UNIVERSITY OF SZEGED
Faculty of Science and Informatics
Doctoral School of Environmental Science
Department of Ecology

Food sources, signals or infection focuses – the role of corpses in different ant species (Hymenoptera: Formicidae)

Summary of the PhD thesis

István Elek Maák

Scientific supervisor: Dr. Bálint Markó associate professor
Internal thesis advisor: Prof. Dr. László Gallé professor emeritus

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1. Introduction

Social life, besides its advantages involves major negative effects, since the intensive contacts among individuals can contribute to the fast spread of pathogens. Further on, social activities and lifestyle can lead to the accumulation of waste materials in high amounts, among which corpses are the most important components. The accumulation of wastes inside a nest can promote the establishment of pathogen microorganisms and fungi, therefore waste management, although essential for the colony's survival, represents risk for the performing workers due to the increased probability of getting infected.

In order to counterbalance these negative effects, many social defensive mechanisms have evolved, from which the most effective is the disposal of corpses on waste piles, i.e. the formation of cemeteries. Corpses can also be used as food sources, and the consumption of insect remnants, including those of other ant species, is a widespread phenomenon among ants. Corpse cannibalism is mentioned only in a few works, but it seems that corpses that appear inside the nest or during a battle can be consumed as food. Some recent researches also highlighted the use of corpses during interspecific conflicts; that is, the appearance of corpses may have negative effects on the behavior of the attacked colony. This behavior let us hypothesize that ants are able to recognize the corpses of different species, and react appropriately. Thus, corpses of different origin may have important signal properties.

2. Aims

In our study, we investigated (1) the response of different *Formica* species and that of the slave-maker *Polyergus rufescens* towards corpses of different rival and non-rival ant species. Besides the above, we also analyzed the differences in the reaction towards nestmate corpses in various situations. We tested (2) the use of these corpses as potential food sources and (3) their role in spread of infestations. Furthermore, we analyzed (4) the division of labor during waste management at different levels.

3. Materials and methods

3.1. Study setup and methods

In order to answer our questions, we performed investigations under field and laboratory conditions. Field observations were made in the case of *Formica cinerea*. The plastic plates used in our experiments were placed 50 cm-s before the main nest entrances. Each study period consisted of 12, 1-minute observations, repeated after 10 minutes through 2 hours. Our laboratory studies, besides *F.* cinerea, were also performed on two slave-maker species, *Formica sanguinea* and *Polyergus rufescens*, and on the territorial *Formica polyctena.* Each box containing a colony was linked with a 10 cm long plastic tube to a foraging arena (60 cm × 30 cm × 15 cm). Experimental colonies were kept under standard laboratory conditions (temperature 22±3 ºC; relative humidity 42-43%; 12 L and 12 D cycle from 7 am to 7 pm). These 1-minute observation periods were repeated after 3 minutes, because distances are shorter under laboratory conditions, and so the reactions are faster.

Before the start of our work, we placed 10 freeze-killed corpses in front of the main entrances and inside the search arenas, respectively, and we observed the number of nestmate workers around the corpses of different rival species, the transport rate and direction of the different corpses, and the behavioral reactions of resident workers towards them (i.e., ignoring, antennation, mandible spreading, biting, dragging and retreat). We used several kinds of corpses, namely corpses of nestmates (*F. cinerea, F. sanguinea, Polyergus rufescens* and *F. polyctena*) as control, non-nestmates, submissive *Formica fusca* and in some cases *Formica rufibarbis*, slave-makers and their slaves, and territorial wood-ants (*F. polyctena*, *Formica pratensis* and *Formica truncorum*). In addition, we compared the reactions of the two slave-maker species (facultative *F. sanguinea* and obligate *P. rufescens*) towards each other, their slaves, and corpses of potential slave species under laboratory conditions.

The role of corpses as food sources was tested in the case of the nestmate corpses of *F. polyctena* and the corpses of *Drosophila melanogaster*. The reactions to these corpses were also investigated after submerging them in oleic acid of 90% (Sigma-Aldrich) to test the response to artificial corpse smell. The amount of nestmate corpses used as food sources were further investigated with the help of individually paint-marked corpses in the case of starved (for 7 days) and satiated (normally fed for 7 days) colonies, and 7-day-old nestmates and rival *Camponotus vagus* corpses. The experimental corpses were measured both before their intake

into the nest and after their placement on the cemetery with an OHaus Explorer Pro EP 214 analytical scale (10000 g precision).

For the analyses of the possible role of corpses as infection focuses, we tested the reactions towards the corpses of nestmate *F. polyctena* treated with the spores and hyphae of the entomopathogenic fungi *Beauveria bassiana* (Hypocreales: Clavicipitaceae). 20 nestmate corpses per colony were submerged in 10^8 spore suspension for a few seconds, and left to dry for another 15 minutes. Afterwards, 10 corpses were used for the experiment with corpses infected with spores, and another 10 individuals were kept in darkness (25°C) for 3 days until the appearance of fungal hyphae on their surfaces. In both cases, we used untreated nestmate corpses kept under the same conditions as controls.

The division of labor in waste management activities at caste and individual level was analyzed in the polymorphic ant species *Camponotus aethiops*, which has workers that can be divided in different size castes, namely minor, media and major. For one week before the experiments, foragers collected from the arenas were individually paint-marked. Observations were performed for 5 minutes in the 1^{st}, 2 minutes in the 2^{nd}, 3^{rd} and 4^{th} trials, and for 1 minute repeated after 5 minutes for 3 hours. During the experiments, we noted the behavioral responses given to corpses, such as eating, drinking, eating corpses, dragging corpses and working on the dump sites. Our observations were also repeated with the corpses of *C. vagus*, a species with almost the same worker size, and those of *Apheanogaster subterranea*, a species with smaller worker size.

3.2. Statistical analysis

Generalized linear mixed models (GLMM, Poisson errors, maximum likelihood fit) were used to test the effect of corpse origin and other variables on the number of ant workers present on the plates, and on the behavioral responses recorded in the course of each 1 min observation. An aggression index was calculated for each 1 min observation where the number of negative reactions (i.e., mandible spreading, biting, dragging and retreat) was divided by the total number of behavioral responses. The effect of corpse origin on the decision whether or not to remove corpses from the plates, or to take them inside the nest or away from it was analyzed using GLMM (binomial error, maximum likelihood fit). The corpse removal rate was tested with the help of Cox regression models.

The same model approaches were used in the analysis of the reaction to the corpses of *D. melanogaster* and nestmates treated with oleic acid, and also to the corpses treated with hyphae and spores of the entomopathogenic fungi *B. bassiana*. The effects of the treatments of the colonies and the different corpse types (nestmate and *C. vagus* rivals) on the decision to bring the corpses inside the nest, to bring them out to the arenas in pieces or to consume them as food were analyzed with the help of GLMMs (binomial error, maximum likelihood fit). The corpse removal rate from the plates, and the rate of bringing them out from the nests were analyzed with the help of Cox regression models.

GLMMs (binomial error, maximum likelihood fitting) were used to analyze the relationship between behavioral categories during waste management, worker size categories and origin of corpse. We summed waste management activities such as biting and dragging corpses and working in the waste yard, and other activities such as eating food or drinking. The activities of individual workers observed during the reactions towards the different corpse types were compared with paired Wilcoxon tests.

All statistical analyses were carried out in R Statistical Environment. GLMMs were performed using the *glmer* function in the *lme4* package, while automated model selection with the help of the *dredge* function in the *MuMIn* package. Cox regression analysis was carried out with the use of the *survival* package. The *relevel* function was used to carry out post hoc sequential comparisons among factor levels when performing GLMM and Cox regression analyses. We applied a table wide sequential Bonferroni-Holm correction to reveal the exact significance levels in these cases.

4. Results

4.1. Cues or meaningless objects: differential responses of different *Formica* species to corpses of rivals

On the basis of our findings, *F. cinerea* responded clearly different towards the different corpses of its competitors. The corpses of the slave-maker *F. sanguinea* and those of the territorial wood ants elicited more aggressive reaction, and they were transported much more quickly than the corpses of the submissive species *F. fusca,* and those of the non-nestmate and nestmate *F. cinerea.* The majority of corpses were transported inside the nest. During our laboratory experiments with *F. cinerea*, we found similar reactions, at least towards the major

rivals, but there were differences compared to the field observations, due to the different habitat origin of the study colonies. Similarly, we found intensive reactions towards the corpses of the slave maker *F. sanguinea*, its slave species, and the territorial *F. pratensis*.

Comparing the reaction of the two slave maker species, we found that in *F. sanguinea*, the corpses of its rival *P. rufescens* and its slave species elicited the most intensive reaction, which was followed by the reaction towards the corpses belonging to non-nestmates and their slaves. The corpses of species that our study species do not meet under natural conditions, were transported slowly, and elicited a similar reaction to food consumption. *P. rufescens* reacted (with small differences) similarly towards the different types of corpses, except the corpses of the non-nestmate *P. rufescens* and its slave, which elicited an intensive reaction.

Interestingly, in the territorial *F. polyctena*, the corpses of another territorial species (*F. truncorum*) did not elicit an intensive reaction, which was even less pronounced than the reaction towards the corpses of the submissive *F. fusca*. The most intensive reaction was elicited by the corpses of *F. sanguinea*, which was followed by the reaction elicited by the corpses of non-nestmates.

On the basis of our results, we can conclude that there is a relationship between the origin of corpses and the intensity of response towards them. The differences in reactions towards corpses belonging to different species depended mostly on the nature of the relationship between the two species under study. In the two slave-maker species, we found a difference in the reaction towards the corpses of nestmates, non-nestmates, their slaves and the potential slave species, so we can suppose that the slave maker species can differentiate between these corpses despite the similarities in their CHC-profile. In each studied species, the majority of corpses were transported inside the nest, which may have an important role in the familiarization of the young, naive individuals residing the nest interior with potential rivals.

4.2. Corpses, as food source

Besides the differentiation between the corpses of nestmates and alien species, *F. polyctena* were able to differentiate corpses treated with concentrated oleic acid from the untreated ones. Corpses treated with oleic acid elicited a fast burial, and, after a while, they

were transported inside the nest. The reaction towards the untreated corpses of *D. melanogaster* elicited a higher level of aggressivity and a more rapid transport compared to the reactions towards every other corpse type.

The analysis of the nestmate corpse consumption rate showed an elevation in the case of satiated colonies, and this remained high even after the retake of normal feeding after the starvation-stress. We also found a rather elevated consumption rate in the case of old corpses and those of the rival *C. vagus*. In this latter case, the highest rate of corpses taking apart was observed.

Our results support the hypothesis that the consumption of nestmate corpses may be much more common than previously supposed, mostly in periods with food shortage. The nestmate corpse consumption rate depends on the state of the colony and other food supplies.

4.3. The recognition and handling of corpses as threat of infections

The reactions towards the infected corpses of different stages showed an exponential response, and these corpses were clearly differentiated by the workers. Those with spores elicited an intensive grooming, while those with hyphae were surrounded by many aggressive individuals, which cleaned them heavily, and after a while, both types were transported inside the nests.

The possibility of infection by consumption of an infected corpse seems to be very low in *F. polyctena*, because a very sophisticated parasite recognition system is present, namely the workers are able to distinguish the corpses infected with hyphae from those infected with the spores of entomopathogenic fungi.

4.4. Corpse management and division of labor

The analysis of the division of labor showed that a smaller waste management activity was observed in the case of major workers compared to the other two castes (minor, media). In the case of the minor and major workers, we observed individual differences in the waste management and other activities, as well. Workers belonging to the major size class performed their tasks in a generalist matter. We found differences in the reactions towards the

corpses of different sizes. *A. subterranea*, which is smaller than the nestmate, elicited a higher number of hygienic tasks, whereas *C. vagus*, a species with a similar size, showed no significant difference compared to nestmates. 15% of workers (independent from caste) were specialized at least temporarily at waste management, while around 67% were present as generalists.

Despite the fact that we did not find a worker caste specialized on waste management in *Camponotus aethiops*, it seems that the efficiency of this labor is enhanced by the temporary specialization of some foragers, thereby reducing the contamination probability, contributing to colony survival. Ant corpses, besides being waste elements and representing the risk of contamination inside the nest, may have other roles, as well.

5. Publications related to the topic of the thesis

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