

## Unique habits of stomodeal trophallaxis in the ponerine ant *Hypoponera* sp.

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### Summary

The present paper describes for the first time that adult-to-adult trophallaxis exists in ponerine ants. Furthermore, it shows that the adult castes of the ponerine and *Hypoponera* sp. have different habits of trophallaxis. Workers display a soliciting behavior toward queens, males and workers, but receive regurgitated food only from workers. The workers are forced to stop soliciting for regurgitated food by the “whipping behavior” of the queen. Callow queens solicit regurgitated food from workers and ergatoid males and receive it, while mature queens do not solicit regurgitation from workers. Ergatoid males receive regurgitated food from workers and regurgitate it to queens. Alate males show no trophallactic food exchange with workers and queens. Trophallactic behavior was never observed between males of either winged or ergatoid types.

### Introduction

Although stomodeal trophallaxis has been considered fundamental to the organization of ant colonies, reaching its extreme in ants, its existence in ponerines was considered absent until now (Hölldobler, 1985; Hölldobler and Wilson, 1990). As the Ponerinae is considered a primitive ant subfamily, it has been hypothesized that this is the reason why trophallaxis never evolved in this subfamily (Eisner, 1957). However, recent studies suggest that Formicinae and Dolichoderinae, both of which present trophallaxis, were the first subfamilies to diverge very early from the ant basic stock (Hashimoto, 1991; Baroni Urbani et al., 1992). We were able to observe that ponerine ants Japanese *Hypoponera* sp. (JFC\* 11104) perform adult-to-adult trophallaxis, while larva-to-adult trophallaxis has been described in *Platythyrea* (Villet et al., 1990). Furthermore, we found that the adult casts of this species, which

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\* Japanese Formicidae Code by M. Terayama (1992)

produces both winged and ergatoid (wingless workerlike) types of females and males, possessed different trophallactic habits towards each other. In particular, the queens showed a unique behavior of rejecting the solicitation of regurgitated food by workers, and the ergatoid males showed the regurgitating behavior toward calow queens.

In this paper, we report the unique habits of the stomodeal trophallaxis among the adult castes of *Hypoponera* sp. (JFC 11104).

**Methods**

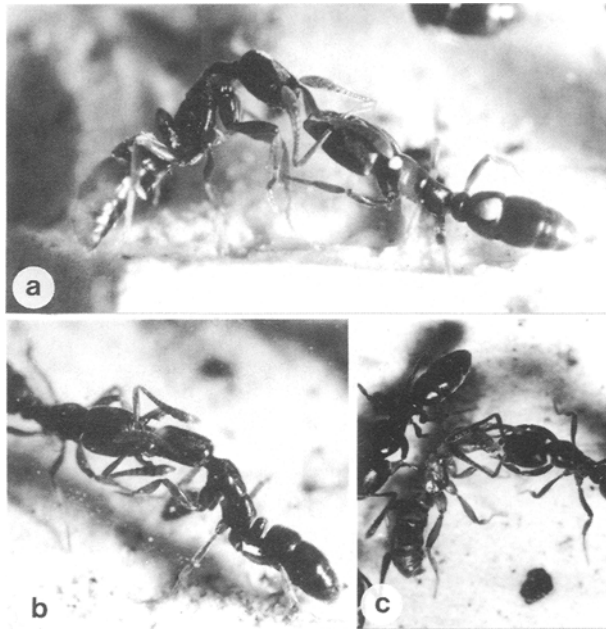
All colonies for this study were collected on the riverbank of the Yodo, Osaka Prefecture, west Japan in 1991 and 1993 (Table 1). Of 18 colonies collected, the trophallaxis behavior of 4 colonies (colony A, B, D and C) was recorded in detail with a videocamera though a stereomicroscope in the laboratory. Colony A comprised 2 dealate and 3 ergatoid queens and 15 workers, colony B ergatoid queen and 10 workers, colony C 5 ergatoid females and 6 ergatoid males just eclosed and 34 workers, and colony D 26 alate females and 49 alate males just eclosed and 46 workers. These colonies were kept at room temperature in plastic petri dishes with a plaster floor. The ants were reared on Collembola and honeywater.

To confirm the occurrence of trophallaxis, the ants were fed honeywater stained red and then dissected to determine the contents of the crop was demonstrated that liquid food stored in the crop was regurgitated to nestmates (Fig. 2).

**Table 1.** Colony composition of the adult castes in *Hypoponera* sp. (JFC 11104)

Date	Dealate Queen(s)	Ergatoid Queens	Workers	Alate Females	Alate Males	Ergatoid Females	Ergatoid Male(s)	Observed Colony code
20.i.91		3	82					
21.iv.91	1	6	126					
19.iv.91	2	3	15					colony A
19.iv.93	4	6	20					
1.v.93		2	10					colony B*
17.vii.93		13	25					
26.vii.93		2	133			2	1	
26.vii.93		7	124			3	6	
31.vii.93		11	132					
1.viii.93			34			5	6	colony C
4.viii.91			30	48	26			
5.viii.93		2	45				1	
13.ix.93			46	26	49			colony D
27.xi.91		5	52					
27.xi.91	1		19					
4.xii.91			231			2	7	
4.xii.91	1	7	48					
4.xii.91	1	13	77					

\* An ergatoid queen is eliminated to observe trophallactic behaviors between a queen and workers.



**Figure 1.** Trophallactic behavior among the adult castes of *Hypoponera sp.* (JFC 11104). a: an ergatoid queen whipping a worker; b: trophalactic food exchange between workers; c: an ergatoid male receiving regurgitated food from a worker

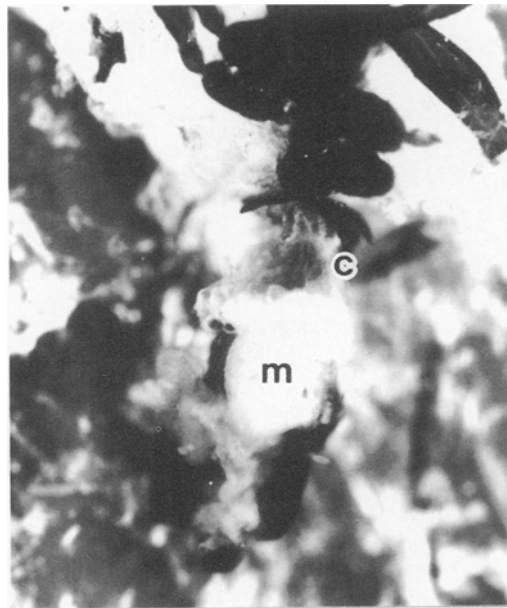
## Results

### *Composition of colonies*

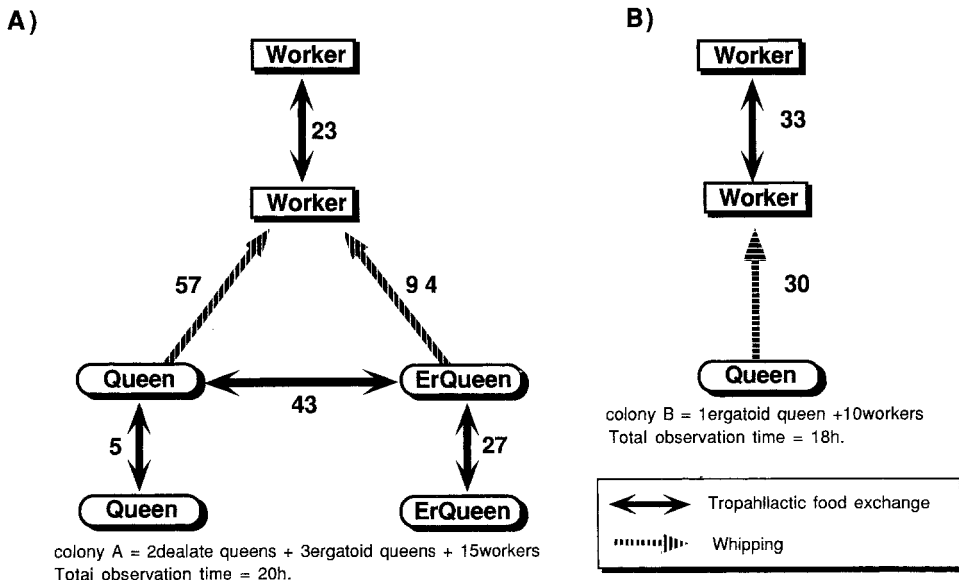
Colonies of *Hypoponera sp.* (JFC 11104) consisted of between approximately 12 and 240 individuals (Table 1). Only one colony contained a single dealate queen; the others were polygynous, with a range of 2 to 14. Colonies may not produce both alate and ergatoid types of new queens and males simultaneously, as seen in our experiment. The ergatoid males were observed to conduct intranidal mating with all eclosing or still inactive, scarcely pigmented females. On the other hand, alate males were not observed to mate with alate females in the nest. Multiple ergatoid males (maximum of 7) in single nests were found without the special action of the attacking male, unlike the cases of *Hypoponera punctatissima* (Hamilton, 1979) and *Cardiocondyla wroughtoni* (Kinomura and Yamauchi, 1987).

### *Description of trophallactic and “whipping” behaviors*

A typical sequence of trophallactic behavior is as follows: when two individuals approach each other head on, the soliciting ant tilts her head sideways almost 90 degrees and strikes the donor's head with her antennae. The solicitor then re-



**Figure 2.** Dissection of the abdomen of a worker to show the stained contents stored in the crop (social stomach). c, crop; m, midgut



**Figure 3.** A) Frequency of trophallic and whipping behaviors of queens and workers in colony A. B) Frequency of trophallic and whipping behaviors of an ergatoid queen and workers in colony B

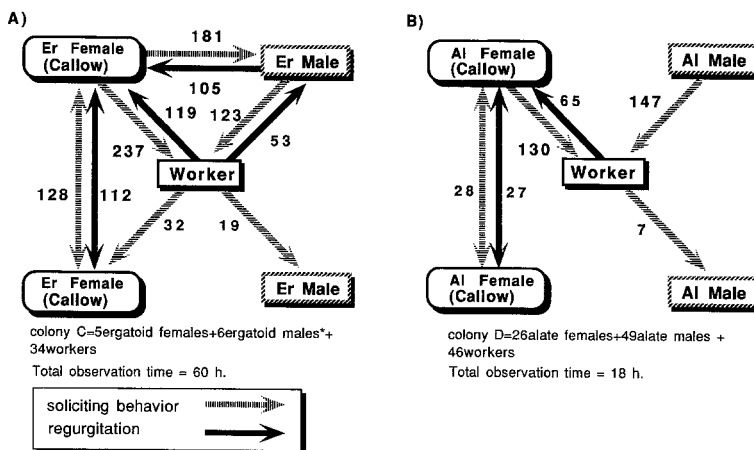
peatedly rips importunately the donor's mandibles with its mandibles and jerks its body back and forth rapidly with antennation, until the donor regurgitates a droplet (Fig. 1 b). Dealate and ergatoid queens show a unique behavior of rejecting the soliciting workers, which is called "whipping" in this paper. In this behavior, the queen takes a standing posture by rising on the middle and hind legs and beats down the solicitor with her antennae until it ceases the soliciting behavior (Fig. 1 a). Alate males had no trophallactic habits, while ergatoid males showed trophallactic behavior similar to that of the workers (Fig. 1 c).

*Trophallactic behavior of queens and workers*

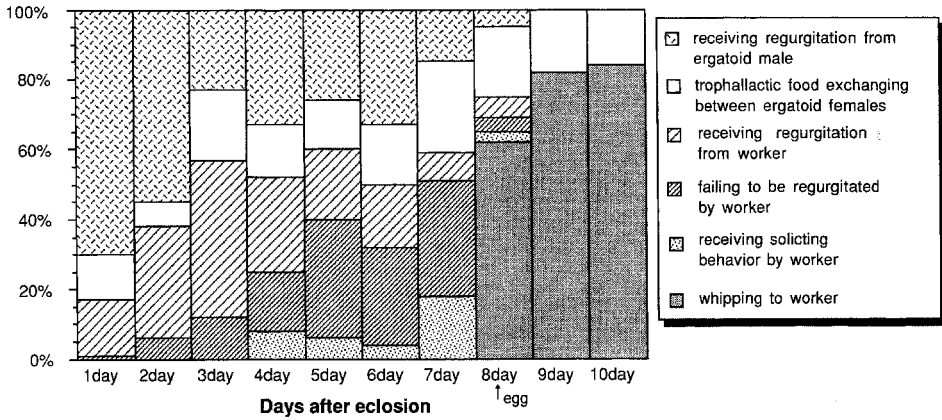
Of the colonies collected in the field, trophallactic food exchange was observed between workers and between queens, but not between workers and queens (except between workers and callow queens; see below). "Whipping behavior" was observed between workers and queens. The VTR observations of colony A for a total of 20 h and B for a total of 18 h confirmed these unique habits, indicating that no trophallaxis occurs between workers and queens, even when the colony only has one queen (Fig. 3). Some differences in trophallactic habit, however, were found between workers and the queen casts. The workers spent much more time in the soliciting behavior of trophallaxis than did queens, so that the time required by workers for the trophallactic food exchange was longer than that of queens. The duration required for trophallactic food exchange of workers was  $124 \pm 143.8$  s on average ( $349-7$  s), while that of queens was  $18 \pm 7.6$  s ( $40-7$  s), in the colony A measured with VTR.

*Trophallactic behavior of ergatoid females and males*

The observations with colony C indicated that the ergatoid females (callow queens) received regurgitated foods from workers (Fig. 4). As no trophallaxis was observed



**Figure 4.** A) Frequency of trophallactic behaviors of ergatoid females and ergatoid males in the colony C (\* Number of the males is 6 at the beginning and 2 at end of observation). B) Frequency of trophallactic behaviors of alate females and alate males in the colony D



**Figure 5.** Frequency percentage of trophallactic-behavioral acts by ergatoid females in colony C for 6 h each day from 1 to 10 days after eclosion

between workers and mature queens, this behavioral change of the queens is of interest. The cocoons of 5 ergatoid females were collected (colony C) to study the trophallactic behavior of these ergatoid females 1 to 10 days after the eclosion. Figure 5 shows that the ergatoid females receive regurgitated foods from workers until 8 days after eclosion; the frequency of successful attempts to be regurgitated by the workers starts to decrease 4 days after eclosion. On the other hand, the frequency of soliciting behavior by workers toward ergatoid females started to increase 4 days after eclosion; the ergatoid females crouched until the workers ceased their soliciting behavior. Starting on Day 8 after eclosion, when the ergatoid females started to lay eggs, they showed no soliciting behavior toward workers and displayed the “whipping behavior” toward the soliciting worker. Ergatoid females did receive regurgitated food from ergatoid males and exchanged regurgitated food with other ergatoid females, starting on the first day after eclosion.

Ergatoid males received regurgitated food from workers and regurgitated it to queens, but not vice versa, as shown by our observations of colony C. Trophallactic behavior was never observed between the males (Fig. 4).

*Trophallactic behavior of alate females and males*

In the observation of colony D, alate females received regurgitated food from workers and exchanged it with other alate females, but did not receive regurgitated food from alate males (Fig. 4). Furthermore, the soliciting behavior of workers toward the alate females was not observed in colony D. Because we missed collecting the cocoons of alate females, behavioral changes of alate females with regard to trophallaxis could not be observed.

Alate males showed soliciting behavior toward workers, but all their attempts failed (Fig. 4). No trophallactic behavior was observed between alate males.

## Discussion

Hölldobler (1985) concluded that the existence of adult-to-adult trophallaxis was probably absent in ponerines, based on the observation of two Australian *Hypoponera* species, *Pachycondyla villosa* and *P. obscuricornis*. We, however, discovered that Japanese *Hypoponera* sp. (JFC 11104) do perform adult-to-adult trophallaxis. This may be the first, such finding in ponerine ants. Since trophallaxis is widespread among wasps (Wilson, 1971), it is clear that its presence among ants is a “primitive” character. Ponerine species not exercising trophallaxis have probably lost this behavior secondarily. Furthermore, we found that the habits of trophallaxis differ among the casts in this species. This may also be the first such discovery in ants. In *Hypoponera* sp. (JFC 11104), the worker displays the soliciting behavior towards queens, males and workers, but receives regurgitated food only from workers. The worker is forced to stop soliciting for regurgitated food by the queen’s “whipping behavior”. Callow queens solicit regurgitated food from workers and ergatoid males and receive it, while mature queens do not solicit regurgitated food from workers. Ergatoid males receive regurgitated food from workers and regurgitate it for queen. Alate males show no trophalactic food exchange with workers and queens. Trophalactic behavior was never observed between males of either winged or ergatoid types.

Generally, male ants are made for mating and little else (self-grooming and dispersion, etc.). In a small number of species, males are wingless and more or less closely resemble typical ant workers (i.e., ergatoid male). This phenomenon is found in four genera; *Hypoponera*, *Cardiocondyla*, *Formicoxenus*, and *Techonomyrmex* (Hölldobler and Wilson, 1990). Because of their worker-life morphology, ergatoid males are expected to participate in worker-like social function; however, until now no evidence has ever been adduced of participation by the males in any social function (Kinomura and Yamauchi, 1993; Hölldobler and Wilson, 1990). The ergatoid male of *Hypoponera* sp. (JFC 11104) does engage in social activities other than the mating: he receives food from workers and regurgitates it to callow queens. Because the ergatoid male shows the loss of between-colony dispersal with a tendency toward pairing with female nestmates, the reason for losing its wings is clear. However, the reason why this type of male is similar to the worker cast is unclear. The findings presented in this paper provide a clue. In ants, the worker cast is generally indifferent to the males (Boomsma and Isaaks, 1985; Hölldobler and Wilson, 1990). To stay in the maternal nest to mate with sisters, the ergatoid males need to avoid aggressive behavior and receive nursing by workers. The ergatoid males of *Hypoponera* sp. (JFC 11104) were fed by workers, whereas the alate males were not. A reason for the ergatoid modifications of the male could be to mimic the worker cast and thus receive regurgitated food.

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