

**BEHAVIOURAL PATTERNS AND MORPHOLOGICAL ADVANTAGES FAVOUR  
SUCCESSFUL USE OF *Crematogaster schmidtii* TRAILS BY *Camponotus lateralis*  
WORKERS (HYMENOPTERA: FORMICIDAE)**

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**ABSTRACT**

The paper examines the relationship between two ant species: *Camponotus lateralis* and *Crematogaster schmidtii* in the neighboring habitat in the biocenoses of the Southern Coast of the Crimea (Ukraine). The ecological characteristics of the species are given, the structure of forage areas is described, as well as the daily activity of ants in shared habitats. It was shown that *Camponotus lateralis* accesses the food resources of *Crematogaster schmidtii* using their trails. As a result of a frame-by-frame analysis of the video recordings, a number of behavioural responses have been identified for each species that it displays during interspecific contacts on the trails. It was shown that *Camponotus lateralis* successfully avoids contact by changing its trajectory at a distance of about 1 cm from *Crematogaster schmidtii* workers. The aggressive reaction of *Crematogaster schmidtii* was only recorded in few cases after antenna contacts. In most cases, *Camponotus lateralis* reacted more quickly than *Crematogaster schmidtii* after antennal contact and changed its trajectory. The structural characteristics of the antennae and eyes of workers of both species were compared. *Camponotus lateralis* workers were shown to have longer antennae on average. The eyes of *Camponotus lateralis* have, on average, more facets than those of *Crematogaster schmidtii* and, on average, more facets per unit of eye area. The significance of these morphological advantages of *Camponotus lateralis* for the successful use of *Crematogaster schmidtii* trails is discussed.

**Keywords:** Ants, behavioural reaction, antennal contact, trails, trajectory of movement

**ABSTRAK**

Kajian ini menilai hubungan antara dua spesies semut *Camponotus lateralis* and *Crematogaster schmidtii* di habitat sekitaran di dalam *biocenoses* di Pantai Selatan Crimea (Ukraine). Ciri-ciri ekologi spesies diberikan, struktur mencari makanan diperlihatkan serta aktiviti harian semut di habitat yang sama. Hasil menunjukkan *Camponotus lateralis* mencari sumber makanan iaitu *Crematogaster schmidtii* menggunakan laluan mereka. Hasil analisis *frame-by-frame* dari rakaman video, beberapa respon kelakuan telah dicamkan untuk setiap spesies yang menunjukkan hubungan intraspesifik di laluan mereka. *Camponotus lateralis* juga berjaya menunjukkan dan

mengelak bersentuhan dengan mengubah laluan lintasan pergerakannya pada jarak 1 cm dari pekerja *Crematogaster schmidti*. Reaksi agresif *Crematogaster schmidti* hanya direkodkan pada beberapa kes selepas sentuhan antena. Dalam kebanyakan kes, *Camponotus lateralis* reaksi dengan cepat dari *Crematogaster schmidti* selepas sentuhan antena dan perubahan laluan. Ciri struktur antena dan mata pekerja pada kedua-dua spesies dibandingkan. Pekerja *Camponotus lateralis* menunjukkan antena yang lebih panjang secara purata. Mata *Camponotus lateralis* secara purata, mempunyai lebih facets dari *Crematogaster schmidti* dan purata lebih facet per unit kawasan mata. Signifikan dari kelebihan morfologi *Camponotus lateralis* ini adalah kejayaan menggunakan laluan *Crematogaster schmidti* juga dibincangkan.

**Katakunci:** Semut, reaksi kelakuan, sentuhan antena, laluan, pintasan pergerakan

## INTRODUCTION

Most ant species known to science live in separate nests (Hölldobler & Wilson 1990; Radchenko 2016; Seifert 2018). There are a number of specific forms of coexistence between and of different species such as plesiobiosis, parabiosis, commensalism. In some cases, ants of different species may build nests in close proximity to each other. This rudimentary form of interspecific association in ants is called plesiobiosis. There is no mixing of the population; each of the nests is an independent unit. Such relationships can form as a result of a lack of nesting sites, as has been shown for *Lasius niger* (Linnaeus 1758)/*Lasius flavus* (Fabricius, 1782), *Lasius platythorax* Seifert, 1991/*Myrmica rubra* (Linnaeus 1758) (Czechowski 2004; Stukalyuk & Goncharenko 2020).

There are known ant species that can live in the same nest without showing aggression towards each other such as (*Crematogaster carinata* Mayr, 1862 and *Camponotus femoratus* (Fabricius 1804) (Swain 1980); *Crematogaster modiglianii* Emery, 1900 and *Camponotus rufifemur* Emery, 1900 (Menzel et al. 2008); *Crematogaster levior* Longino, 2003 and *Camponotus femoratus* (Vantaux et al. 2007); *Apterostigma urichii* Forel, 1893 and *Mycetophylax faunulus* (Wheeler 1925) (Sanhudo et al. 2008) and these ant species are able to share the same feeding routes. This type of coexistence is known as parabiosis. Parabiosis is mutually beneficial to both species and is a form of symbiosis. For example, *Camponotus* workers follow *Crematogaster* pheromone trails when foraging (Menzel et al. 2012; 2013).

Relationships between ants can take the form of commensalism, as described for *Camponotus* sp. (Ito et al. 2004). Workers of *Camponotus* sp. feed on food residues of *Crematogaster inflata* Smith, F., 1857, which are detected by their trace pheromones and did not harmed their host. At the same time, the successful actions of *Camponotus* sp. contribute to the similarity in colour to *Crematogaster inflata*, i.e. Batesian mimicry (Ito et al. 2004). Batesian mimicry has also been reported for some other species pairs: *Colobopsis truncata* (Spinola 1808) / *Dolichoderus quadripunctatus* (Linnaeus 1771) (Wagner, 2019); *Colobopsis imitans*/ *Crematogaster scutellaris* (Olivier 1792) (Schifani et al. 2022).

Similar interactions, characterised by one species attempting to access the food resources of another, have been described in several ant species, such as *Gnamptogenys menadensis* (Mayr 1887) and *Polyrhachis rufipes* Smith, F., 1858 (Gobin et al. 1998), *Camponotus lateralis* (Olivier 1792) and *Crematogaster scutellaris* (Gene, 1842; Emery, 1886, 1915; Zimmermann, 1934; Goetsch, 1942, 1951, 1953; Kaudewitz, 1955; Baroni Urbani, 1969; Menzel et al. 2010a), *Camponotus lateralis* and *Crematogaster schmidti* (Mayr 1853) (Stukalyuk & Radchenko 2011). When moving along trails, *Camponotus lateralis* orient

themselves to the trail pheromone of *Crematogaster scutellaris*, but not vice versa (Menzel et al. 2010a). *Crematogaster scutellaris* workers were shown to attack *Camponotus lateralis* workers upon encounter in all cases (Menzel et al. 2010a). The same behaviour was also recorded for the pair of *Crematogaster schmidtii* and *Camponotus lateralis* (Stukalyuk & Radchenko 2011). Apparently, in this case, Batesian mimicry is not able to completely protect *Camponotus lateralis* workers from *Crematogaster scutellaris* aggression. There is probably a set of behavioural responses that allow *Camponotus lateralis* to avoid *Crematogaster scutellaris* aggression.

Most of the known works in this area are devoted to the study of colour similarity between pairs of interacting species, as well as the chemical composition and structure of trace pheromones. In some works, the authors note a high movement speed of *Camponotus* species workers, but without objective measurements (Menzel & Bluthgen 2010; Stukalyuk & Radchenko 2011; Schifani et al. 2022). Unfortunately, the ethological responses during interaction in the *Camponotus-Crematogaster* pair have not been sufficiently studied.

In this study, we investigated the ecological characteristics of *Camponotus lateralis* and *Crematogaster schmidtii* on the Southern Coast of the Crimea (Ukraine). The main aim of this study was to identify the factors that allow *Camponotus lateralis* to successfully coexist with *Crematogaster schmidtii* within the latter's foraging areas. In addition, we hypothesised that certain behavioural traits and morphological advantages help *Camponotus lateralis* workers to avoid aggression from *Crematogaster schmidtii* when encountering dominant trails. Therefore, the primary objective of this research is to identify some of the factors that facilitate the harmonious coexistence of both species within the foraging infrastructure of the 'host' species, *Crematogaster schmidtii*.

## MATERIALS AND METHODS

### Study Design

Data on the ecological characteristics of both ant species (nesting conditions, co-occurrence, daily activity) were collected. The second part includes observations of the interaction between *Crematogaster schmidtii* and *Camponotus lateralis* workers on the trails. The third part includes comparative morphological studies.

### Study Region

The studies were carried out in June-August 2013 on the territory of the Crimean Peninsula (Ukraine) (mapping of forage areas of ant colonies, video recording of ant movements along the trails). For mapping, we selected areas with two plant communities typical for the Crimean Mountains and the Southern Coast of Crimea: oak-pistachio woods (*Quercus pubescens*, *Pistacia mutica*) of the Karadag mountain range (up to 150 m a.s.l.) and juniper woods (*Juniperus excelsa*) on the Southern slope of Cape Aya (less than 100 m a.s.l.) (Figure 1).

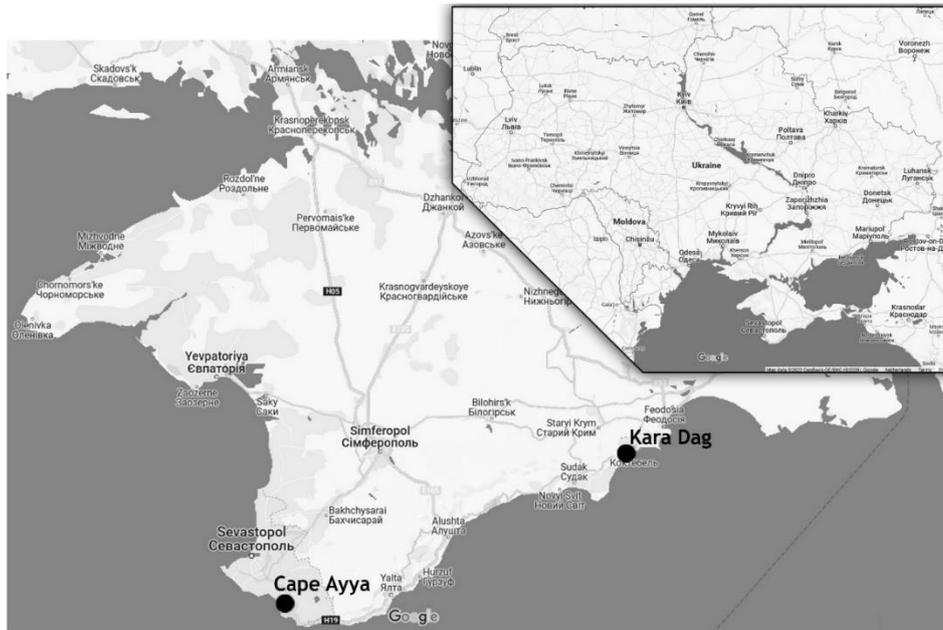


Figure 1. Sampling sites in Crimea (Ukraine)

### Ecological Characteristics

In the sampling area, 10 x 10 m plot has been established to survey the trees and shrubs inside and to record the foraging behavior of *Crematogaster schmidtii* and *Camponotus lateralis* (Figure 2). The number of nests, number of forage trees and the number of trails of these two species has been recorded. The forage areas of the colonies were mapped on graph paper at a scale of 1:100 (Dlussky 1965). *Crematogaster schmidtii* can have several nests at the same time - the main (central) nest, which contains the queen and brood, and auxiliary (peripheral) nests, which contain some of the workers and brood. The *Crematogaster schmidtii* colony is therefore polycalic (Stukalyuk & Radchenko 2011).



Figure 2. General lateral view of workers. A, *Camponotus lateralis*, major worker (above) and minor worker (below). B, *Crematogaster schmidtii*. Scale bar, 1 mm

### Studies on the Activity and Behavior of Ants on the Trails

In order to study the daily activity of the ants, one colony of *Crematogaster schmidtii* was selected, along the trails of *Camponotus lateralis* workers also moved. To record the activity the wire gates has been installed above the trail. The number of worker ants passing in both directions has been counted every 5 minutes in 30 minutes. Temperatures (in °C) were recorded using a mercury thermometer. Observations were made in July 2013, around the clock, in triplicate by the same one colony.

Ant behaviour on the trails was videotaped using a Sony DVCAM camera (frame rate 25/1 second, avi format). The camera was mounted on a tripod above the trail. The total duration of the recorded video is 46 minutes 27 seconds. The footage was analysed frame by frame in Movavi Video Editor 14 (Movavi, Russia). In total, we analysed the movement of ants of both species on 6 trails of four *Crematogaster* colonies. The scoring system was used to analyse the video frequency of ant-antennal contacts, the reactions after ant-antennal contacts and the visual reactions of the ants. one point was given if the reaction was observed, 0 points if there was no reaction. Thus, if the reaction occurred frequently throughout the observation period, its average value is closer to 1, and if it occurred rarely, closer to 0. For four types of reactions during interspecies contacts, the trajectories of the ants' movements relative to each other and to stationary objects in the frame were visualised by drawing the position of the insects' bodies frame by frame. The resulting diagrams make it possible to understand the peculiarities of the ants' movements, and to evaluate the difference in the speed of their movements.

### Morphological Studies

Workers of *Crematogaster schmidtii* are monomorphic (3-5 mm in size), *Camponotus lateralis* has two size classes of workers (Seifert 2019): minors (4-5 mm) and majors (7 mm). The sizes of the minors of *Camponotus lateralis* workers and *Crematogaster* workers are comparable. This made it possible to distinguish minors and majors of *Camponotus* in the video. For comparative morphological studies, samples of workers from both ant species were fixed in 70% alcohol. Thirty workers of each species were sampled. Under laboratory conditions, samples were prepared for research. Both 70% ethanol preserved and dried insects from the collection were used for comparative morphological studies. The antennae were prepared by removing them from the specimens (10 specimens of each species) using dissecting needles and forceps, and then mounted in Faure's medium. The preparations were photographed through an Olympus CX41s microscope (Tokyo, Japan) with a Canon EOS 600D camera (Taichung, Taiwan).

The tpsDig version 2 program (developed by F. James Rohlf of the State University of New York at Stony Brook, USA) was used to measure antenna size. Only one antenna of each individual was measured. The eyes and surrounding cuticle were separated from the insect's head and macerated in 10% KOH. These preparations were then washed in distilled water, mounted in Faure's medium and photographed using an Olympus CX41s microscope (Tokyo, Japan) with a Canon EOS 600D camera (Taichung, Taiwan). The number of facets on one eye of each specimen (18 specimens of *Crematogaster schmidtii* and *Camponotus lateralis*) was counted on the photographs.

In addition, to compare the resolution of the eyes of *Crematogaster schmidtii* and *Camponotus lateralis*, the number of facets superimposed in the predetermined square on the photo in the central region of the eye was counted (13 specimens of *Crematogaster schmidtii* and 11 of *Camponotus lateralis*). SEM photographs of the structure were taken by V.G. Radchenko (Institute for Evolutionary Ecology NAS Ukraine) using a scanning electron

microscope (JEOL JCM 6000) connected to Semafore software (JEOL, Sollentuna, Sweden). The samples for the SEM study were coated with a thin gold film using the JEOL Smart Coater.

### Statistical Analysis

The Paleontological Statistics Software (PAST) program (version 4.09.32) was used for data analysis, performed in two directions: a) the average frequency of occurrence of a behavioural response (the number of responses from the total analysis time of 46 minutes 27 seconds); b) the average duration of a behavioural response (in seconds). Such calculations were made both for general behavioural responses of the two species on the trails and for specific interactions between the species. The significance of the common behavioural responses of *Crematogaster schmidtii* and *Camponotus lateralis* between the obtained parameters in terms of frequency and mean time was calculated using the Kruskal-Wallis test (K-W,  $P \leq 0.05$ ), taking into account the normality of the sample. The Mann-Whitney test was used for pairwise comparisons of parameters (M-W,  $P \leq 0.05$ , with Bonferroni-corrected p-values). The same tests were used for the analysis of morphological characteristics (number of facets in eyes, average number of facets per unit area, total length of antennules, length of the funiculus of antenna, length of antennal scape).

Bivariate regression was used to calculate a possible relationship between the parameters (between the number of workers of both species on the trails in the analysis of daily activity). To analyse the influence of independent (time of day, temperature) and dependent (number of workers of both species on the trails) factors, multivariate multiple regression analysis was used for the dependent and independent variables. To establish a possible relationship between the elements of the structure of the forage area (number of trees per one *Crematogaster schmidtii* colony vs. number of *Camponotus lateralis* nests; number of *Camponotus lateralis* nests vs. number of *Crematogaster schmidtii* nests in the colony; trees per one *Crematogaster schmidtii* colony vs. number of *Crematogaster schmidtii* nests in the colony), MANOVA analysis was used. Correlation analysis (Pearson's correlations) was used to determine a possible relationship between the frequency of occurrence of behavioural responses.

## RESULTS

### Structure of the Foraging Areas of the Studied Ant Species

Twelve colonies of *Crematogaster schmidtii* were mapped and seven of *Camponotus lateralis* on five plots in the juniper forest (Karadag), 16 colonies of *Crematogaster schmidtii* and eight of *Camponotus lateralis* on five plots in the oak-pistachio forest (Cape Aya). The number of nests per *Crematogaster schmidtii* polycalic colony is lower than the number of forage trees visited by this species (Figure 3). In general, the structure of the forage area of *Camponotus lateralis* is simpler than that of *Crematogaster schmidtii*, with fewer nests and fewer trees visited (K-W:  $P \leq 0.001$ ; Figure 3), i.e. *Camponotus lateralis* colonies are smaller. *Camponotus lateralis* has a lower nest density than *Crematogaster schmidtii* (Figure 3).

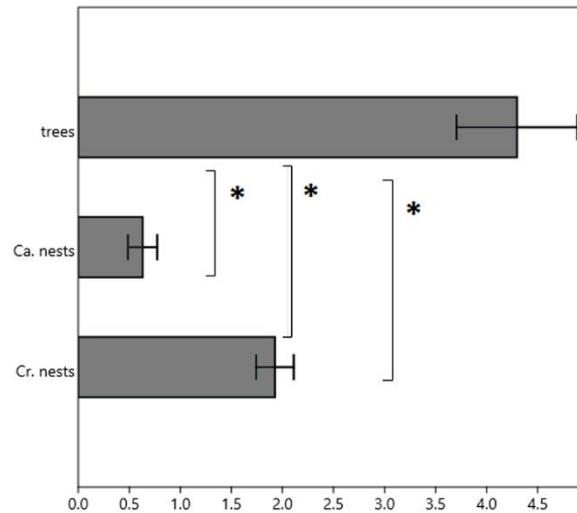


Figure 3. Mean number of *Crematogaster schmidti* (Cr. nests), *Camponotus lateralis* (Ca. nests) nests per *Crematogaster schmidti* colony, average number of trees per *Crematogaster schmidti* colony.  
 Note: The average number of trees per colony of *Camponotus lateralis* is identical to the average number of nests per colony in this species. \*  $P \leq 0.001$  (Mann-Whitney test)

The more nests in a *Crematogaster schmidti* polycalic colony, the more forage trees were visited (Table 1). Of the 28 *Crematogaster schmidti* colonies, *Camponotus lateralis* colonies were found in 15, i.e. the co-occurrence of the two species in the Crimean population was about 50%. For *Camponotus lateralis*, the number of nests corresponds to the number of trees visited (Table 2). In four colonies of *Camponotus lateralis* the presence of two visited trees was recorded, in the remaining colonies only one tree was visited. Therefore, in most cases in the Crimean population, *Camponotus lateralis* is associated with visiting a single tree where its nest is located.

Table 1. Behavioural reactions of *Camponotus lateralis* and *Crematogaster schmidti* workers on the trails

Type of Reaction by Ant Species	The Number of Cases
<b>Reactions of <i>Camponotus lateralis</i></b>	
Change in trajectory without acceleration after antenna contact with <i>Crematogaster schmidti</i>	88
Change of movement trajectory with acceleration (escape) after antennal contact with <i>Crematogaster schmidti</i>	11
<b>Reactions of <i>Crematogaster schmidti</i></b>	
Continued linear movement after antennal contact with <i>Camponotus lateralis</i>	88
Prolonged stop after antennal contact with <i>Camponotus lateralis</i>	3
Threatening posture after antennal contact with <i>Camponotus lateralis</i>	4
Chasing of <i>Camponotus lateralis</i> after antennal contact	10
<b>Visual Reactions</b>	
Change in the trajectory of <i>Camponotus lateralis</i> workers at a distance of less than 1 cm from <i>Crematogaster schmidti</i>	28
Change in movement trajectory of <i>Camponotus lateralis</i> workers at a distance of more than 1 cm from <i>Crematogaster schmidti</i>	81

Table 2. Results of MANOVA analysis and regression analysis between the number of *Camponotus lateralis*, *Crematogaster schmidtii* nests per 100 m<sup>2</sup> and the number of trees visited by *Crematogaster schmidtii*

Category	Trees per 1 <i>Crematogaster schmidtii</i> nest vs Number of <i>Camponotus lateralis</i> nest	Number of <i>Camponotus lateralis</i> nests vs Number of <i>Crematogaster schmidtii</i> nests in colony	Trees per 1 <i>Crematogaster schmidtii</i> nest vs Number of <i>Crematogaster schmidtii</i> nests in colony
Multivariate linear regression (1 independent, n dependent)			
R2:	0.02017	0.01855	0.4803
MSE:	9.275	0.5541	4.919
MANOVA			
Wilks' lambda:	0.9798	0.9815	0.5197
F:	0.5352	0.4914	24.03
df1:	1	1	1
df2:	26	26	26
p(regr):	0.471	0.4895	4.36E-05

### Daily Activity Parameters of *Crematogaster schmidtii* and *Camponotus lateralis*

The active time of *Crematogaster schmidtii* and *Camponotus lateralis* were different and *Crematogaster schmidtii* has been recorded active in 24 hours. The activity period of *Camponotus lateralis* is shorter and does not cover part of the night (Figure 4). *Crematogaster schmidtii* showed a negative correlation between the intensity of traffic on foraging trails and air temperature (-0.64,  $P \leq 0.05$ ; Tables 3, 4). For *Camponotus lateralis*, no significant relationship with temperature was found (0.48,  $P \geq 0.05$ ; Tables 3, 4). A weak negative correlation was found between the number of *Crematogaster schmidtii* and *Camponotus lateralis* workers on the trail during the 5-min observation period (Figure 5). This suggests that the foraging activity of *Camponotus lateralis* is lower during the period of maximum activity of the host species.

Table 3. Multivariate multiple regression analysis for dependent and independent variables

Tests on independent variables	Wilks lambda	F	df1	df2	P
Temperature	0.2995	23.39	2	20	5.81E-06
time, hours	0.472	11.19	2	20	0.000549
Tests on dependent variables	R <sup>2</sup>	F	df1	df2	P
Number of <i>Crematogaster schmidtii</i> workers per 5 min	0.7189	26.86	2	21	1.63E-06
Number of <i>Camponotus lateralis</i> workers per 5 min	0.2542	3.578	2	21	0.046

Table 4. Regression coefficients and statistics

Category		Coeff.	Std.er.	T	P	R <sup>2</sup>
Number of <i>Crematogaster schmidtii</i> workers per 5 min	Constant	60.206	7.3495	8.1918	5.62E-08	
	Temperature	-1.8382	0.27281	-6.7379	1.15E-06	0.41562
	time. hours	0.6534	0.13725	4.7605	0.000106	0.1113
Number of <i>Camponotus lateralis</i> workers per 5 min	Constant	-3.7241	1.9951	-1.8667	0.075975	

Temperature	0.16855	0.074057	2.2759	0.033446	0.23851
time. hours	0.024733	0.037259	0.66381	0.51403	0.070193

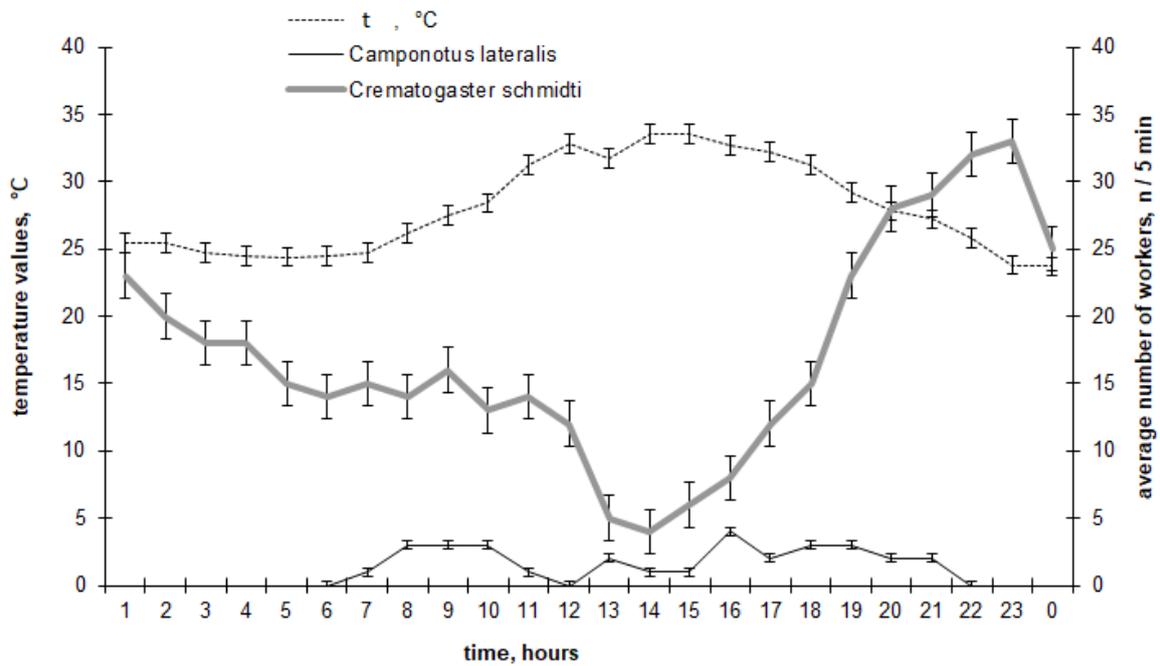


Figure 4. Mean indicators of daily activity of *Crematogaster schmidtii*, *Camponotus lateralis* on one stern trail (number of workers / 5 minutes of recording)

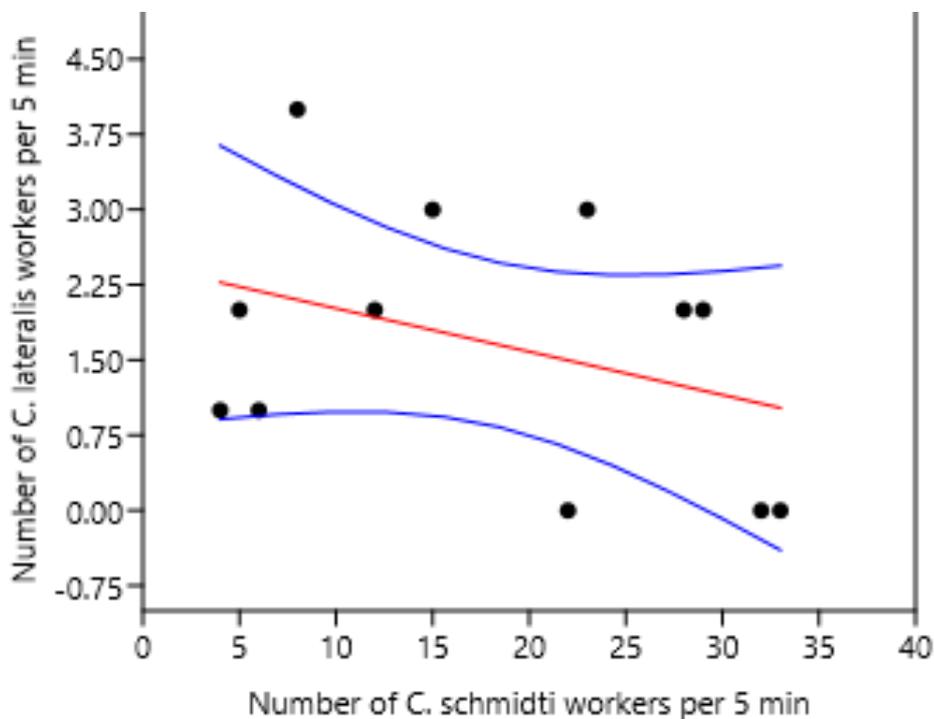


Figure 5. Bivariate regression of the number of *Camponotus lateralis* workers on the number of *Crematogaster schmidtii* workers on the trail. 95% regression is marked in blue.  $r=-0.26971$ ;  $r^2=0.072744$ ,  $P=0.20247$

The activity of *Camponotus lateralis* is linked to the activity of *Crematogaster schmidtii*, whose trails it uses to move to food sources (aphid colonies) (Figure 5). The morning emergence of *Camponotus lateralis* workers from nests begins at 05-00-06-00, when air temperatures are still relatively low. The peak of activity falls at 08-00-10-00, and then, with a gradual increase in temperature to 28-31°C, *Camponotus lateralis* workers begin to reduce their activity. In the evening, the last peak of activity of workers returning to the nest is observed at 21-00.

### Antennal Contacts

The frequency of occurrence of all reaction types was significantly different throughout the observation period (K-W:  $P \leq 0.001$ ). A total of 271 antennal contacts were recorded during the observation period. In the videos, intraspecific antennal contacts of *Crematogaster schmidtii* (162 cases, Figure 6A) significantly (12.5 times) outnumbered intraspecific contacts of *Camponotus lateralis* (10 cases, Figure 6A). Obviously, this is due to the presence of more *Crematogaster schmidtii* workers on the trail. During the analysis of the video recordings, 99 interspecific antennal contacts were recorded.

A separate type of contact is when *Camponotus lateralis* makes unilateral antennal contact, for example with the abdomen of *Crematogaster schmidtii* (88 cases). Among the movement trajectories (301 points in total, one point - movement of *Camponotus lateralis* along the trail of *Crematogaster schmidtii*, two points - away from the trail), *Camponotus lateralis* workers most often moved towards the trail (117 cases), less often along the trail (92 cases). The frequency of failed interspecific contacts (88) is almost the same as that of successful contacts (99). Significant differences were found between the duration of antennal contacts for *Camponotus lateralis* and *Crematogaster schmidtii* (K-W:  $P \leq 0.001$ ; Figure 6B). Intra- and interspecific antennal contacts of *Camponotus lateralis* were found to be of approximately the same duration and two times shorter than intraspecific contacts of *Crematogaster schmidtii* (Figure 6B).

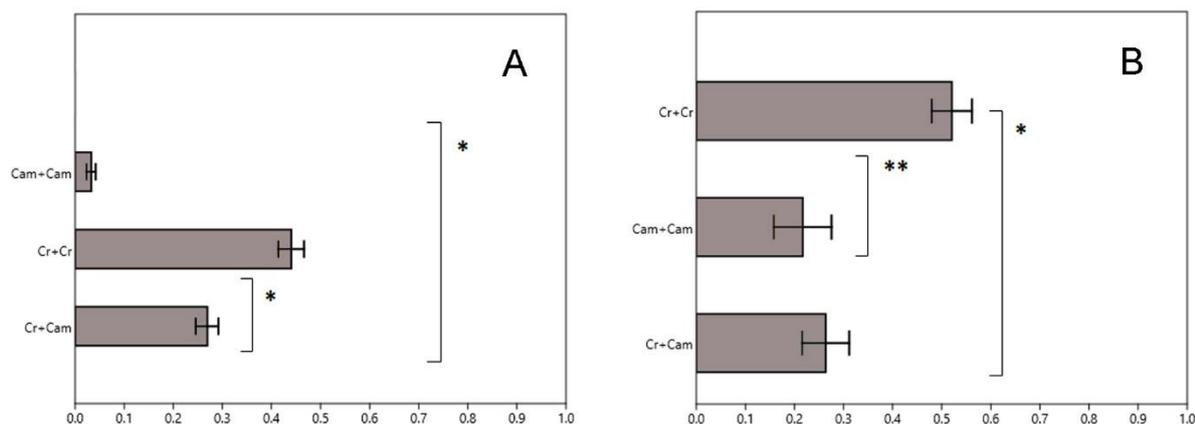


Figure 6. Mean number of single-species and interspecies antennal contacts (6A, number of reactions in 46 minutes 27 seconds) for the entire observation time and their duration (6B, seconds)

Designations: \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$  (Mann-Whitney test), Cr+Cam – interspecific contact, Cam+Cam, Cr+Cr – single-species contact, deviation – deviation of the *Camponotus lateralis* movement trajectory during the opposite movement of *Crematogaster schmidtii*; Cr-Cam – unrealized interspecies antennal contact

### Reactions After Antennal Contact

By analysing the video recordings, we identified several types of responses that ants showed after antenna contact (Table 1; Figure 7A & B). We did not consider antenna-antenna and antenna-body (leg) contacts separately. Unfortunately, the quality of the video did not allow us to clearly see the moment of contact in all cases. However, where possible, we saw *Camponotus* touching the body or limbs of *Crematogaster schmidtii* workers with its antennae first. We did not record a single case of *Crematogaster schmidtii* touching the body or limbs of *Camponotus lateralis* with its antennae first.

A negative correlation was observed between intraspecific antennal contacts of *Crematogaster schmidtii* and interspecific antennal contacts (-0.52), as well as between intraspecific contacts of *Crematogaster schmidtii* and a change in the movement trajectory of *Camponotus lateralis* after antennal contact (-0.81). In other words, *Camponotus lateralis* probably avoid approaching *Crematogaster schmidtii* aggregations on the trail.

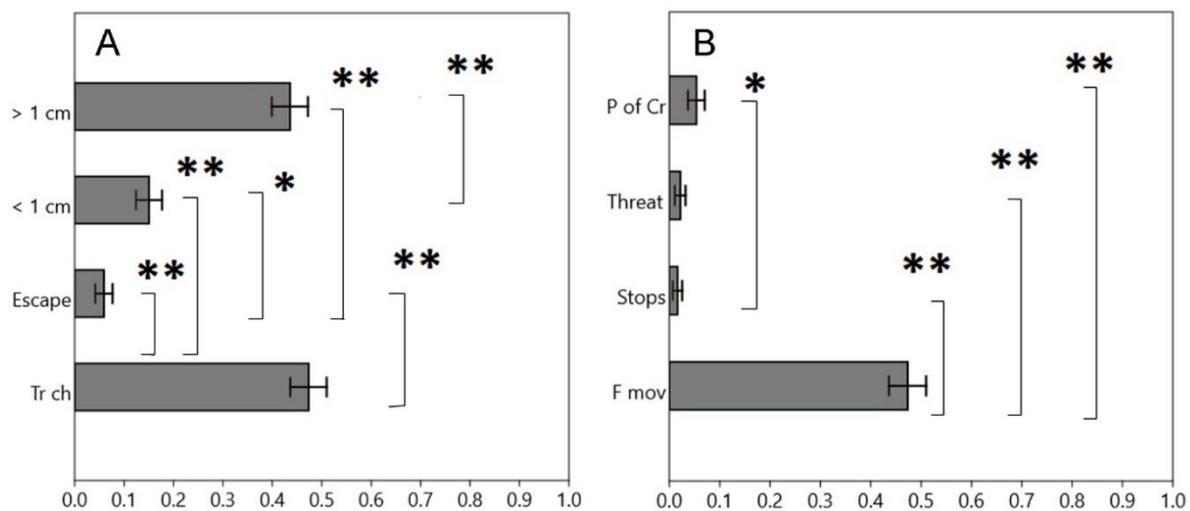


Figure 7. Mean number of reactions after antennal contacts and visual contacts (7A, number of reactions in 46 minutes 27 seconds) for the entire observation time and their duration (7B, seconds)

Designations: \* $P \leq 0.05$ ; \*\* $P \leq 0.001$  (Mann-Whitney test)

Reactions of two species after antennal contacts:

Reactions of *Crematogaster schmidtii* (7A): Threat Cr – threatening pose of *Crematogaster schmidtii*; P of Cr, Pursuit of *Crematogaster schmidtii* (worker pursuit of *Crematogaster schmidtii*); stops of *Crematogaster schmidtii* workers; f mov – forward movement of *Crematogaster schmidtii* (continuation of movement)

*Camponotus lateralis* reactions (7B): Escape – flight of *Camponotus lateralis* on contact with *Crematogaster schmidtii*; Tr ch – change of motion trajectory without acceleration after antennal contact. Visual reactions of *Camponotus lateralis*: < 1 cm – deviation from the opposite trajectory at a distance of up to 1 cm; > 1 cm – more than 1 cm

### Visual reactions

We also identified a number of responses exhibited by *Camponotus lateralis* at some distance from *Crematogaster schmidtii* workers (Table 1, Figure 7B). The time spent by ants in different

interspecific behavioural responses differed significantly (K-W:  $P \leq 0.013$ ). When the distance between workers of two species is less than 1 cm, *Camponotus lateralis* spends twice as much time deciding on an action (Figure 7B). *Crematogaster schmidtii* takes twice as long to decide to move forward when the distance between workers of both species is less than 1 cm (Figure 7B; 8). Correlations were found between *Crematogaster schmidtii* stopping after antennal contact with *Camponotus lateralis* and escape of *Camponotus lateralis* (0.66), escape of *Camponotus lateralis* and pursuit of *Crematogaster schmidtii* (0.54), and between escape of *Camponotus lateralis* and distance between workers less than 1 cm (0.76).

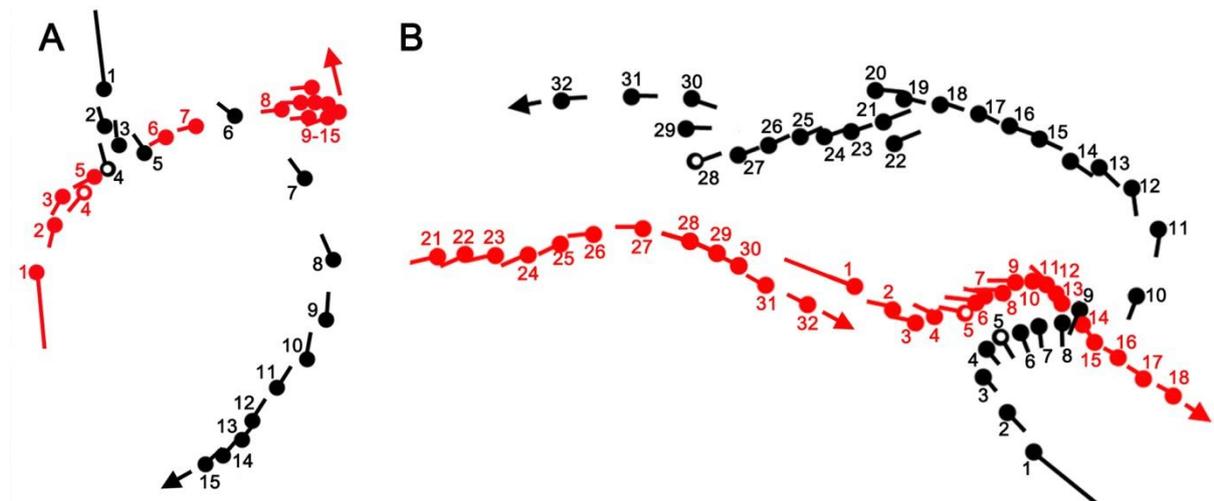


Figure 8. Examples of the behavior of *Camponotus lateralis* and *Crematogaster schmidtii* during interspecific contacts on the trail. Frame-by-frame video recordings. Drawn every third frame

A, pursuit of *Crematogaster schmidtii* (frames 4-8) of the escaping (frames 4-9) worker *Camponotus lateralis* after interspecific antennal contact, B, change in the trajectory (evasion) of *Camponotus lateralis* after interspecific antennal contact (frames 5-13) and after probable visual contact (frames 28-32). *Crematogaster schmidtii* does not respond to *Camponotus lateralis* after antennal contact (frames 5-18)

Notation. Black, *Camponotus lateralis*. Red, *Crematogaster schmidtii*. The dots indicate the head of the worker, the lines indicate the orientation of the body. The first frame shows the length of the ant's body in the frame. The arrows indicate the further direction of the ant's movement. White dots in A (frame 4), moment of antennal contact. White dots in B, moment of antennal contact (frame 5) and probable visual contact (frame 28)

### Some Morphological Characteristics of the Species Studied

Some morphological characteristics of the eyes and antennae of the studied species were compared. It was found that, on average, the eyes of *Crematogaster schmidtii* workers consist of fewer ommatidia than those of *Camponotus lateralis* minor workers ( $151 \pm 2$  vs.  $232 \pm 3$ ) and also have a lower density of ommatidia per unit area ( $22 \pm 0.4$  vs.  $30 \pm 0.5$ , Figure 9A,B; Figure 10). In addition, *Camponotus lateralis* was shown to have a longer antennal scape ( $0.85 \pm 0.01$  mm vs.  $0.76 \pm 0.01$ ) and funiculus of antenna ( $1.40 \pm 0.03$  vs.  $1.09 \pm 0.01$  mm) on average than *Crematogaster schmidtii*, and thus a longer total antenna length (Figure 9C & D; Figure 11).

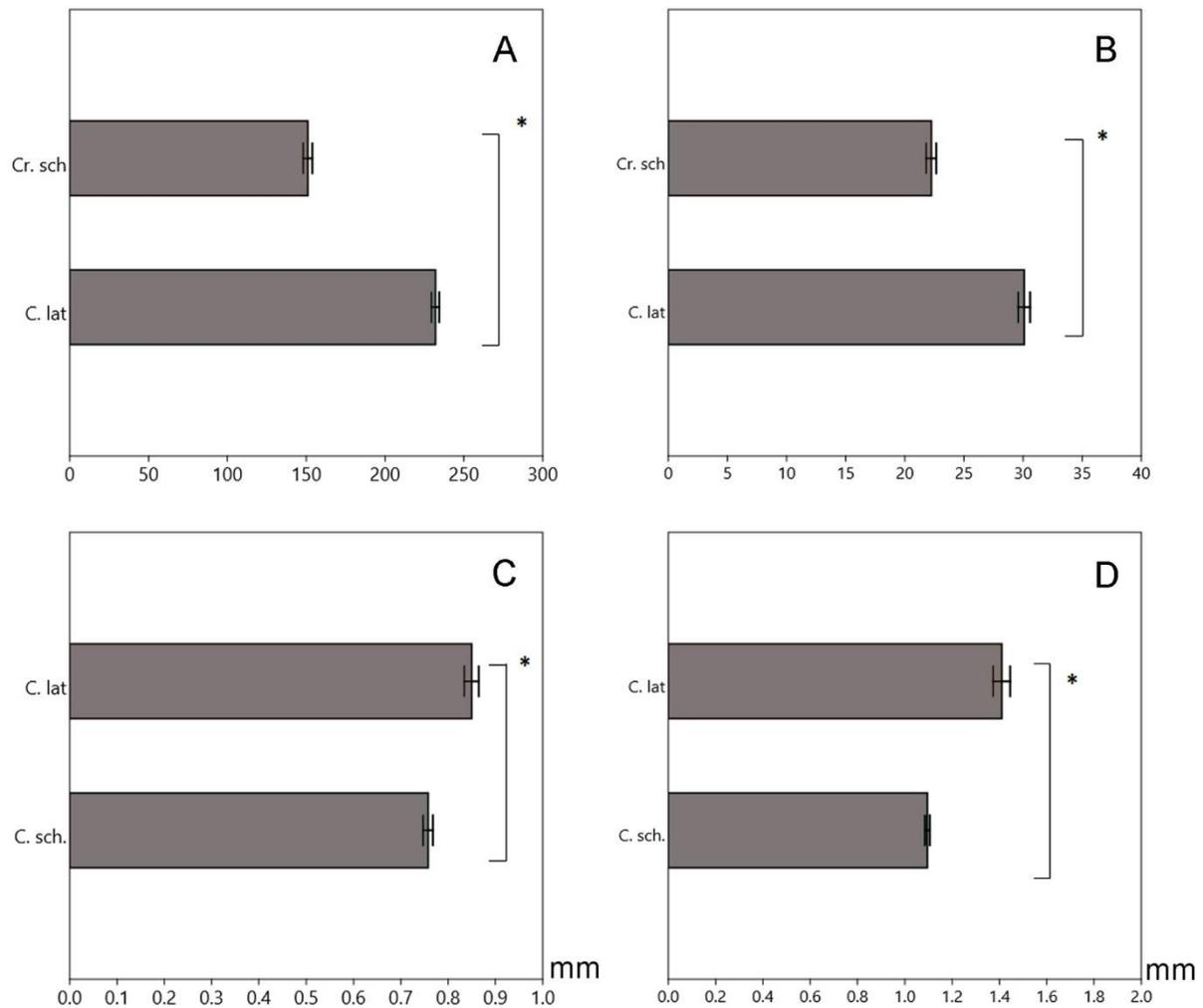


Figure 9. Morphological Characteristics Of *Camponotus Lateralis* (C. Lat) And *Crematogaster Schmidtii* (Cr. Sch). A: Mean Number Of Ommatidia Per Eye In *Crematogaster Schmidtii* (N=18), *Camponotus Lateralis* (N=18) Workers; B: Mean Number Of Ommatidia Per Measurement Area In The Central Part Of The Eye In *Crematogaster Schmidtii* (N=13), *Camponotus Lateralis* (N=11); C: Mean Length Of Antennal Scape In *Crematogaster Schmidtii* (N=10), *Camponotus Lateralis* (N=10); D: Average Length Of The Funiculus Of Antenna In *Crematogaster Schmidtii* (N=10), *Camponotus Lateralis* (N=10). Legend: \* $P \leq 0.001$  (Mann-Whitney Test)

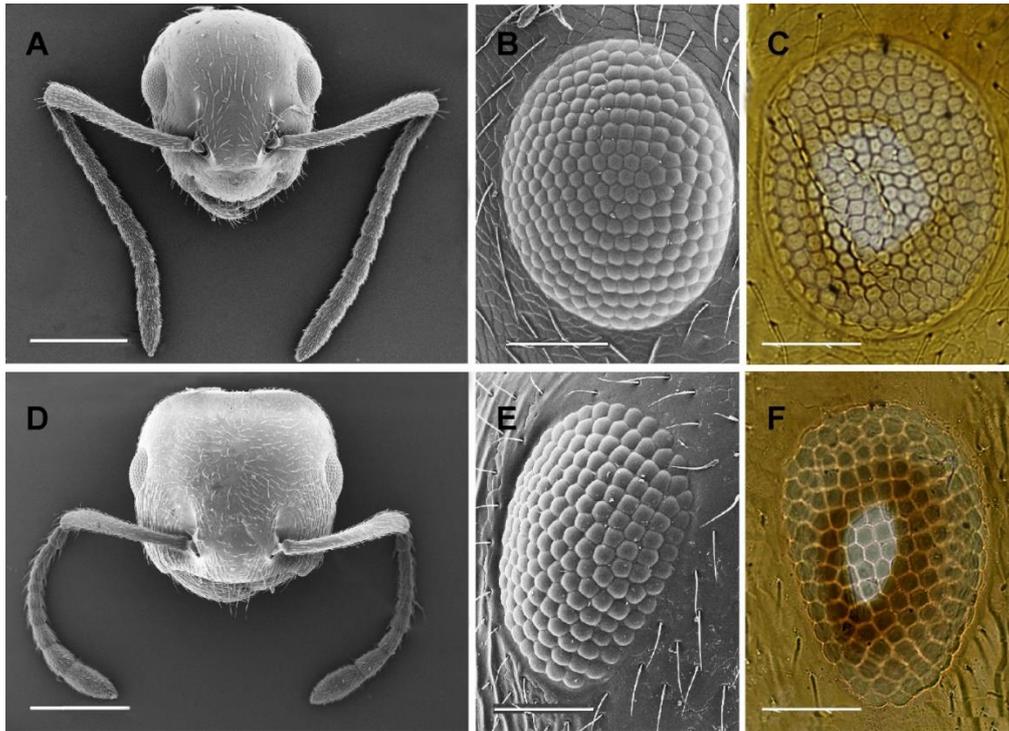


Figure 10. Heads (front view) and eyes of *Camponotus lateralis* (A-C) and *Crematogaster schmidti* (D-F)  
Scale bars, A, D, 500 mkm; B, C, E, F, 100 mkm

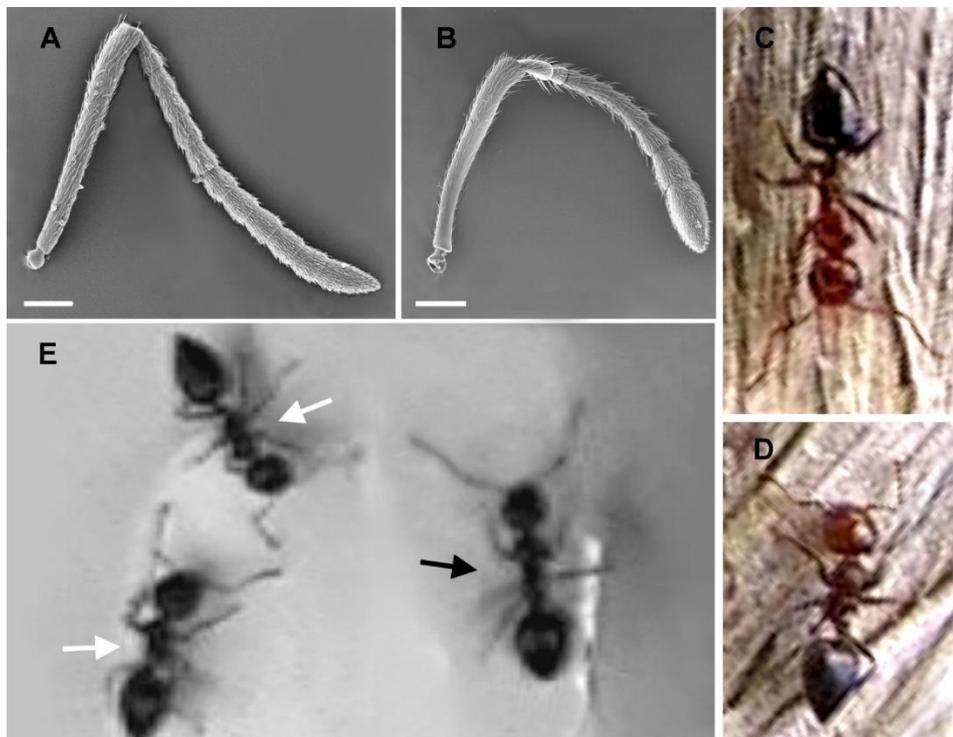


Figure 11. The antennae of *Camponotus lateralis* (A) and *Crematogaster schmidti* (B), and also, antennae position while ants' walking along the trail (C-E). C, *Camponotus lateralis*. D, *C. schmidti*. E, *C. schmidti* (white arrows) and *Camponotus lateralis* (black arrow) on the stretch of trail covered with white paper. C-E, frame from video. Scale bar, 200 mkm

## DISCUSSION

### Joint Visits to Forage Trails by Ants of Different Species

The size of *Crematogaster schmidtii* colonies in the Crimean population can vary from 25 to 100 thousand workers (Stukalyuk et al. 2022), while the population of a *Camponotus lateralis* colony does not exceed several hundred individuals (Radchenko 2016). This is confirmed by the more complex structure of the forage area of *Crematogaster schmidtii* compared to *Camponotus lateralis* (Figure 3). For large colonies of *Crematogaster schmidtii* in the Crimea (Ukraine), we recorded several hundred individuals in a 2-minute count on the trail (Stukalyuk et al. 2022). Our data on the traffic intensity of *Crematogaster schmidtii* on trails are quite low for this species in this region (Figure 4). It is likely that *Camponotus lateralis* prefers to settle near relatively small colonies of the host species.

The activity of major workers of *Camponotus lateralis* outside the nest is reduced (up to 38% of the total number of workers in European populations (Seifert 2018)), we also mainly observed minor workers on trails. In the video recordings that we analysed, the absolute majority (46 out of 48) of *Camponotus lateralis* workers belonged to the smallest size class (minors). We analysed the responses to antennal interspecific and intraspecific (for *Crematogaster schmidtii*) contacts, as well as the behaviour of ants at the distance of presumed interspecific visual contact. According to Brandstaetter et al. (2008), *Camponotus* ants are able to distinguish workers from their colony from strangers at a distance of 1 cm. Therefore, we considered responses at a distance of less than and more than 1 cm separately.

When analysing the frequency of behavioural responses, evasion by *Camponotus lateralis* along the trajectory was one of the most frequent responses. Despite the small number of workers of this species on the trails, the frequency of their encounters with numerous *Crematogaster schmidtii* workers was very high, and *Camponotus lateralis* workers have to make constant decisions about the choice of behaviour in a given situation (Figure 5). In large colonies of *Crematogaster schmidtii* there will be high activity on the trails and the frequency of such decisions will increase. In this case, *Camponotus lateralis* workers may simply not be able to cope. Therefore, even if *Camponotus lateralis* are able to colonise the territory of such large colonies of *Crematogaster schmidtii*, we expect that they will do so to a greater extent on the periphery, near auxiliary nests. Apparently, the frequency of co-occurrence of two species can vary greatly depending on conditions and location - in the Crimean population, about 50% of *Crematogaster schmidtii* colonies were with commensals of *Camponotus lateralis*, while for the commensal *Colobopsis*, together with *Crematogaster scutellaris*, this data can vary from 20 to 97% (Schifani et al. 2022). *Crematogaster schmidtii* ants from different polycalic colonies are aggressive towards each other; according to our observations, the same is known for *Crematogaster scutellaris*, although workers from the nearest nests belonging to the same cluster do not show aggression (Santini et al. 2011).

### Reactions of Ants During Interspecific Contacts on the Trails

Parabiotic ant species inhabit the same nest and/or share the same trails. A number of species with such relationships have been described. In some cases, the two species coexist peacefully. Sanhudo et al. (2008) described the coexistence of two leaf-cutter species, *Apterostigma urichii* Forel, 1893 and *Mycetophylax faunulus* (Wheeler 1925), in the same nest. Workers of both species moved along the same trails and made antenna contacts without any signs of aggression. Furthermore, antennal contacts were made without aggression between workers and queens of different species. Some other species show similar relationships: *Camponotus*

*femoratus/Crematogaster levior* (Sprenger et al. 2021), *Crematogaster modiglianii/Camponotus rufifemur* (Menzel et al. 2012; 2013).

It is known that in some cases one of the interacting species can act as a commensal and covertly visit the food resources of the dominant using its trails. There is no direct competition for food between the species. For example, according to Schifani et al. (2022), *Colobopsis* workers often use *Crematogaster scutellaris* pheromone trails to find food resources. When *Crematogaster* activity is low, *Colobopsis* move in a straight line directly along the trail, sometimes simply following the host workers. However, when activity was high and the gaps between moving *Crematogaster* were small, *Colobopsis* moved off to the side of the trail. At the same time, the authors (Schifani et al. 2022) recorded the movement of *Colobopsis* at a distance of one cm from the trail, as well as movement along the trace pheromone of *C. scutellaris*.

Representatives of some species of the genus *Camponotus* show parabioc relationships with representatives of the genus *Crematogaster*, depending on habitat conditions and species characteristics, ranging from parasitism to commensalism to mutualism (Menzel et al. 2014). In the pair of species we studied, the relationship between them can be interpreted as commensalism, if the role of the commensal *Camponotus lateralis* is reduced to visiting aphid colonies hidden from the dominant, and there is no direct competition for food resources. However, the relationship between these species is far from being as 'friendly' as those mentioned above. In a number of cases we recorded an aggressive response from *Crematogaster schmidti* towards *Camponotus lateralis* after interspecific antennal contact (Table 1; Figures 7 & 8). Thus, in order to successfully use the trails and food resources of the host, *Camponotus lateralis* had to develop mechanisms that would allow it to minimise the aggression of *Crematogaster schmidti*.

These mechanisms include behavioural responses that allow them to avoid contact with an adversary or to flee after contact. According to our data, *Camponotus lateralis* most often avoided contact with *Crematogaster schmidti* by changing trajectory in its immediate vicinity (Figure 8). It is possible that frequent trajectory changes by *Camponotus lateralis* are related to the high activity of *Crematogaster schmidti* workers on the trails. It should be noted that according to Brandstaetter et al. (2008) ants of the genus *Camponotus* are able to distinguish the workers of their colony from strangers at a distance of one cm by significant acceleration (Figure 8). It is known that workers from the same colony recognise each other tactilely during antennal contact (Popp et al. 2018). In most cases, *Crematogaster schmidti* did not respond to *Camponotus lateralis*. After interspecific antennal contact, *Crematogaster schmidti* usually resumed its linear movement after a short pause. Only in rare cases did *Crematogaster schmidti* show aggressive behaviour after antennal contact, such as a threatening posture or unsuccessful chasing of *Camponotus lateralis* (Figures 6 & 8). Obviously, factors that ensure effective detection of the enemy are also important for the successful behavioural strategy of *Camponotus lateralis* when moving along the trails of *Crematogaster schmidti*.

### **Significance of Trace Pheromones and Cuticular Hydrocarbons in the Interaction of Different Ant Species**

Chemical communication plays a crucial role in the life of an ant colony. Ants use trail pheromones to mark trails leading to food resources, allowing colony workers to forage efficiently (Czaczkes et al. 2013, 2015; Evison et al. 2008; Widihastuty & Fadhillah 2021). In some ant species (*L. niger*), the most important orientation factors are not only vision and finding landmarks, but also movement along the trail pheromone (Evison et al. 2008). However,

some ant species are able to detect not only the trail pheromones of their own species, but also the trail pheromones of species with which they are associated through parabiogenic, parasitic, symbiotic and other relationships (Hangartner 1967; Menzel et al. 2010b; Stukalyuk et al. 2021).

Ant species whose nests are not in close proximity are also able to recognise the tracks of other ants in nature. For example, *Lasius fuliginosus* (Latreille 1798) is able to recognise the pheromone trails of *Lasius emarginatus* (Olivier 1792) and *Lasius niger* (Linnaeus 1758), but the latter two species do not recognise the trails of *Lasius fuliginosus* (Hangartner 1967). More recent studies have shown that dominants may be attracted to the scent of submissive species, while submissive species try to avoid visiting sites with traces of dominants (Binz et al. 2014; Wüst & Menzel 2016). It is known that some dominants use pheromone traces of submissive species to find food sources more efficiently (Reznikova 1983). Włodarczyk (2012) showed that in a mixed colony of *Formica polyctena* Foerster, 1850 / *Formica sanguinea* Latreille, 1798 established under laboratory conditions, workers of these species learned to recognise each other's pheromone traces.

Menzel et al. (2010b) investigated the relationships between the species pair *Camponotus lateralis* / *Crematogaster scutellaris*. The authors showed that *Camponotus lateralis* moves along trails with *Crematogaster scutellaris* trace pheromones, while *Crematogaster scutellaris* ignores *Camponotus lateralis* trace pheromones. We assume that the same relationships are characteristic of the species pair we studied. It is likely the *Crematogaster schmidti* pheromones that guide *Camponotus lateralis* to food resources. There are a number of studies demonstrating the important role of cuticular hydrocarbons in the recognition of individuals by ants within their colony (Menzel et al. 2010a; 2013). However, cuticular hydrocarbons can also be exchanged between species in close parabiogenic or parasitic relationships (Menzel & Bluthgen 2010; Stukalyuk et al. 2021; Toshiharu & Ryohei 2002). Such an exchange has also been demonstrated in a mixed *Formica polyctena* / *Formica sanguinea* colony established under laboratory conditions (Włodarczyk 2012; Włodarczyk & Szczepaniak 2014).

Toshiharu and Ryohei (2002) suggested that such interbreeding is only possible when species share the same nest for a long time. However, other researchers believe that mixing of cuticular hydrocarbons can also occur when trails are shared (Lenoir et al. 1997; Menzel & Bluthgen 2010). Menzel and Bluthgen (2010) showed that *Crematogaster modiglianii* and *Camponotus rufifemur* can use the same trails. At the same time, *Crematogaster modiglianii* is able to distinguish *Camponotus rufifemur* from a neighbouring colony from ants of this species from other colonies. This is facilitated by mixing of cuticular hydrocarbons that can occur during trail sharing as well as within the nest.

It is known that the cuticular hydrocarbons of *Crematogaster scutellaris* and *Camponotus lateralis* differ in composition (Menzel et al. 2010a). We assume that a significant difference is also characteristic of the species pair we studied. In our opinion, there is not enough mixing of cuticular hydrocarbons during *Crematogaster schmidti*/*Camponotus lateralis* interactions to allow reliable chemical mimicry of *Camponotus lateralis*, as in a number of cases we recorded an aggressive reaction of *Crematogaster schmidti* during antennal contacts with *Camponotus lateralis* (Figure 7A).

Based on our data (Figure 8), we can assume that on average *Camponotus lateralis* spends significantly less time on chemical recognition during antennal contact than

*Crematogaster schmidtii*. This may be one of the factors for successful avoidance of aggression from the dominant. On the other hand, some mixing may be taking place, as in most cases *Crematogaster schmidtii* workers quietly continued their movement after a short antennal contact (Figure 7A). It should also be noted that for ant species using the same trails, tolerance of a dominant species to another (less aggressive, submissive) species is associated with habituation of one species to another (Menzel et al. 2010b).

### Morphological Features

Fundamental to learning and foraging is the ability of ants to find landmarks using visual and tactile analysers (i.e. eyes and antennae) (Seidl & Wehner 2006). These organs play a crucial role in the orientation of ants in space.

Contact chemoreceptors on the antennae of worker ants are responsible, among other things, for recognising individuals from their nest and strangers (Barsagade et al. 2013; Nakanishi et al. 2009). We have shown that *Camponotus lateralis* minor workers has on average longer antennae than *Crematogaster schmidtii* for similar body sizes (Figure 10A & D; Figure 11). In addition, the antennae of *Camponotus lateralis* workers adopt a wider position than those of *Crematogaster schmidtii* when moving along the trail (Figure 11 C & D). In *Crematogaster schmidtii*, the funiculus of the antenna and the antennal scape form an angle of almost 90°. Thus, the apices of their antennae are directed more anteriorly than laterally, and their span is much smaller than that of *Camponotus lateralis*.

These morphological features give *Camponotus lateralis* some advantage in antennal contact with *Crematogaster schmidtii* were suggested. The long length and wide position of the antennae increase the likelihood that *Camponotus lateralis* will be the first to touch and recognise *Crematogaster schmidtii*. It should be noted that *Camponotus lateralis* reacted much more quickly than *Crematogaster schmidtii* to antennal contacts (usually abruptly changing trajectory), while *Crematogaster schmidtii* in most cases simply continued on its way, sometimes after a short pause. We have shown that the duration of intraspecific antennal contacts in *Camponotus lateralis* is, on average, significantly shorter than in *Crematogaster schmidtii* (Figure 6B). It is likely that *Camponotus lateralis* are able to assess the composition of cuticular hydrocarbons more quickly than *Crematogaster schmidtii* during antennal contacts, allowing them to avoid aggression from the latter.

The most important component of ant orientation is vision. It is known that *Gigantiops destructor* (Fabricius 1804), which has the largest eyes among ants, is able to move away from the nest up to 20 m without using trace pheromones, relying instead on visual orientation (Beugnon et al. 2001; Gronenberg & Hölldobler 1999). Many ant species (e.g. *Formica polyctena* Foerster, 1850, *Camponotus atriceps* (Smith 1858)) with large eyes have colour vision (Menzel & Knaut 1973; Briscoe & Chittka 2001; Perl & Niven 2016). Later, this phenomenon was also confirmed for ants with small eyes, such as *Myrmica sabuleti* Meinert, 1861 (Cammaerts 2007).

Cathemeral ant species have eyes with lower resolution than diurnal species (Yilmaz et al. 2014). The facet diameter of nocturnal ant species is usually larger than that of diurnal species (Greiner et al. 2007; Moser et al. 2004). It has also been found that ant species with a smaller number of facets have lower resolution, while the number of facets correlates with eye size (Palavalli-Nettimi & Narendra 2018; Palavalli-Nettimi et al. 2019). There is some evidence that nocturnal ant species have a greater visual range, and that nocturnal ant species have larger eyes and facet diameters (Johnson & Rutowski 2022). Although nocturnal ant species see better in the dark, their daylight vision is inferior to that of diurnal species (Ogawa et al. 2022).

Therefore, it can be assumed that *Crematogaster schmidtii* does not have a specialisation for nocturnal activity, as evidenced by its round-the-clock activity. Consequently, *Crematogaster schmidtii* does not have eyes specialised for night vision, and its daytime vision may be inferior to that of *Camponotus lateralis*.

Some morphological characteristics (total number of facets, number of facets per unit area) of the eyes of the studied species were compared. *Camponotus lateralis* has, on average, a higher total number of facets and their density, and thus a higher resolution than *Crematogaster schmidtii*. The described adaptations of *Camponotus lateralis* are probably explained by the fact that this species is active only during the day, whereas the activity of *Crematogaster schmidtii* is reduced during the day (Figure 4). We therefore assume that the eyes of *Camponotus lateralis* are better adapted to daytime conditions than those of *Crematogaster schmidtii*. We did not make precise measurements of eye size and facet diameter in the species studied. However, we can state that "visually" (Figure 10) *Camponotus lateralis* have larger eyes and smaller facets on average, which may further indicate their visual advantage over *Crematogaster schmidtii*. *Crematogaster schmidtii* workers seem to have difficulty tracking *Camponotus lateralis* due to their poor visual performance. In a number of cases we observed that *Crematogaster schmidtii* started to chase *Camponotus lateralis* after antennal contact, but broke off rather quickly, probably having lost visual control over the enemy (Figure 8). Thus, the safety of *Camponotus lateralis* workers is likely to be mediated by their behavioural responses based (among other factors) on morphological advantages. It is possible that similar factors also characterise the relationships of other described species pairs in which one species is a commensal of another: *Colobopsis truncata* (commensal) and *Dolichoderus quadripunctatus*; *Colobopsis imitans* (commensal) and *Crematogaster scutellaris* (Schifani et al. 2022).

## CONCLUSION

It was found that *Crematogaster schmidtii* reduces the intensity of traffic on trails with increasing air temperature (-0.64). For *Camponotus lateralis*, there was no significant relationship with temperature (0.48). An inverse relationship was found between the number of *Crematogaster schmidtii* and *Camponotus lateralis* workers on the trail during the 5 minute count, i.e. *Camponotus lateralis* workers prefer less busy *Crematogaster schmidtii* trails. The duration of intraspecific antennal contacts of *Camponotus lateralis* was approximately the same as the duration of interspecific contacts between *Camponotus lateralis* and *Crematogaster schmidtii* workers. Interspecific antennal contacts and antennal contacts between *Camponotus lateralis* workers lasted two times less than intraspecific contacts of *Crematogaster schmidtii*. On average, *Camponotus lateralis* reacts two times faster than *Crematogaster schmidtii* in each behavioural response. *Camponotus lateralis* workers are not only able to effectively avoid encounters with *Crematogaster schmidtii* workers, but also to react faster in case of antennal contact, to orient themselves in the choice and speed of implementation of a behavioural response. *Camponotus lateralis* has a number of morphological advantages over *Crematogaster schmidtii*: a greater total number of facets, a more significant number of facets per unit area (i.e. greater ocular resolution) and a greater length of antennae. These advantages may contribute to the successful use of *Crematogaster schmidtii* trails by *Camponotus lateralis* workers, despite the aggressive behaviour of the dominant.

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## **AUTHORS DECLARATIONS**

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### **Conflict of Interest**

The authors declare that they have no conflict of interest.

### **Ethics Declarations**

No ethical issue is required for this research.

### **Data Availability Statement**

Data available on request.

### **Authors' Contributions**

SS conceptualized this research and designed experiments; SS, DG and AA participated in the design and interpretation of the data; SS, DG and AA wrote the paper and participated in the revisions of it. All authors read and approved the manuscript.

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