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## THE EFFECT OF LABORATORY COLONY CONDITION ON THE TROPHALLACTIC INTERACTIONS OF *CAMPONOTUS VAGUS* (HYMENOPTERA: FORMICIDAE)

ORSOLYA KANIZSAI<sup>1</sup>, ISTVÁN MAÁK and GÁBOR LÓRINCZI

<sup>1</sup>*Department of Ecology, University of Szeged, 52 Közép fasor, Szeged 6726, Hungary*  
E-mail: [orsi.kanizsai@gmail.com](mailto:orsi.kanizsai@gmail.com)

In this study, our aim was to give a detailed evaluation of the trophallactic interactions among foragers of *Camponotus vagus* in outside-nest situation, and to find out which properties of trophallaxis may have a role in the information-flow among workers about current nutritional state of the colony. Measured parameters were the number and frequency of trophallactic interactions, the duration of trophallaxes, the frequency of different duration interactions, and the number and size-class of workers participating in trophallactic events outside the nest. Experiments were conducted both with starved and satiated colonies to examine the effect of feeding condition. We demonstrated that the dynamics of trophallaxis is a stable parameter; it was independent from the starvation level. Similarly, the number of partners and the size class distribution of the different sized worker pairs did not differ between the two colony states. Starvation level influenced both the frequency and mean duration of trophallactic interactions. The frequency-distribution of the duration of trophallactic events showed an exponential trend, i.e., the short term interactions were more frequent than the prolonged ones in both colony states. However, the rate of these two distinguished types of trophallaxis was different in the case of the two colony conditions. Different rates of the short term and prolonged interactions may provide information about the current nutritional requirements of the colony, enhancing the speed and efficiency of colony responses to feeding stress. Frequent short term trophallaxis may not only contribute to a high level of cooperation during retrieval of food among foragers, but also maintain the integration of colony members even outside their nest.

Key words: cooperation, feeding stress, food-sharing, foragers, information-flow.

### INTRODUCTION

Trophallaxis, the exchange of liquid food by regurgitation is a highly evolved form of food sharing among colony members of social insects (WILSON 1971, HÖLLDOBLER & WILSON 1990). Besides this important function, it also contributes to the continuous flow of hydrocarbons facilitating the dynamic formation of the unique and uniform colony odour (BOULAY & LENOIR 2001, SOROKER *et al.* 1995, SOROKER *et al.* 1998, DAHBI *et al.* 1999, BOULAY *et al.* 2000, BOULAY *et al.* 2004). Furthermore, trophallaxis can also have its share in the transfer of immune factors promoting a colony-level immune competence against infection and disease transmission (HAMILTON *et al.* 2011).

Trophallaxis is much more common among ant species belonging to phylogenetically advanced subfamilies (e.g., Formicidae) and genera (e.g., *Camponotus* spp.), than in the more primitive subfamilies such as the ponerine ants, which typically carry the liquid droplets between their mandibles (WILSON 1971, HÖLLDOBLER 1985, DEJEAN & SUZZONI 1997, RICHARD *et al.* 2004).

Frequent trophallactic interactions among nestmates maintain a continuous contact, which is essential to the plasticity in the division of labour, enhancing social cooperation, and it also allows the exchange of information about the current requirements of the colony (SØRENSEN *et al.* 1985, HÖLLDOBLER & WILSON 1990, FARINA 2000). In the case of *Formica fusca* Linnaeus, 1758 and *Solenopsis invicta* Buren, 1972 it was demonstrated that the frequency of trophallaxis increased with worker and colony hunger (i.e., with starvation) (WALLIS 1964, HOWARD & TSCHINKEL 1981). SANADA *et al.* (1997) also reported that trophallaxis was more frequent among starved workers of *Camponotus yamaokai* Terayama & Satoh, 1990 than among satiated ones.

Under an artificial outside-nest condition, we investigated the trophallactic interactions among the foragers of the polymorph carpenter ant, *Camponotus vagus* (Scopoli, 1763). Our main question was which parameters of trophallactic interactions promote and contribute to the information-sharing among workers about current feeding condition and needs of the colony. We aimed to determine whether there is a difference between the starved and satiated colonies regarding 1) the number and frequency of trophallactic interactions, 2) the duration of trophallaxes and the frequency of different duration interactions, and 3) the number and size-class of workers participating in trophallactic events outside the nest.

## MATERIAL AND METHODS

### *Study species*

Owing to their high trophallactic activity, *Camponotus* species are ideal objects for studying these interactions in ants (BONAVITA-COUGOURDAN & MOREL 1988, PROVECHO & JOSENS 2009, SANADA *et al.* 1999, BOULAY *et al.* 2000, LENOIR *et al.* 2001, HAMILTON *et al.* 2011). *Camponotus* species are considered to be polymorphic because they show a gradient of size variation from the smallest minor workers to the largest majors. At least two different subcastes can be distinguished (e.g., in *C. foreli* Emery, 1881) (ESPADALER *et al.* 1990), but three size classes can also occur in some species of this genus (e.g., in *C. sericeiventris* (Guérin-Méneville, 1838), BUSHER *et al.* 1985). Similarly to other members of the *Camponotus* genus, *C. vagus* is strongly polymorphic with a wide range of worker sizes (BONAVITA-COUGOURDAN & MOREL 1985).

We previously measured the head width (HW: maximum width of head, including eyes, measured in full-face view) of 73 workers from the same habitat where the collection of experimental colonies took place. These measurements also demonstrated a wide range

of worker sizes of *C. vagus*, but still, three main size-classes were securely distinguishable by visual inspection. This was important, because we wanted to record the trophallactic events without disturbing the ants, and this way these events were easily followed without using cameras. On the basis of the previous measurements, the distinguished classes were minor ("S"=small; HW: mean 3.12 mm  $\pm$  0.18 SD), intermediate ("M"=medium; HW: mean 3.82 mm  $\pm$  0.18 SD) and major workers ("L"=large; HW: mean 5.19 mm  $\pm$  0.32 SD). Beside the size and the form of the body, the shape of the head also helped us in visual separation: workers with wide, "heart shaped" head were considered as majors ("L"), while those with "short" head as minors ("S"). All intermediate forms were grouped into the intermediate category ("M"), which contained more sizes, not distinguishable by only visual inspection; therefore this category was a mixed class.

Our study species, *C. vagus* is a Euro-Siberian species distributed mainly in Central and Southern Europe (KUTTER 1977, CZECHOWSKI *et al.* 2012). In the Carpathian Basin it is common in warm and dry habitats, especially in open forests and forest edges (GALLÉ *et al.* 2005). It nests mostly in decaying wood, but also under stones (KUTTER 1977, SEIFERT 2007, CZECHOWSKI *et al.* 2012). Colonies are monogynous with a few thousand (up to ten thousand) workers (SEIFERT 2007, CZECHOWSKI *et al.* 2012).

The four experimental colonies of *C. vagus*, each composing of ca. 200 workers and broods, were collected in March 2012 in the Kiskunság National Park (Central Hungary). Acclimatisation period for laboratory condition was about a month before experiments, which were all conducted in May 2012.

### Experimental setup

Colonies were kept in plastic nest boxes (38 l each) containing fragments of the original wood nest material (i.e., artificial nests). The nests were regularly moistened, and the colonies were kept at a temperature of 22 ( $\pm$  3 SD) °C with a 12 h photoperiod. Ants were fed with a commonly used artificial diet (BHATKAR & WHITCOMB 1970), but during the experiments a honey-water solution (2:1) was applied as liquid bait. Just before the start of the trials, the nest box of the experimental colony was connected to the external foraging arena (i.e., outside-nest situation) with a plastic tube.

The external foraging arena (L: 180 cm, W: 65 cm, H: 35 cm) was divided into 468 grid squares of 5 cm  $\times$  5 cm for the random arrangement of baits. Before the start of the trials, 12 liquid baits were randomly placed, four in each third (60 cm long) part of the arena. Each trial lasted for one hour. The connecting tubes towards the arena were opened just before the experiments. The evaluation period started when the first worker entered the arena. For each colony we conducted one trial in starved and one in satiated condition. We recorded only those trophallactic events that took place in the external foraging arena but those within the nests were not recorded.

We tested the trophallactic events in the case of each experimental colony both in starved and satiated conditions. The first set of trials were conducted with starved colonies (i.e., the colony was not fed within ten days before the experiment), while the second set of trials was conducted with the same but satiated colonies (i.e., the colony was fed one day before the experiment). That is one day passed between the two sets of trials of one colony.

During the experiments we recorded the duration (in sec) of each trophallactic interaction, the number and size-class of participants, and the size-class (S = small, M = medium and L = large) of the participant initiating the interaction. We measured the total number

of trophallactic events/hour both in the case of the starved and satiated colonies. For the analysis of the dynamics of trophallaxis we summarised the number of trophallactic events in intervals of five minutes (12 intervals/hours).

### Data analysis

Each of the four experimental colonies was tested in starved and satiated condition. Different colonies were analysed only together. We tested both the dynamics of trophallactic interactions and the frequency-distribution of the different duration trophallactic interactions in both colony conditions with Curve Fit Estimation Regression. To identify whether the colony condition has an influence on the number of partners, the size-class of different partners and the initiator of the interaction, we built a GLMM model with Poisson error term, with the different experimental colonies as random factor. The same approach was used for testing, whether the number of partners and the colony state has an effect on the duration of trophallaxis. The best model was chosen with automated model selection on the basis of the AIC value, with the help of “dredge” function from the MuMIn package (BARTOŃ 2013). We also tested whether the size-class of partners influences the duration of trophallaxis, but because of lacking data, with a smaller sample size. The differences between the five size-class pairs were analysed with pair-wise comparisons (function “relevel”) and Bonferroni-Holm corrections. We compared the mean number of trophallactic interactions for every five-minute interval of experiments between the different colony conditions with the help of paired t test.

Statistical analyses were carried out with R (R CORE TEAM 2013) and SPSS package (version 17.0.0) for Windows (SPSS Inc., Chicago, IL, USA).

## RESULTS

Overall, a total of 1152 trophallactic interactions were recorded and analysed among the workers of *C. vagus* in outside-nest situation.

In the case of starved colonies 2–5 workers, while in the case of satiated ones 2–3 workers participated in each trophallactic event, but most of them took place between two workers in both colony conditions (Table 1). The number of participants in trophallactic interactions was not influenced significantly by the starvation level of colonies (GLMM  $z = -0.845$ ,  $N = 620$ ,

**Table 1.** The number of participants in trophallactic events.

| No. of participants | Starved colonies |       | Satiated colonies   |              |       |
|---------------------|------------------|-------|---------------------|--------------|-------|
|                     | No. of cases     | %     | No. of participants | No. of cases | %     |
| 2                   | 656              | 88.05 | 2                   | 401          | 98.53 |
| 3                   | 73               | 9.80  | 3                   | 6            | 1.47  |
| 4                   | 15               | 2.01  | 4                   | 0            | 0.00  |
| 5                   | 1                | 0.13  | 5                   | 0            | 0.00  |
| Total               | 745              | 100   | Total:              | 407          | 100   |

**Table 2.** Size-class distribution of trophallactic partners ("S"=small, "M"=medium, "L"=large): the number and frequency of trophallactic events between different size-class pairs. The total numbers of cases for starved and satiated colonies were 656 and 401, respectively.

| Size-class distribution | Starved colonies   |               |       | Satiated colonies  |               |       |
|-------------------------|--------------------|---------------|-------|--------------------|---------------|-------|
|                         | Total no. of cases | Mean (SD)     | %     | Total no. of cases | Mean (SD)     | %     |
| S-S                     | 84                 | 14.00 (5.87)  | 12.97 | 62                 | 10.33 (8.98)  | 15.59 |
| S-M                     | 102                | 17.00 (10.49) | 15.14 | 67                 | 11.17 (8.68)  | 17.53 |
| S-L                     | 48                 | 8.00 (5.93)   | 7.69  | 42                 | 7.00 (6.90)   | 12.83 |
| M-M                     | 231                | 38.50 (16.88) | 34.82 | 119                | 19.83 (15.04) | 27.55 |
| M-L                     | 147                | 24.50 (5.96)  | 22.4  | 79                 | 13.17 (10.21) | 18.79 |
| L-L                     | 44                 | 7.33 (2.66)   | 6.98  | 32                 | 5.33 (7.03)   | 7.70  |

$p = 0.40$ ). Most of the trophallactic interactions involving two partners occurred between the medium size-class workers in both cases (Table 2). There were no significant differences between the starved and satiated colonies regarding the size-class distribution of trophallactic partners (GLMM  $z = -0.962$ ,  $N = 575$ ,  $p = 0.34$ ).

Trophallaxes were initiated mostly by the small size-class workers when their partner belonged to the medium size-class, while the initiators of interactions were mostly the large workers when their partner was a small or medium size-class worker (Table 3). The size-class of the initiators did not differ significantly between the two colony conditions (GLMM  $z = 0.353$ ,  $N = 1152$ ,  $p = 0.72$ ).

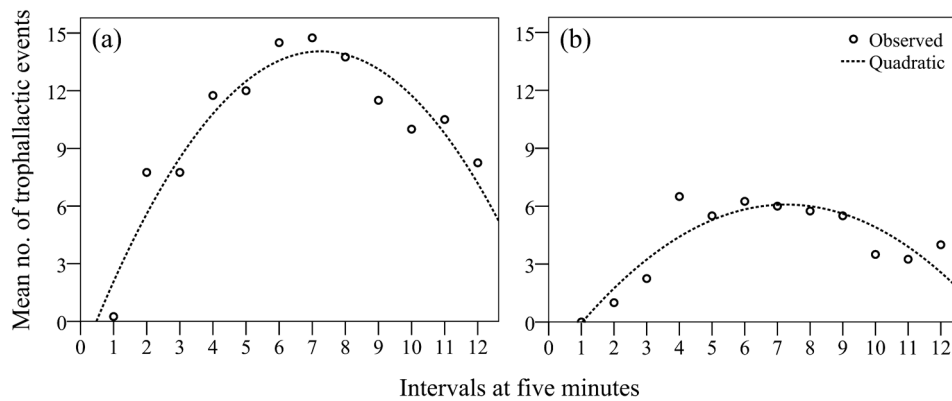
The number of trophallactic interactions within the five minutes intervals showed a significant quadratic curve fit both in starved (Curve Fit Estimation Regression  $R^2 = 0.89$ ,  $F = 37.90$ ,  $df_1 = 2$ ,  $df_2 = 9$ ,  $p < 0.001$ ,  $b_1 = 4.44$ ,  $b_2 = -0.31$ ,  $N = 12$ ) and satiated colonies ( $R^2 = 0.79$ ,  $F = 17.33$ ,  $df_1 = 2$ ,  $df_2 = 9$ ,  $p = 0.001$ ,  $b_1 = 2.28$ ,  $b_2 = -0.16$ ,  $N = 12$ ) (Fig. 1). The two colony conditions had significant

**Table 3.** Frequencies (%) of the different size-class initiator of interactions in the different trophallactic pairs. "S"=small, "M"=medium, "L"=large.

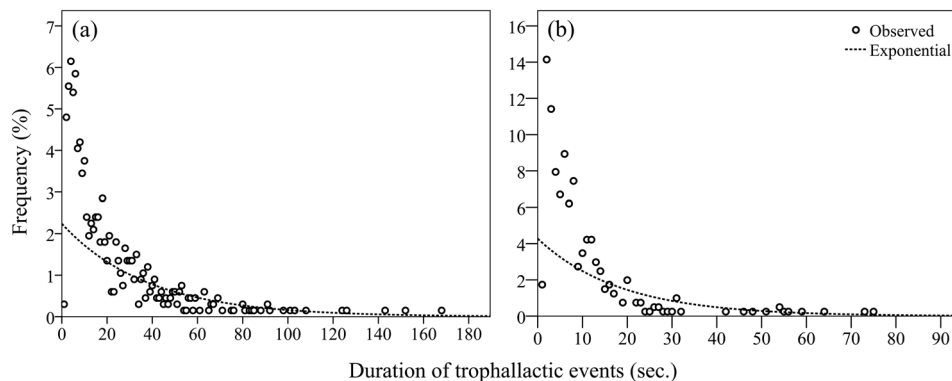
| Initiator of interactions | Size-class distribution |     |       |
|---------------------------|-------------------------|-----|-------|
|                           | S-M                     | S-L | M-L   |
| S                         | 64.91                   | 12  | –     |
| M                         | 35.09                   | –   | 33.74 |
| L                         | –                       | 88  | 66.26 |
| Total no. of cases        | 57                      | 25  | 83    |

differences in the mean number of trophallactic interactions within the five minutes intervals of the experiments (paired samples t-test:  $t = 9.37$ ,  $p < 0.001$ ).

The duration of trophallactic events lasted from one to 181 sec with a median of 16.68 sec ( $\pm 19.79$  SD). The frequency-distribution of trophallactic interactions showed an exponential trend, where the short term trophallactic events were more frequent than the longer ones both in starved and satiated colonies (Curve Fit Estimation Regression, exponential model: 1) starved colonies:  $R^2 = 0.676$ ,  $F = 173.461$ ,  $df1 = 1$ ,  $df2 = 83$ ,  $p < 0.001$ ,  $b1 = -0.026$ ,  $N = 85$ ; 2) satiated colonies:  $R^2 = 0.655$ ,  $F = 73.946$ ,  $df1 = 1$ ,  $df2 = 39$ ,  $p < 0.001$ ,  $b1 = -0.054$ ,  $N = 41$ ) (Fig. 2). These interactions lasted significantly longer in the case of starved, than in the case of satiated colonies (GLMM  $z = -17.63$ ,  $N = 620$ ,  $p < 0.001$ ). The duration of trophallaxis was influenced also by the number of



**Fig. 1.** The hourly dynamics of trophallactic events in *Camponotus vagus*. (a): Starved colonies; (b): Satiated colonies.



**Fig. 2.** Frequencies of duration of trophallactic interactions in *Camponotus vagus*. (a): Starved colonies; (b): Satiated colonies.

**Table 4.** Differences in the duration of trophallactic interactions between the five size-class pairs. "S"=small, "M"=medium, "L"=large.

|     | S-M         | S-L         | M-M         | M-L         | L-L        |
|-----|-------------|-------------|-------------|-------------|------------|
| S-S | Z = -7.20** | Z = -6.68** | Z = -4.94** | Z = -2.28** | Z = 3.41** |
| S-M | -           | Z = -0.27   | Z = 3.23**  | Z = 5.63**  | Z = 9.42** |
| S-L | -           | -           | Z = 3.01**  | Z = 5.13**  | Z = 8.76** |
| M-M | -           | -           | -           | Z = 2.99**  | Z = 7.75** |
| M-L | -           | -           | -           | -           | Z = 5.52** |

partners (GLMM  $z = 30.57$ ,  $N = 620$ ,  $p < 0.001$ ), and it was significantly different between most of the size class pairs, except S-M and S-L (GLMM  $z = -0.27$ ,  $N = 575$ ,  $p = 0.79$ ) (Table 4).

## DISCUSSION

The state of hunger of foragers plays an important role in regulating food distribution in the colony. Ants respond to colony starvation by taking up more food and sharing it in a greater proportion with their nestmates (HOWARD & TSCHINKEL 1980). Our results also revealed a significant effect of starvation both on the frequency and duration of trophallactic events among the foragers of *Camponotus vagus*. However, the length of food deprivation significantly influenced the readiness to regurgitate, but the hourly dynamics of trophallactic events was independent from the condition of the colonies. In both cases there were relatively few trophallactic events during the first five minutes of the observations. The maximal frequency of interactions was measured at the half time (30 min) of the experiments.

The duration of worker-larva trophallaxis is reportedly brief and relatively constant (<15 s) (CASSIL & TSCHINKEL 1999) and neither larval size, nor larval starvation has a significant effect on it. The allocation of liquid food to larvae by workers is regulated by the frequency of trophallactic interactions, and the frequency of trophallaxis increases with larval size and hunger (CASSIL & TSCHINKEL 1996). In contrast with the worker-larva trophallaxis, the duration of worker-worker interactions is highly variable and usually longer (<360 s) (CASSIL & TSCHINKEL 1999). According to the study by CASSIL and TSCHINKEL (1996), the duration of trophallaxis among workers of different sizes is similar in fire ants. Similarly to that study, our results showed that the duration of interactions was not influenced by the size-class distribution of trophallactic partners of *C. vagus*. We observed a higher number of prolonged interactions between foragers from starved colonies than from satiated ones, although short-term interactions were more frequent in both colony condi-

tions. Short-term (i.e., 1–10 sec) trophallaxis may have a crucial role in the information-flow among the foragers of *C. vagus* about current colony needs, working as a continuous feed-back whether the foraging activity is intense enough, or more workers need to be retrieved. Moreover, it may also help to adjust the foraging behaviour of workers outside the nest. The need for further studies to elucidate the exact role of short term trophallaxis is apparent. The assessment and collection of food is undertaken by the foraging ants, which can solve nutritional challenges for the colony by making intricate adjustments to their feeding behaviour and nutrient processing (DUSSUTOUR & SIMPSON 2009). Individual foragers must be responsive to a number of variable factors, including the availability and distribution of resources in their environment (HIRSH & GORDON 2001). Owing to their trophallactic interactions outside the nest, the information-flow among foragers may contribute to an enhanced efficiency of food discovery and retrieval, promoting a fast stress response concerning foraging activity of the colony in concordance with its nutritional requirements.

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## REFERENCES

- BARTOŇ, K. (2013) MuMIn: Multi-model inference. *R package version 1.9.13*. <http://CRAN.R-project.org/package=MuMIn>.
- BHATKAR, A. & WHITCOMB, W. H. (1970) Artificial diet for rearing various species of ants. *The Florida Entomologist* **53**: 229–232.
- BONAVITA-COUGOURDAN, A. & MOREL, L. (1985) Polyethism in social interactions in ants. *Behavioural Processes* **11**: 425–433.
- BONAVITA-COUGOURDAN, A. & MOREL, L. (1988) Interindividual variability and idiosyncrasy in social behaviours in the ant *Camponotus vagus* Scop. *Ethology* **77**: 58–66.
- BOULAY, R. & LENOIR, A. (2001) Social isolation of mature workers affects nestmate recognition in the ant *Camponotus fellah*. *Behavioural Processes* **55**: 67–73.
- BOULAY, R., SOROKER, V., GODZINSKA, E., HEFETZ, A. & LENOIR, A. (2000) Octopamine reverses the isolation-induced increase in trophallaxis in the carpenter ant *Camponotus fellah*. *The Journal of Experimental Biology* **203**: 513–520.
- BOULAY, R., KATZAV-GOZANSKY, T., HEFETZ, A. & LENOIR, A. (2004) Odour convergence and tolerance between nestmates through trophallaxis and grooming in the ant *Camponotus fellah* (Dalla Torre). *Insectes Sociaux* **51**: 55–61.



- BUSHER, C. E., CALABI, P. & TRANIELLO, J. F. A. (1985) Polymorphism and division of labor in the Neotropical ant *Camponotus sericeiventris* Guerin (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* **78**: 221–228.
- CASSIL, D. R. & TSCHINKEL, W. R. (1996) A duration constant for worker-to-larva trophallaxis in fire ants. *Insectes Sociaux* **43**: 149–166.
- CASSIL, D. R. & TSCHINKEL, W. R. (1999) Information flow during social feeding in ant societies. Pp. 69–81. In: DETRAIN, C., DENEUBOURG, J. L. & PASTEELS, J. M. (eds): *Information Processing in Social Insects*. Birkhäuser Verlag, Basel.
- CZECHOWSKI, W., RADCHENKO, A., CZECHOWSKA, W. & VEPSÄLÄINEN, K. (2012) *The ants of Poland with reference to the myrmecofauna of Europe*. Fauna Poloniae 4, Warszawa.
- DAHBI, A., HEFETZ, A., CERDÁ, X. & LENOIR, A. (1999) Trophallaxis mediates uniformity of colony odor in *Cataglyphis iberica* ants (Hymenoptera, Formicidae). *Journal of Insect Behavior* **12**: 559–567.
- DEJEAN, A. & SUZZONI, J. P. (1997) Surface tension strengths in the service of a Ponerine ant: a new kind of nectar transport. *Naturwissenschaften* **84**: 76–79.
- DUSSUTOUR, A. & SIMPSON, S. J. (2009) Communal nutrition in ants. *Current Biology* **19**: 740–744.
- ESPADALER, X., RETANA, J. & CERDÁ, X. (1990) The caste system of *Camponotus foreli* Emery (Hymenoptera: Formicidae). *Sociobiology* **17**: 299–312.
- FARINA, W. M. (2000) The interplay between dancing and trophallactic behavior in the honey bee *Apis mellifera*. *Journal of Comparative Physiology [A]* **186**: 239–245.
- GALLÉ, L., MARKÓ, B., KISS, K., KOVÁCS, É., DÜRGŐ, H., KÓVÁRY, K. & CSÓSZ, S. (2005) Ant fauna of Tisza River Basin (Hymenoptera: Formicidae). Pp. 149–197. In: GALLÉ, L. (ed.): *Vegetation and fauna of Tisza River Basin I*. Tiscia Monograph Series, Szeged.
- HAMILTON, C., LEJEUNE, B. T. & ROSENGAUS, R. B. (2011) Trophallaxis and prophylaxis: social immunity in the carpenter ant *Camponotus pennsylvanicus*. *Biology Letters* **7**: 89–92.
- HIRSH, A. E. & GORDON, D. M. (2001) Distributed problem solving in social insects. *Annals of Mathematics and Artificial Intelligence* **31**: 199–221.
- HÖLLDOBLER, B. (1985) Liquid food transmission and antennation signals in Ponerine ants. *Israel Journal of Entomology* **19**: 89–99.
- HÖLLDOBLER, B. & WILSON, E. O. (1990) *The Ants*. Harvard University Press, Cambridge, 732 pp.
- HOWARD, D. F. & TSCHINKEL, W. R. (1980) The effect of colony size and starvation on food flow in the fire ant, *Solenopsis invicta* (Hymenoptera: Formicidae). *Behavioral Ecology and Sociobiology* **7**: 293–300.
- HOWARD, D. F. & TSCHINKEL, W. R. (1981) The flow of food in colonies of the fire ant, *Solenopsis invicta*: a multifactorial study. *Physiological Entomology* **6**: 297–306.
- KUTTER, H. (1977) Hymenoptera, Formicidae. In: *Insecta Helvetica*, Fauna Bd. 6. Schweizerische Entomologische Gesellschaft, Zürich, 298 pp.
- LENOIR, A., HEFETZ, A., TOVIT, S. & SOROKER, V. (2001) Comparative dynamics of gestalt odour formation in two ant species *Camponotus fellah* and *Aphaenogaster senilis* (Hymenoptera: Formicidae). *Physiological Entomology* **26**: 275–283.
- PROVECHO, Y. & JOSENS, R. (2009) Olfactory memory established during trophallaxis affects food search behaviour in ants. *The Journal of Experimental Biology* **212**: 3221–3227.
- R DEVELOPMENT CORE TEAM (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>.
- RICHARD, F. J., DEJEAN, A. & LACHAUD, J. P. (2004) Sugary food robbing in ants: a case of temporal cleptobiosis. *Comptes Rendus Biologies* **327**: 509–517.

- SANADA, S., SATOH, T. & OBARA, Y. (1997) Trophallaxis and genetic relationships among workers in colonies of the polygynous ant *Camponotus yamaokai*. *Ethology, Ecology and Evolution* **9**: 149–158.
- SANADA, S., SATOH, T. & OBARA, Y. (1999) How average relatedness affects the frequency of trophallaxis between workers in an experimental colony of the polygynous ant, *Camponotus yamaokai*. *Journal of Ethology* **16**: 43–48.
- SEIFERT, B. (2007) *Die Ameisen Mittel- und Nordeuropas*. Lutra-Verlags- und Vertriebsgesellschaft, Görlitz, 368 pp.
- SORENSEN, A. A., BUSCH, T. M. & VINSON, S. B. (1985) Control of food influx by temporal subcastes in the fire ant, *Solenopsis invicta*. *Behavioral Ecology and Sociobiology* **17**: 191–198.
- SOROKER, V., VIENNE, C. & HEFETZ, A. (1995) Hydrocarbon dynamics within and between nestmates in *Cataglyphis niger* (Hymenoptera: Formicidae). *Journal of Chemical Ecology* **21**: 365–378.
- SOROKER, V., FRESNEAU, D. & HEFETZ, A. (1998) Formation of colony odor in Ponerine ant *Pachycondyla apicalis*. *Journal of Chemical Ecology* **24**: 1077–1090.
- WALLIS, D. I. (1964) The foraging behaviour of the ant, *Formica fusca*. *Behaviour* **23**: 149–176.
- WILSON, E. O. (1971) *The Insect Societies*. Harvard University Press, Cambridge, MA, 562 pp.

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