponera eduardi* Forel. *Comptes rendus hebdomadaires des séances de l'Académie des Sciences, Paris* 235:1549-1551.
- Lenoir, A. 1973a. Les communications antennaires durant la trophallaxie entre ouvrières du genre *Myrmica*. Proceedings of the VIIth Congress of the International Union of the Study of Social Insects, London 1973, pp. 226-233.
- Lenoir, A. 1973b. Influence de sections de tarsi antérieurs sur le comportement de trophallaxie de deux espèces de fourmis *Myrmica scabrinodis* Nyl et *Lasius emarginatus* Olf., Comptes rendus 96e Congrès national des sociétés savantes, Toulouse, 1971, Sciences 3:531-540.
- Lenoir, A. and P. Jaisson. 1982. Evolution et rôle des communications antennaires chez les insectes sociaux. In: Social Insects in the Tropics (ed. P. Jaisson), Vol. 1, p. 157-180; Presses de l'Université de Paris XIII, Paris.
- Maschwitz, U., B. Hölldobler, M. Möglich. 1974. Tandemlauf als Rebrutierungsverhalten bei *Bothroponera tesserinoda* Forel (Formicidae, Ponerinae). *Zeitschrift für Tierpsychologie* 35:113-123.
- McCluskey, E.S. and W.L. Brown. 1972. Rhythms and other biology of the giant tropical ant *Paraponera*. *Psyche* (Cambridge) 79:335-347.
- Taylor, R.W. 1978. *Nothomyrmecia macrops*: A living fossil ant rediscovered. *Science* 201:979-985.
- Traniello, J.F.A. and B. Hölldobler. 1984. Chemical communication during tandem running in *Pachycondyla obscuricornis* (Hymenoptera: Formicidae). *Journal of Chemical Ecology* 10:783-794.
- Wallis, D.J. 1961. Food-sharing behavior of the ants *Formica sanguinea* and *Formica fusca*. *Behaviour* 17:17-47.
- 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, E.O. 1971. *The Insect Societies*. The Belknap Press of Harvard University Press, Cambridge, MA.

- Wilson, E.O. and T. Eisner. 1957. Quantitative studies of liquid food transmission in ants. *Insectes Sociaux* 4:157-166.
- Young, A.M. 1977. Notes on the foraging of the giant tropical ant *Paraponera clavata* (Formicidae: Ponerinae) on two plants in tropical wet forest. *Journal of the Georgia Entomological Society* 12:41-51.
- Young, A.M. and H.R. Hermann. 1980. Notes on foraging of the giant tropical ant *Paraponera clavata* (Hymenoptera: Formicidae: Ponerinae). *Journal of the Kansas Entomological Society* 53:35-55.