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Mobilization Strategies in Ants (Hymenoptera: Formicidae)

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Abstract
The mobilization strategies of ants have been studied quite well, but the questions of how far foragers of different species are able to move away from the nest remain unclear. The study of changes in foraging strategies depending on the type of habitat remains relevant. The aim of the work is to study mobilization strategies in 31 ant species. The study was conducted in 2019-2021 on the territory of 2 countries – Ukraine (Kyiv region and Kyiv) and Uzbekistan (Tashkent region, Tashkent). Pairs of baits (one carbohydrate and one with tuna) were laid out at a distance of 3 m from each other, in the form of transects. In total, 16 transects (417 pairs) were laid out in Ukraine in 9 types of habitats, in Uzbekistan – 5 transects (70 pairs of baits) in one type of habitats. The number of ants on each type of bait was recorded every 10 minutes, for 0-90 minutes. The distance to the nest from where the mobilization took place was also determined. It has been established that all ant species can be divided into 4 clusters according to the average distance to the nest from which foragers mobilize on the bait. Cluster 1 included 3 species of dominants, which were able to move away from the nest at a distance of up to 50 m, cluster 2 included 4 species of dominants, whose foragers could move up to a distance of 20 m. Cluster 3 included 23 species that moved away from nest at a distance of 0.2-2.0 m, cluster 4 – 1 species, foragers of it moved to a distance of up to 7 m. Preferences of bait types were noted in 15 ant species. The distance to the nest ($F=9.02$, $p<0.001$) had the greatest influence on the number of ants on baits among the considered factors, followed by species of ants ($F=6.75$, $p<0.001$) and habitat type ($F=4.17$, $p<0.001$). In habitats where an ant species mobilizes a smaller number of foragers, they have to travel, on average, long distances to a food source. Consequently, the abundance of food resources in the habitat of ants is determined by the average distance of mobilization from the nest – the smaller it is, the more resources.

Key words: foragers, mobilization strategies, baits, nest distance.

Introduction

The search for food resources is one of the central activities of the ant colony (Traniello 1989). The flow of food collected by ants, after entering the nest, is distributed among the entire population. As a rule, food is collected by worker ants (foragers) in liquid form and is in the goiter. Between workers there is an exchange of food – trophallaxis. An interesting aspect is that the collected carbohydrate food is mainly consumed by the workers, while the protein food is consumed by the queens, as well as by the larvae. After the forager brings food to the nest, it transfers it by trophallaxis to several more workers who distribute the food among the rest of the ants (Hölldobler & Wilson 1990). If there is not enough food, foragers actively search for it. In the feeding area of ants, there are permanent food resources – trees with aphid colonies, to which forage trails have been laid in dominant species. The search for protein food is associated with hunting for small invertebrates. For example, red wood ants (*Formica rufa* group) have hunting trails, at the end of which workers disperse across the territory of the forage area (Zakharov 2015). Thus, the role of foragers in the life of an ant colony is very important.

Among the foragers, two groups of individuals are distinguished. The first includes active foragers who hunt or forage alone. This group of foragers is also engaged in the exploration of new food resources. The functions of active foragers, in addition to hunting and reconnaissance, also include protecting the territory of the colony from competing ant species. The second group of workers, passive foragers, is mainly engaged in collecting honeydew from aphid colonies. These ants move along one route, for example, along a trail leading to trees with aphid colonies (Hölldobler & Wilson 1990; Zakharov 2015). Workers form groups that are quite constant in terms of the number of individuals – for example, in red wood ants, foragers make up 13% of the total population of the colony, about 8% of workers participate in construction activities, 30% of ants are a reserve group, the rest have to perform functions inside the nest – care for brood, and so on (Zakharov 1991). Depending on the species, these numbers may vary, for example, in *Lasius alienus* (Foerster, 1850), foragers make up 15% of the total population, while the reserve workers for 40% (Nielsen 1974). There may also be changes in the ratio of food in an ant colony – in a growing colony, protein (consumed mainly by larvae) predominates in the diet, in an aging colony, on the contrary, carbohydrate.

The effectiveness of foraging will be determined by the type of mobilization strategy. Among different ant species, two prevail: the strategy of mass mobilization and the strategy of secondary division of the territory of the forage area (Carroll & Janzen 1973; Traniello 1989; Zakharov 2015). Mass mobilization is carried out when scouts attract passive foragers to the place where a food resource is found. In the most primitively organized ant species (*Temnothorax*, *Leptothorax*), mobilization occurs only after the arrival of the scout to the nest. At the same time, the road to the food source is marked by trace pheromones, which lead passive foragers (Hölldobler & Wilson 1990). Some species prefer to forage alone, such as *Formica fusca* Linnaeus, 1758, *Camponotus fallax* (Nylander, 1856). There is also another type of mobilization – tandem, when one worker leads another or a chain of passive foragers to a food source. Tandem mobilization is known in some species of *Myrmica* (Kipyatkov 1991). For more highly organized ants, for example, *Lasius fuliginosus* (Latreille, 1798), mass mobilization can be carried out from the nearest section of the forage trail (or tunnel). The most advanced type of mobilization is the secondary division of the territory; it is typical for red wood ants. A certain area is assigned to each forager, and if prey is found, workers from neighboring areas can be mobilized to the right place. The density of foragers in the forage area is high and can significantly increase in the place where prey is found (Zakharov 1991; 2015).

Some ant species can combine two types of mobilization—mass mobilization and secondary division of territory, as is observed in *Lasius fuliginosus*, *Liometopum microcephalum* (Panzer, 1798), *Camponotus vagus* (Scopoli, 1763), and also in large polycalytic colonies of *Myrmica rubra* (Linnaeus, 1758) (Zakharov 2015).

Mass mobilization is usually effective in species with small forage areas that are not protected from the penetration of other ants. Secondary territorial division is effective in dominant ants with large protected forage areas.

The mobilization strategies of ants are well studied (Dlussky 1981; Traniello 1989; Kipyatkov 1991). It is known how ants forage on different types of resources. For some species, there are preferences in the type of a resource; *Lasius fuliginosus* prefers protein food to carbohydrate food (Czechowski et al. 2013). In such cases, this is due to the fact that most of these ant species are trophobionts and are initially provided with carbohydrate food. It remains unclear how effective mobilization is in ants of the same species in different habitats. For many ant species, it is not known how far they can forage from their nest. Comparison of the efficiency of mobilization (distances that ants can move away from the nest) in different ant species can give an answer to why these species use one or another type of mobilization strategy.

This study provides information on preferences in choosing the type of bait, effective foraging distances in different habitats, and mass mobilization in 31 ant species inhabiting the temperate continental climate zone and the arid climate zone of Eurasia. We have shown that the studied ant species can be divided into 4 groups according to the efficiency of mobilization, depending on the distance from the nest to which foragers are able to go. We found that in habitats with a smaller amount of food resources, ants of the same species can forage at greater distances compared to habitats where there is an abundance of food resources.

The purpose of the study is to study the mobilization strategies of ants. The authors suggest that the distance from the nest is a key factor in determining the effectiveness of mobilization.

Material and methods

Research region

The study was conducted in June-August 2019-2021 on the territory of two countries – Ukraine (Eastern Europe) and Uzbekistan (Central Asia) (Fig. 1). In Ukraine, the sampling points were the Kyiv region and the city of Kyiv (Fig. 2). In Kyiv, samples were taken in 4 locations, in the Kyiv region – in 2 (Fig. 2). The locations correspond to the following types of habitats: steppe areas, pine forests (coniferous), deciduous forests, mixed forests, floodplain forests, urbanized habitats, meadows, gardens, semi-urbanized habitats.

In Uzbekistan, samples were taken on the territory of Tashkent and the region. In Tashkent and the region, samples were taken for one location – urbanized habitats (the territory of the city, Fig. 3). A detailed description of the dominant vegetation is given in Stukalyuk et al., 2022a.

Bait installation

The laying out of the baits was carried out in pairs – at a distance of 5 cm from the carbohydrate bait (water solution of sugar), the protein bait (tuna) was laid out. Each pair of baits was 3 m apart from the other. All baits were laid out in the form of a transect, each transect included 15-40 baits. In some cases, if the territory of the forage area of the dominant species was too large, 30-40 pairs of baits were included in the transect. All transects were laid out in the form of a line. In total, 16 transects and 417

Table 1 – Habitat types and number of observations for the studied ant species.

Species	Region	Habitat	Number of observations of ants on sugar baits, 0-90 min	Number of observations of ants on tuna baits, 0-90 min	Number of distances	Number of colonies
Camponotus aethiops	Kyiv region	Natural (Steppe areas)	21	31	6	3
Camponotus vagus		Suburban (lines of trees); Natural (pine forests)	86	89	29	3
Crematogaster subdentata	Tashkent region	Urban (gardens, parks in city)	159	166	17	6
Dolichoderus quadripunctatus	Kyiv region	Natural (deciduous forests); urban (gardens in city)	102	117	15	7
Formica cinerea		Natural (pine forests)	254	109	70	25
Formica clara	Tashkent region	Urban (parks in city)	50	19	11	6
Formica cunicularia	Kyiv region	Natural (meadows)	15	0	3	3
Formica fusca		Natural (deciduous forests)	21	5	27	n/a
Formica polyctena		Natural (pine forests)	289	434	50	1
Formica pratensis		Natural (pine forest edge)	3	139	15	1
Formica rufa		Natural (pine forests)	79	207	33	3
Formica rufibarbis		Natural (meadows)	20	6	15	3
Formica truncorum		Natural (pine forests)	90	171	79	2
Lasius brunneus		Natural (deciduous forests)	8	15	2	2
Lasius emarginatus		Natural (deciduous forests)	135	52	77	30
Lasius fuliginosus		Natural (deciduous, pine, riparian forests)	79	304	44	3
Lasius neglectus	Tashkent region	Urban (parks, gardens, lines of trees)	138	21	20	7
Lasius niger	Kyiv region	Natural (meadows)	365	336	205	202
Lasius platythorax		Natural (pine forests)	26	14	7	7
Leptothorax acervorum		Natural (pine forests)	55	30	11	11
Messor muticus		Natural (steppe areas)	29	36	5	3
Myrmica rubra		Natural (meadows)	220	45	38	36
Myrmica ruginodis		Natural (meadows)	126	46	29	27
Myrmica salina	Tashkent region	Urban (parks in the city)	48	16	7	6
Plagiolepis pallescens		Urban (parks in the city)	50	18	6	6
Plagiolepis tauricus	Kyiv region	Natural (steppe areas)	5	32	5	5
Solenopsis fugax		Natural (pine forest edge)	31	39	5	5
Tapinoma erraticum	Tashkent region	Urban (parks in the city)	14	3	2	2
Temnothorax sp.	Kyiv region	Natural (deciduous forests)	6	0	3	3
Tetramorium armatum	Tashkent region	Urban (parks in the city)	17	11	3	3
Tetramorium caespitum	Kyiv region	Natural (pine forests); Suburban (lines of trees); steppe areas	178	189	198	190

pairs of baits were laid out in Kyiv and the region. Transect 1 included 40 pairs of baits, 2, 6, 7, 15 – 30 pairs each; 3 – 25 each; 4, 9, 10, 11, 14 – 20 pairs each; 5 – 34; 8, 12 – 31 pairs; 13 – 15 pairs; 16 – 21 pairs. In Tashkent and the region, 5 transects were laid out, out of 70 baits. Transect 1 included 10 pairs of baits, transect 2 – 20 pairs of baits; 3 – 15 pairs of baits; 4 – 8 pairs, 5 – 17 pairs.

For different habitats, the following number of baits and transects has been laid out: 1) Kyiv and the region (Ukraine). a) pine forests (transects 1, 7, 12, 13, 15, 16), meadows (transects 2, 11), deciduous forests (transect 3), orchards (transect 4), steppe areas (transect 5), mixed forests (transects 6, 14), floodplain forests (transects 8, 9), semi-urbanized habitats (transect 10). 2) Tashkent and re-

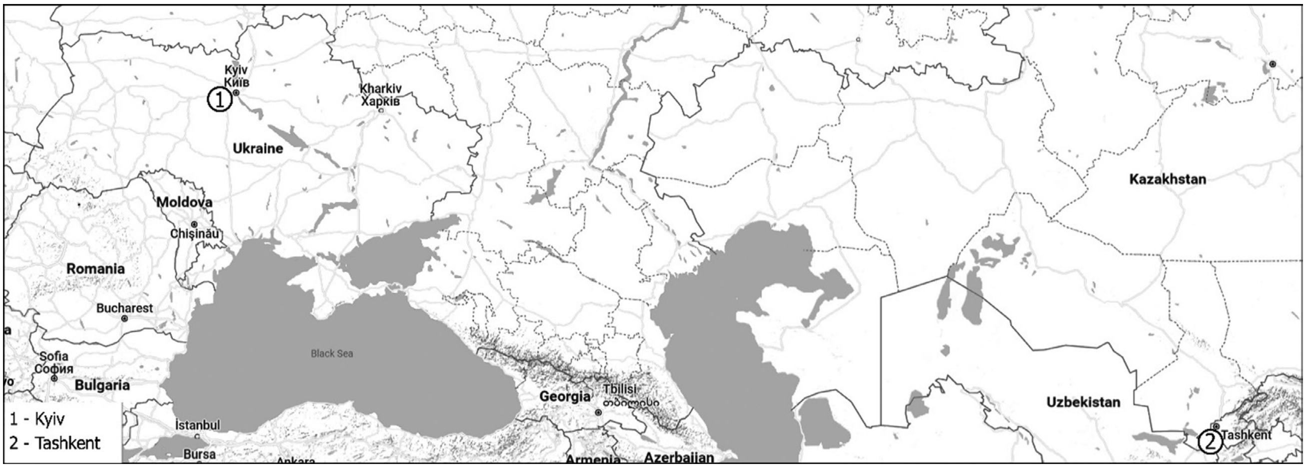

Fig. 1 – Sampling locations in Ukraine and Uzbekistan.

gion (Uzbekistan): all transects are in urbanized habitats. The number of observations for each ant species in different habitats and regions is given in Table. 1. The different number of transects is due to the fact that the studied habitats had different areas. In addition, a larger number of baits were required in the transect, which crossed large forage areas of dominant ants, for example, *Formica polyctena* Foerster, 1850. The number of examined colonies turned out to be large for subordinate ant species, while for dominants it was small (Table 1). This is due to the fact that the area of the forage area is much larger in dominants.

Field Research Methods

In our work, we used a modified methodology proposed by Czechowski et al. (2013). Before laying out the baits, the number of ants was measured on areas 0.5 by 0.5 m ("nudum" observations, 0 minutes). After that, the baits were laid out and the number of ants on them was counted for 1.5 hours (total time of observation 0-90 minutes). For each time period, the number of mobilized ants (ant species, number of foragers) was recorded. In addition, the distance to the nest from where the forager ants were mobilized was taken into account. For species with clearly visible nests (red wood ants, *Lasius fuliginosus*, *Formica cinerea*), this was not a problem. The search for nests of other ant species was more difficult, but the intensive movement of foragers in most cases made it possible to find their nests (*Lasius niger*, *L. platythorax*, *Formica clara*, *Myrmica* species, *Tetramorium caespitum*). For some ant species, nests were not found in most cases (*Formica fusca*, *Temnothorax* and *Leptothorax* species). The distance to the nest was recorded in meters (m). The studies were carried out in the morning, from 9-00 to 11-00 local time. This period was chosen by us, since most of the ant species are active at this time. Thus, for *Formica*, *Lasius*, *Camponotus* species, this is the first, morning peak of activity, while the second peak occurs in the evening (Dlussky 1967; Mershchiev 2010; Zakharov 2015). In the morning (before 13:00) there is a peak in the activity of most ant species in Mediterranean communities as well (Sanchez-Garcıa et al. 2022).

Study design

In this study, we analyzed two data sets. The first data array is the number of ants on different types of baits, depending on the time interval. The second data array is the number of ants on baits depending on the distance to the

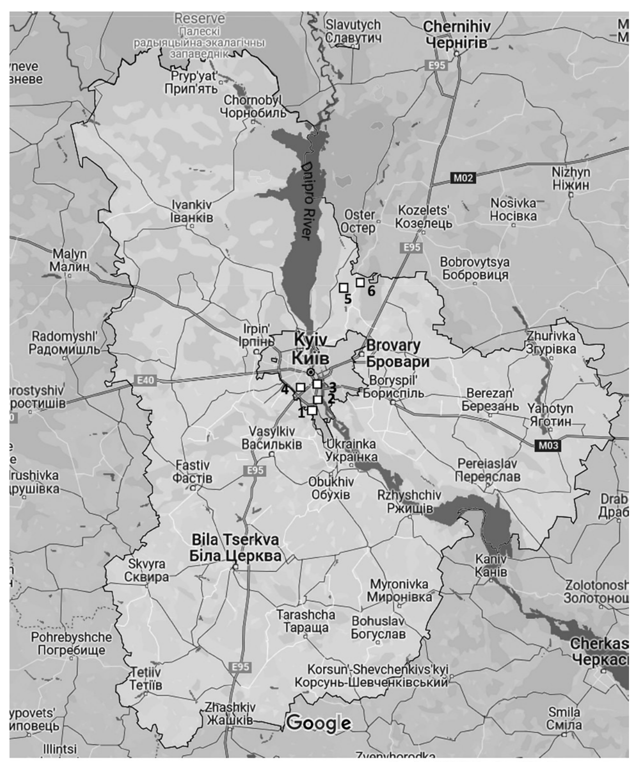

Fig. 2 – Sampling points in Kyiv and Kyiv region (Ukraine). Squares are sampling points. Habitats: Kyiv: 1 – deciduous forests (Feofaniya); 2 – mixed forests (Goloseevsky forest), 3 – steppe areas (Lysa Hora), 4 – gardens (Expocenter «Ukraine»); Kyiv region, with Litky and surroundings: 5- urbanized areas, 6 – mixed forests, pine forests, floodplain forests.

Table 2 – Test results for the influence of factors determining the intensity of ant mobilization to baits.
Model: capscale(formula = sp ~ spec + dist + habi, data = a2, distance = "bray").

Factor	Df	SumOfSqs	F	Pr(>F)
species	29	44.808	6.7539	0.000999 ***
distance	1	2.064	9.0228	0.000999 ***
habitat	8	7.627	4.1675	0.000999 ***
Residual	477	109.124	-	-

Table 3 – Average, minimum, and maximum distance from the nest (m) for which mobilization for bait was carried out in different ant species.

Species	Min	Average	Max	Forage area (m^2), average value	Forage area (m^2) max value
Camponotus aethiops	2.10	3.33	4.90	34.81915	75.3914
Camponotus vagus	0.10	6.63	22.0	138.0247	1519.76
Crematogaster subdentata	2.00	20.7	51.0	1345.459	8167.14
Dolichoderus quadripunctatus	0.20	1.32	2.40	5.471136	18.0864
Formica cinerea	0.10	2.77	10.5	24.09291	346.185
Formica clara	0.50	2.10	3.70	13.8474	42.9866
Formica cunicularia	1.85	1.70	2.00	9.0746	12.56
Formica fusca	0.40	1.80	2.20	10.1736	15.1976
Formica polyctena	3.60	23.21	47.0	1691.531	6936.26
Formica pratensis	1.00	7.20	16.0	162.7776	803.84
Formica rufa	11.5	21.14	45.0	1403.265	6358.5
Formica rufibarbis	1.50	2.40	4.00	18.0864	50.24
Formica truncorum	1.70	10.67	26.0	357.4855	2122.64
Lasius brunneus	0.50	1.35	2.20	5.72265	15.1976
Lasius emarginatus	0.30	1.92	4.80	11.5753	72.3456
Lasius fuliginosus	0.20	5.46	20.0	93.60842	1256
Lasius neglectus	0.10	0.47	1.50	0.693626	7.065
Lasius niger	0.10	0.98	2.90	3.015656	26.4074
Lasius platythorax	0.20	0.78	1.40	1.910376	6.1544
Leptothorax acervorum	0.05	0.15	0.35	0.07065	0.38465
Messor muticus	0.10	0.96	2.20	2.893824	15.1976
Myrmica rubra	0.10	0.95	1.90	2.83385	11.3354
Myrmica ruginodis	0.30	1.24	2.10	4.828064	13.8474
Myrmica salina	0.10	0.47	1.10	0.693626	3.7994
Plagiolepis pallescens	0.03	0.26	0.50	0.212264	0.785
Plagiolepis tauricus	0.20	0.54	0.80	0.915624	2.0096
Solenopsis fugax	0.05	0.11	0.20	0.037994	0.1256
Tapinoma erraticum	0.90	1.20	1.50	4.5216	7.065
Temnothorax sp.	0.05	0.25	0.40	0.19625	0.5024
Tetramorium armatum	0.20	0.43	0.90	0.580586	2.5434
Tetramorium caespitum	0.05	0.63	1.70	1.246266	9.0746

nest. Thus, the following factors were taken into account: a) type of habitat; b) type of bait; c) species of ant; d) distance to the nest.

Based on the obtained data on the average distance to the nest, we calculated the area of the forage area. Considering that in most models that calculate the area of the foraging, it is considered to be close to a circle (Li et al. 2014), we used the formula for calculating the area of a circle:

$$S = \pi r^2$$

Where r is the radius of the forage area. The radius was considered to be the average distance to the nest. In addition, the area of the foraging was also calculated from the maximum distance from the nest. This was the maximum value of the forage area.

We also calculated the rate of mobilization to baits in ant species that perform mass mobilization. To do this, we compared the number of ants in "nudum observations" and its increase for every 10 minutes of counting.

Statistical analysis

To take into account the influence of factors affecting ant mobilization, we used a permutational test (dbRDA). The type of bait (sugar or tuna) was the dependent variable, and the habitat type, ant species, and distance to the nest were

Table 4 – Minimum, average and maximum number of workers mobilized for different types of baits (for all habitats, the sum of workers in 0-90 minutes). Significant differences are highlighted in bold.

Species	**Sugar baits**			**Tuna baits**			**Wilcoxon paired t-test**	**M-W test, for all species on all baits in all habitats**
	min	**Average**	**Max**	**Min**	**Average**	**Max**		
Camponotus aethiops	7.0	30.6	97.0	22.0	45.5	76.0	0.115	
Camponotus vagus	1.0	25.2	189.0	1.0	9.4	58.0	0.918	
Crematogaster subdentata	56.0	337.7	946.0	115.0	550.0	1343.0	**0.0005**	
Dolichoderus quadripunctatus	2.0	302.9	1309.0	41.0	443.3	1469.0	0.061	
Formica cinerea	2.0	42.3	227.0	1.0	9.2	83.0	**>0.001**	
Formica clara	1.0	24.5	132.0	1.0	12.7	88.0	**0.0009**	
Formica cunicularia	19.0	20.5	22.0	0	0	0	-	
Formica fusca	1.0	1.5	5.0	1.0	0.3	1.0	**0.041**	
Formica polyctena	1.0	140.7	955.0	2.0	89.0	283.0	0.341	
Formica pratensis	1.0	0.2	1.0	14.0	85.7	256.0	**>0.001**	
Formica rufa	1.0	27.1	324.0	12.0	81.9	201.0	**>0.001**	
Formica rufibarbis	3.0	17.6	30.0	1.0	9.6	37.0	0.224	
Formica truncorum	1.0	14.6	58.0	1.0	84.1	206.0	**>0.001**	
Lasius brunneus	0	125.5	251.0	41.0	255.0	469.0	0.499	
Lasius emarginatus	8.0	296.3	753.0	2.0	12.3	56.0	**>0.001**	
Lasius fuliginosus	1.0	6.2	56.0	11.0	914.6	6169.0	**>0.001**	0.9288
Lasius neglectus	6.0	438.2	1448.0	1.0	1.9	13.0	**0.0001**	
Lasius niger	1.0	79.8	644.0	1.0	84.6	613.0	**0.504**	
Lasius platythorax	7.0	55.5	176.0	3.0	10.3	32.0	0.575	
Leptothorax acervorum	2.0	9.9	19.0	1.0	10.2	45.0	0.918	
Messor muticus	25.0	57.6	113.0	27.0	173.4	379.0	0.063	
Myrmica rubra	1.0	64.5	216.0	2.0	14.1	282.0	**>0.001**	
Myrmica ruginodis	1.0	26.9	178.0	1.0	11.7	121.0	**0.00012**	
Myrmica salina	8.0	151.0	460.0	1.0	23.0	101.0	**0.015**	
Plagiolepis pallescens	127.0	336.6	517.0	5.0	14.6	33.0	**0.031**	
Plagiolepis tauricus	0	9.2	46.0	28.0	101.0	339.0	0.0615	
Solenopsis fugax	76.0	248.4	515.0	139.0	767.8	1181.0	0.062	
Tapinoma erraticum	58.0	58.0	58.0	1.0	3.0	5.0	-	
Temnothorax sp.	1.0	3.0	7.0	0	0	0	-	
Tetramorium armatum	27.0	86.0	204.0	11.0	56.6	134.0	-	
Tetramorium caespitum	3.0	146.5	1438.0	2.0	252.3	1201.0	**0.01**	

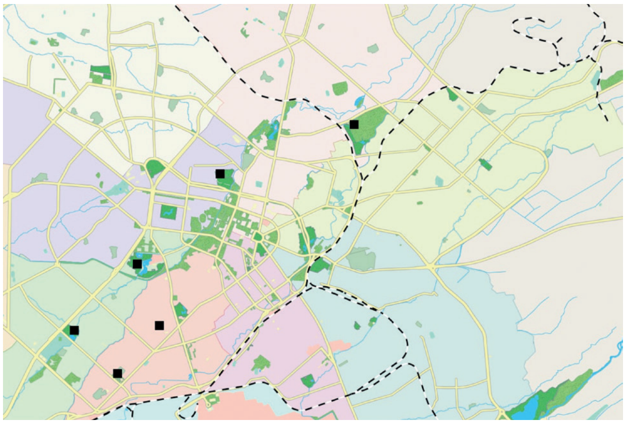

Fig. 3 – Sampling points in Tashkent (Uzbekistan). Sampling points are marked with squares, all of them are urbanized habitats (parks, areas of the botanical garden).

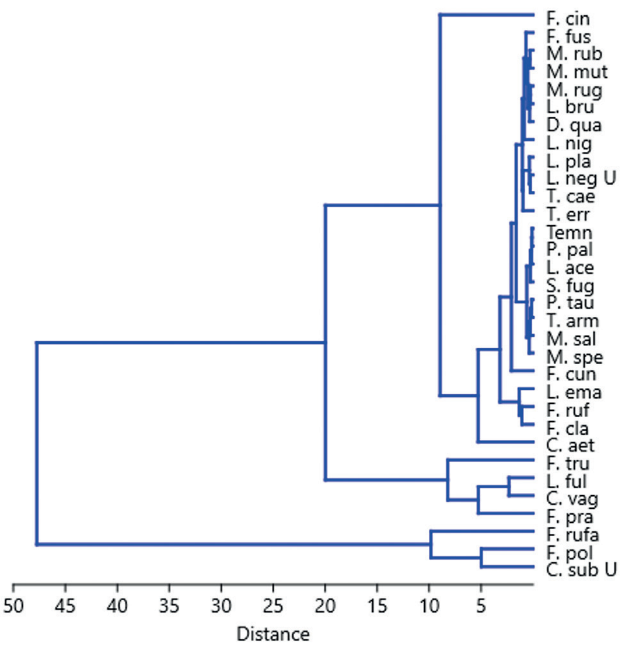

Fig. 4 – Cluster analysis results for the distance from which ants mobilize from the nest. **4th cluster: F cin** – *Formica cinerea*; **3rd cluster: F**. fus – *F. fusca*; M. rub – *Myrmica rubra*; M. mut – *Messor muticus*; M. rug – *Myrmica ruginodis*; L. bru – *Lasius brunneus*; D. qua – *Dolichoderus quadripunctatus*; L. nig – *Lasius niger*; L. pla – *L. platythorax*; L. neg U – *L. neglectus*; T. cae – *Tetramorium caespitum*; T. err – *Tapinoma erraticum*; Temn – *Temnothorax* sp.; P. pal – *Plagiolepis pallescens*; L. ace – *Leptothorax acervorum*; S. fug – *Solenopsis fugax*; P. tau – *Plagiolepis tauricus*; T. arm – *Tetramorium armatum*; M. sal – *Myrmica salina*; M. spe – *M. specioides*; F. cun – *Formica cunicularia*; L. ema – *Lasius emarginatus*; F. ruf – *Formica rufibarbis*; F. cla – *F. clara*; C. aet – *Camponotus aethiops*; **2nd cluster:** F. tru – *Formica truncorum*; L. ful – *Lasius fuliginosus*; C. vag – *Camponotus vagus*; F. pra – *Formica pratensis*; **1st cluster:** F. rufa – *Formica rufa*; F. pol – *F. polyctena*; C. sub U – *Crematogaster subdentata*.

independent variables. The Wilcoxon paired t-test was used to identify the difference between the compared parameters (preference for the type of bait in the same ant species). The Mann-Whitney test (M-W test) was used to identify general differences between all ant species in bait type preference.

Cluster analysis was used to divide ant species into groups depending on the distance from the nest. Bivariate regression was used to construct figures showing the relationship between time and the number of ants of all species on baits. The same regression was used to plot the relationship between distance from the nest and the number of ants mobilized for bait. Such figures were built for each species separately. All analyzes, except for the permutational test (performed in the R software environment), were performed in the Past program (v. 4.08). To display the mobilization rates of the same species in different habitats, figures were plotted with arithmetic means and errors of the mean (in the Origin program, 2021b).

Results

Influence of factors on the mobilization of ants to baits. All the variables had a strong influence on both of the bait variables taken together (tuna, sugar, Table 2). There were large differences among species and this determined the number of workers on baits ($F=6.75$, $p<0.001$). In the same way, there were strong differences in the number of ants at both bait types (the combination of the two//its taking the overall mean for both bait types) among the habitat types ($F=4.17$, $p<0.001$), and the distance had a strong effect ($F=9.02$, $p<0.001$). In connection with the results obtained, the further paragraphs of the article are in accordance with the importance of the factor, from the most powerful to the factors that have less influence.

The distance over which mobilization is carried out in different species of ants. Different ant species can forage at different distances, from 0.2 to 51.0 m (Table 3). Cluster analysis made it possible to identify four groups of species in which mobilization is carried out at different distances from the nest (Fig. 4). The first cluster includes three species (*C. subdentata*, *F. polyctena*, *F. rufa*), it is can forage at a distance of 20-50 meters. Accordingly, the forage areas of these species have an area of 6000-8000 m^2 (Table 3). The second cluster is formed by 4 species (*L. fuliginosus*, *F. truncorum*, *C. vagus*; *F. pratensis*), foraging of which is carried out at a distance of 20-26 m. The forage areas of these species have an of 1200-2000 m^2, only in one species (*Formica pratensis*) it can reach 800 m^2 in the maximum value. The third cluster is formed by the majority of studied species (23). The foraging of workers of these species is carried out over short distances, up to 7 m, usually up to 2-3 m. The forage area is within 0.5-30 m^2. Separately, there is one species, *Formica cinerea*, which forms the fourth cluster. Workers of this species are mobilized for bait at a distance of up to 10 m, the forage area can reach 300 m^2.

Bait type preferences by species. It has been found that ant species in general do not have significant bait preferences (Table 4). However, these differences appear when

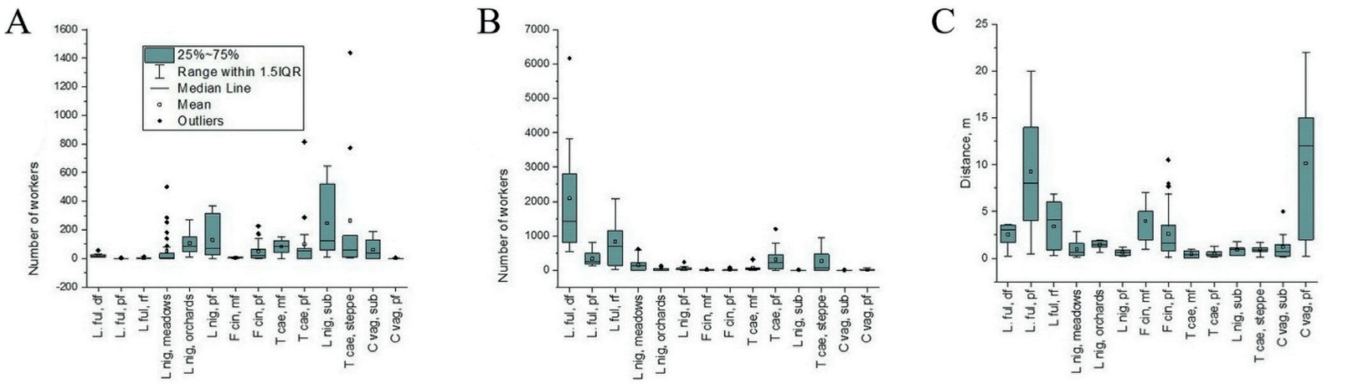

Fig. 5A-C – Mobilization of ant species inhabiting different habitat types (average number of workers per 0-90 minutes). **A** – sugar baits, **B** – tuna baits, **C** – average distance from nest in different habitat types (m). Abbreviations: df – deciduous forests; pf – pine forests, rf – riparian (floodplain) forests, mf – mixed forests, sub – suburban areas.

comparing the number of workers on baits of different types for the same species in pairs. The following species prefer tuna baits to sugar baits: *C. subdentata*, *F. rufa*, *F. pratensis*, *F. truncorum*, *L. fuliginosus*, *S. fugax*, *T. caespitum*. On the contrary, such species as *F. cinerea*, *F. fusca*, *L. emarginatus*, *L. neglectus*, *M. rubra*, *M. ruginodis*, *M. salina*, *P. pallescens*, *F. clara* preferred sugar baits. For some species, despite a large number of measurements, no significant differences were found in visiting different types of baits (*C. vagus*, *D. quadripunctatus*, *F. polyctena*, *L. niger*, *L. platythorax*, *T. caespitum*).

Influence of the type of habitat on the intensity of mobilization. In different habitats, the same species can show different mobilization rates (Fig. 5). For example, *L. niger* on sugar baits had the lowest rates of mobilization in meadows, the high in gardens, pine forest edges, and the maximal in semi-urbanized habitats (Figure 5A). At the same time, on tuna baits, the maximum mobilization of this species was in meadow habitats (Figure 5B). *F. cinerea* mobilized more workers on sugar baits in pine forests than in mixed forests (Figure 5A). *L. fuliginosus* on tuna baits mobilized the maximum number of workers in broadleaf and floodplain forests, and less in pine forests (Fig. 5B). *C. vagus* in semi-urbanized habitats mobilized more workers on sugar baits than in pine forests. For *T. caespitum*, the maximum number of workers for both types of baits is mobilized in the steppe areas. In different types of habitats, there are different distances for which workers are mobilized. For example, for *L. fuliginosus*, the average distance that workers are mobilized for both types of bait is greater in pine forests than in broadleaf forests (Fig. 5C, Table 5). For *C. vagus* in pine forests, the average distance to the nest is greater than in semi-urbanized habitats. *F. cinerea* mobilized its workers over a greater distance in mixed forests than in pine forests (Fig. 5C, Table 5). *L. niger* in meadows and orchards mobilized its workers over a greater distance than in other habitats. Due to different average distances to the nest, these ant species also differ in the areas of forage areas in different habitats (Table 5). It follows that in habitats where the ant species mobilizes a smaller number of workers, these workers have to travel, on average, longer distances to the food source. Consequently, the abundance of food resources in an ant habitat is determined by the average mobilization distance: the smaller it is, the more resources.

The type of bait matters for the distance of mobilization from the nest (Fig. 6). For example, in a pine forest on sugar baits, ant mobilization is effective up to 20 m (Fig. 6A), while ants are mobilized up to 35 m on tuna baits (Fig. 6B).

Mobilization speed. If there is a resource, mobilization can continue throughout the observation period. On sugar and tuna baits, ants are present in large numbers throughout the entire observation period (0-90 min, Fig. 7A, B). However, Fig. 7 shows a general pattern for all ant species. When analyzing the rate of mobilization, carried out for species separately, it is possible to establish which ant species use the mass mobilization (Table 6). The most mass mobilization is typical for *L. fuliginosus*, *C. subdentata*, *S. fugax* (tuna baits), *L. neglectus*, *T. caespitum* (sugar baits). These species show high efficiency of mobilization at different distances from the nest (Table 6). Other species of ants given in Table 6, also mobilize their workers for bait, but less massively, usually dozens of workers for 1 account every 10 minutes. A more detailed description of the effective mobilization distance is shown in Fig. 8. For *C. subdentata* (Fig. 8A, B), this distance is up to 30 m on both types of baits, while red wood ants (*F. polyctena*, *F. rufa*) can also effectively mobilize workers at a distance of up to 30 m. *L. fuliginosus*, *F. pratensis*, *F. truncorum* effectively mobilize workers at a distance of up to 15 m (Fig. 8C, D). For *P. pallescens*, *P. tauricus*, *S. fugax*, mobilization is effective over very short distances, 0.1-0.7 m (Fig. 8E). Finally, most ant species (Fig. 8F, *L. niger*, *L. platythorax*, *L. neglectus*, *M. rubra*, *M. salina*, *T. caespitum*) show efficient mobilization of workers to baits up to 2 m away. All these species correspond to the third cluster (Fig. 4).

Table 5 – Average distance to nest, size of forage area, and multivariate linear regression results* (distance to nest and total number of workers that came to both types of baits within 0-90 minutes) for ant species found in multiple habitats.
*dependent variables – number of workers, independent – distance to the nest. Significant differences are highlighted in bold.

Species	Habitat	Average distance, m Mean±SE	Forage area (m^2), average value	r, p	R^2
Lasius niger	Meadows	0.94±0.14	9.86	**-0.54751; 0.0009**	**0.2998**
	Gardens	1.48±0.14	7.49	**-0.058336; 0.87282**	**0.003403**
	Pine forests	0.62±0.09	1.53	-0.51257; 0.10693	0.2627
	Suburban areas	0.91±0.23	3.48	**-0.90103; 0.014**	**0.8119**
Formica cinerea	Pine forests	2.61±0.42	42.56	**-0.36686; 0.0234**	**0.1346**
	Mixed forests	4.00±1.09	65.31	**-0.896; 0.0392**	**0.804**
Tetramorium caespitum	Mixed forests	0.45±0.15	1.04	-0.52044; 0.28982	0.2709
	Pine forests	0.50±0.09	1.22	**-0.60788; 0.0096**	**0.3695**
	Steppe areas	0.94±0.14	3.34	**-0.63323; 0.049**	**0.401**

Table 6 – The rate of mobilization of different ant species to different types of baits *
* the types of baits for which this species performs maximum mobilization are selected;
** ant species are given with a large number of measurements (more than 30).

Species** and type of bait	Distance, m	Time (minutes) and number of workers on baits									
		0	10	20	30	40	50	60	70	80	90
F. polyctena, tuna	9.0	2	16	28	30	32	40	39	31	30	35
L. fuliginosus, tuna	0.9	10	259	250	550	600	700	800	900	1000	1100
L. niger, sugar	0.3	1	7	10	22	41	67	98	110	135	153
L. emarginatus, sugar	0.3	3	16	62	87	83	90	95	92	102	123
L. neglectus, sugar	0.3	0	30	100	118	127	179	190	261	213	230
C. subdentata, tuna	3.0	11	36	150	236	250	211	100	130	126	93
M. rubra, sugar	0.1	1	14	17	21	22	20	24	29	32	36
S. fugax, tuna	0.07	0	0	11	93	147	162	225	200	194	149
T. caespitum, sugar	0.8	0	3	11	67	154	230	303	270	244	156

Types of mobilization. The studied ant species use different types of mobilization. Mass mobilization is typical mainly for species from the third cluster (*D. quadripunctatus*, *T. caespitum*, *L. neglectus*, *Plagiolepis* species, *S. fugax*). Species with large forage areas can also use mass mobilization (*L. fuliginosus*, *C. subdentata*), although red wood ants do not clearly demonstrate this type of strategy. The species included in the second cluster (except for *L. fuliginosus*) have a less pronounced mobilization; up to several hundred workers come to baits during 90 minutes of observations. Some species (*F. fusca*, *F. cunicularia*, *F. rufibarbis*, *C. aethiops*, *Temnothorax* sp., *Leptothorax* sp.) come to baits singly or mobilize small groups of workers, usually up to several dozens in 90 minutes of observation.

Territoriality. Depending on the territoriality of the dominant species, a different number of other ant species may be present in its forage area (Table 7). Moreover, visiting baits by other species of ants may be related to what type of bait the dominant prefers. Thus, in the territory of *L. fuliginosus*, there were twice as many other ant species on sugar baits because this dominant prefers tuna baits. In some cases, only single dominant foragers (*L. fuliginosus* on sugar baits) can come to baits, which also contributes to it visiting by submissive species. The same is observed for the other two dominants, *F. rufa* and *F. pratensis*. The remaining dominants, visiting mainly sugar baits, have a larger number of other ant species on tuna baits (Table 7).

Discussion

Competition for food resources. Mobilization strategies can vary within the same ant species, depending on a number of factors. Some species are more mass mobilized for a certain type of bait. For example, *L. niger* visits carbohydrate baits more frequently (Portha et al., 2002), although we have not established such a pattern. At the same time, we confirmed the preference of dominants (red wood ants

Table 7 – The number of species for submissive species on the territory of the forage area of the dominants.

Dominant species	% occupied by the dominant sugar baits (of the total number of occupied baits)	% of tuna baits used by the dominant (of the total number of occupied baits)	Total number of submissive ant species on sugar baits	Total number of submissive ant species on tuna baits
C. subdentata	50	50	1	0
L. fuliginosus	35	65	6	3
L. emarginatus	57	43	0	1
L. neglectus	67	33	2	5
F. cinerea	60	40	6	9
F. polyctena	40	60	3	1
F. pratensis	17	83	2	0
F. rufa	39	61	6	2
F. truncorum	41	59	2	0
C. vagus	48	52	6	8

and *L. fuliginosus*) for tuna baits over sugar baits, while *Myrmica* has the opposite preference (Czechowski et al., 2013). The availability of a carbohydrate resource may be the reason for the greater abundance of invasive ant species, such as *Anoplolepis gracilipes* (Smith, F., 1857) (Lach et al. 2020).

Submissive ant species tend to find bait faster than dominant ants (Fellers 1987). Some ant species, when competing for food resources, try not to find food faster, but to displace competitors that have already arrived to the baits (Leonetti et al. 2019). This behavior was recorded by us in many dominants from the genera *Formica*, *Lasius*, *Camponotus*. In urban habitats, most ant species monopolized the bait within 120 minutes after opening the bait, protecting it from other species (Dáttilo & MacGregor-Fors 2021). This was also confirmed by us, not only for urban habitats (*C. subdentata*), but also for natural ones (*Formica rufa* group, *F. truncorum*, *F. pratensis*, *L. fuliginosus*), and already within 90 minutes of observations.

The behavior of some dominant species (*Formica pratensis*) can change, if it inhabit within large territories of other species (*Formica exsecta* Nylander, 1846) they can behave like subordinate species (Maák et al. 2020a). Near the nests of the red wood ants (*Formica polyctena*, *F. rufa*) some of the subordinate species, for example, *Myrmica*, can not only settle, but also switch to feeding mainly on the corpses of red wood ants (Maák et al. 2021). The preference of subordinate ant species for baits to which dominants are less mobilized was shown by the example of *Myrmica*, which visited baits with pollen, while *Formica polyctena* visited baits with animal protein (Erős et al. 2020). This strategy is quite situational – depending on the density of workers of dominant species in the territory, submissive species can switch from one type of bait to another. We confirmed this not only for red wood ants, but also for *L. fuliginosus* and submissive species on their territory. At the same time, the distance to the nest can play a key role, since the density of workers in the territory depends on it.

Another example is that, in order to avoid competition with dominants, submissive species can forage in the grass layer of vegetation, in which there are few or no dominant workers (Stukalyuk 2016). Foraging of ants can be carried out at different times – if red wood ants are active during the day, then *Myrmica* may be more active at night (Zmihorski & Slipinski 2016). Our studies were conducted during the daytime and therefore do not fully reflect the foraging activity of at least some species such as *Myrmica*. However, most of the studied species are still characterized by high activity in the daytime.

Finally, among the factors that can affect the effectiveness of mobilization, the experience of a single forager plays a role. Some older foragers can use tools (clods of earth, Módra et al. 2020; 2022) when collecting liquid food, and thus collect it more efficiently than young foragers (Maák et al. 2020b). Ants from the same colony can feed on the detected baits at different rates, depending on the degree of starvation (Frizzi et al. 2019).

Mobilization strategies in ants. During foraging, ants return to places where they have repeatedly found a food source and avoid areas where they have acquired negative experiences (Tanner 2009). In open areas, dominants may not have a significant effect on submissive species. In this case, the temperature regime has the greatest influence on the feeding time and mobilization in ants (Cerdá et al. 1998; Sanchez-Garcıa et al. 2022). At the same time, high temperature may be a lesser negative factor for ant species that use group mobilization compared to species with mass mobilization of workers for baits. This is due to the fact that trace pheromones of species with group mobilization are less volatile (van Oudenhove et al. 2012). In our study, we

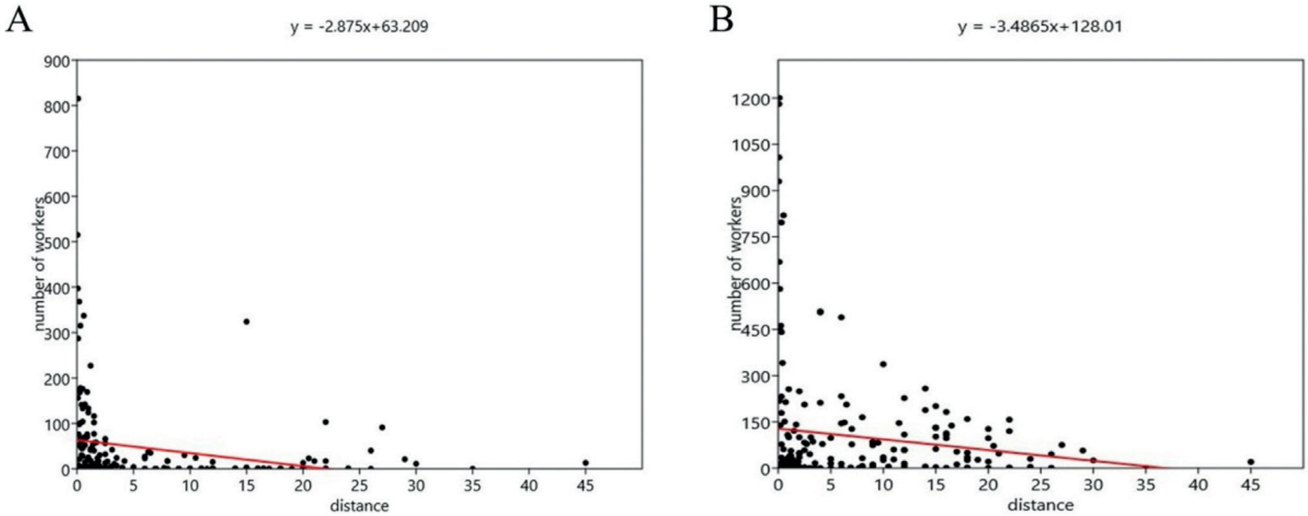

Fig. 6 A, B – Mobilization of ants to carbohydrate baits (A) and to tuna baits (B) on the example of a pine forest, Kyiv region, Ukraine.

chose the temperature interval corresponding to the optimal indicators of daily activity for most ant species, from 20 to 25°C. Therefore, species with mass mobilization (*L. fuliginosus*, *T. caespitum*, *L. neglectus*) showed a high efficiency in attracting workers. *C. subdentata* was the only exception, since in the arid zone of Tashkent it can effectively forage even at 30-35°C. For some invasive species, for example, *Linepithema humile* (Mayr, 1868), the most massive foraging was recorded at 10-15°C (Burford et al. 2018).

There are three types of ant mobilization strategies: mass mobilization, group mobilization, and solitary foraging (Lanan 2014). Among the 402 species studied, about half mainly used solitary foraging (194), followed by species with trunk trails (71), trunk networks (53), the remaining species used one or another type of group mobilization. In our case, out of 31 species studied, mass mobilization was noted in 12 species (more than 100 workers per 1 bait in 90 minutes, Table 4), for 17 species – group mobilization (from 10 to 99 workers), the rest of the species used single foraging (up to 10 workers). At the same time, mass mobilization was not necessarily characteristic of dominant species with large colonies; it was also used by subordinate species (*T. caespitum*). An interesting finding is mobilization in *S. fugax*, a cryptic kleptobiont species. It is possible that the recorded mobilization in this species is associated with the time of the nuptial flight (in August, see Stukalyuk et al. 2022b), when *S. fugax* make their passages closer to the surface and can come to the surface.

The efficiency of mobilization decreased in all studied species with increasing distance from the nest. These distances turned out to be different for different species. While for species from cluster 3 the distances were small (on average, from 0.2 to 2 m), for species from clusters 1, 2 and 4 mobilization was effective at distances of 7–50 m. For 22 ant species in Northern Vietnam, it was found that 16 of them foraged no further than 1 meter from the nest, and only one species (*Liometopum* sp.) foraged at a distance of up to 10 meters (Eguchi et al. 2004). Thus, it can be stated that most ant species do not effectively forage at a distance of more than 1-2 meters from the nest. In large colonies of red wood ants (*Formica aquilonia* Yarrow, 1955) with an anthill population of several mil-

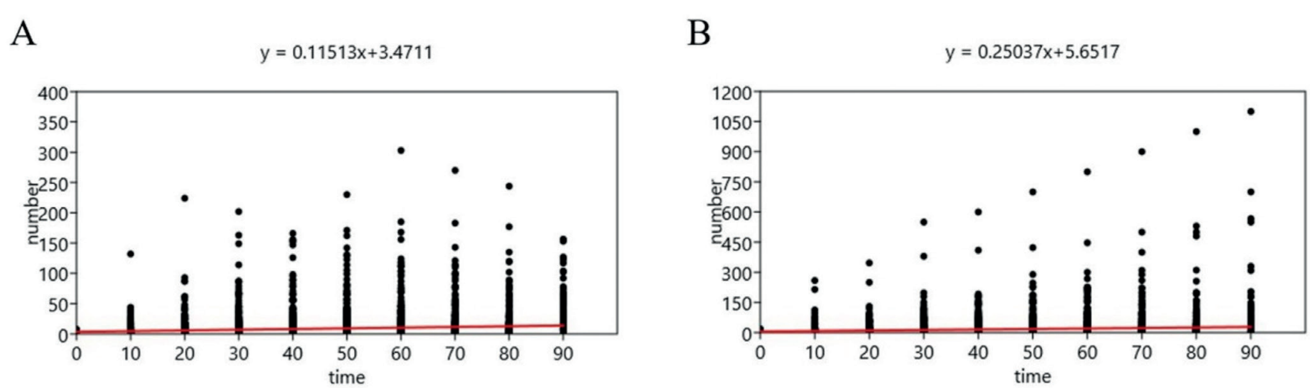

Fig. 7A, B – Dynamics of ant mobilization to sugar baits **(A)** and to tuna baits **(B)** over 0-90 minutes for all ant species in all habitats.

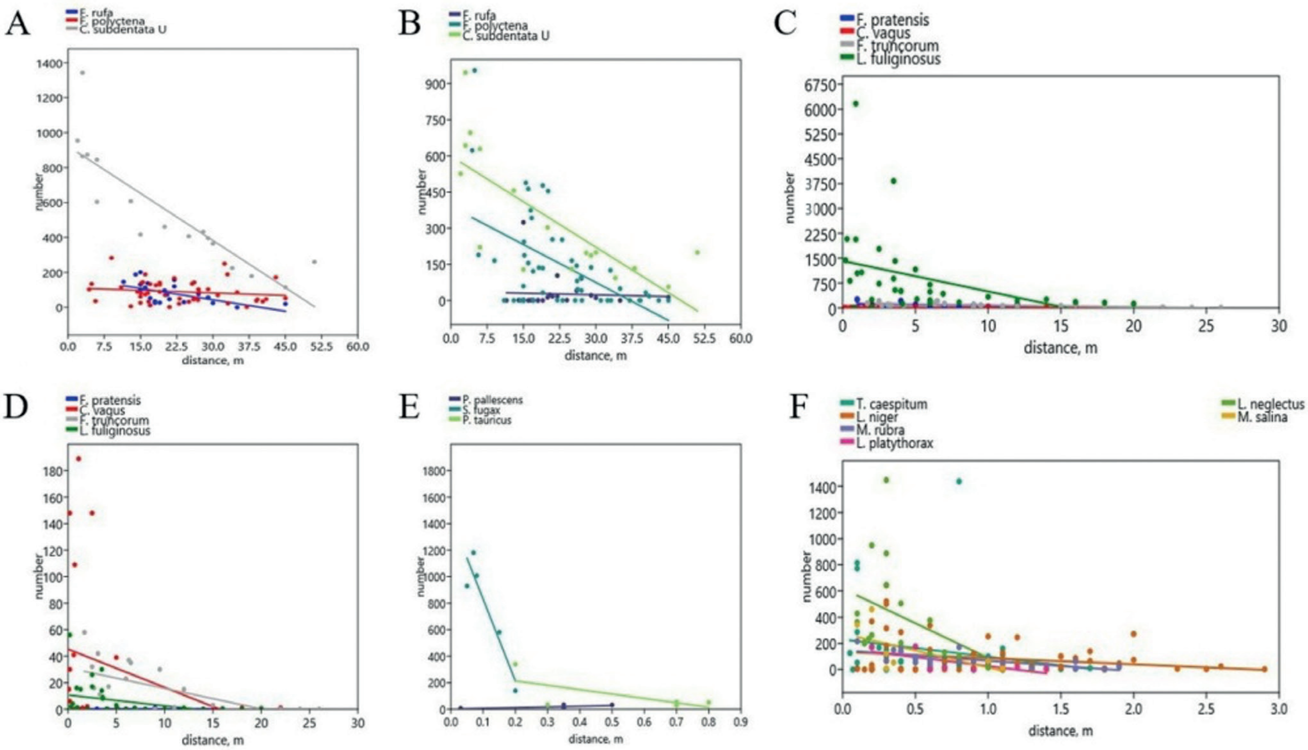

Fig. 8A-F – Distances over which workers of different ant species are mobilized on baits.
Multivariate linear regression: A, sugar baits, *F. rufa* (**R^2=0.3268, p=0.002**); *F. polyctena* (R^2=0.0025, p=0.28); *C. subdentata* (**R^2=0.7512, p≤0.001**).
B: tuna baits, *F. rufa* (R^2=0.0027, p=0.8042); *F. polyctena* (**R^2=0.29, p≤0.001**); *C. subdentata* (**R^2=0.5801, p=0.003**).
C: tuna baits, *F. pratensis* (R^2=0.1036, p=0.2422); *F. truncorum* (**R^2=0.53, p=0.0001**); *L. fuliginosus* (**R^2=0.1503, p=0.025**); *C. vagus* (R^2=3.349E-06, p=0.99).
D: sugar baits, *F. pratensis* (R^2=0.0006, p=0.9287); *F. truncorum* (**R^2=0.444, p=0.0007**); *L. fuliginosus* (**R^2=0.1261, p=0.04**); *C. vagus* (**R^2=0.1465, p=0.044**).
E: tuna baits, *P. pallescens* (R^2=0.5267, p=0.1025); *P. tauricus* (R^2=0.45, p=0.2151); *S. fugax* (**R^2=0.8788, p=0.01859**).
F: sugar baits, *T. caespitum* (R^2=0.037, p=0.2789); *L. niger* (**R^2=0.054, p=0.057**); *L. platythorax* (R^2=0.4856, p=0.081); *L. neglectus* (R^2=0.143, p=0.1345); *M. rubra* (**R^2=0.5463, p≤0.001**); *M. salina* (R^2=0.3377, p=0.1712).

lion individuals, foragers can move up to 250 m from the nest (Zakharov, 2015). Despite the fact that for most of the studied ant species in large colonies, on average, foragers move a greater distance from the nest, for some species of *Temnothorax*, such a dependence on the size of the colony has not been established (Bengston & Dornhaus 2013).

It is known that mass mobilization is most effective when the forage area is small (Zakharov 2015). In dominant territories, which can be hundreds of square meters in area, there is usually a secondary division of the territory, when a high forager density is created situationally, in places with a high concentration of food. Some of the dominants (*L. fuliginosus*) showed high efficiency of mass mobilization even at large distances from the nest. This may be due to the complex structure of the forage area, when, in addition to the main nest, there are auxiliary nests, trails or tunnels from which mobilization can be carried out. At the same time, the mobilization strategy is quite variable (Lanan 2014), and can change even in one species in different habitats (See Table 5).

An important role for the indicators of mobilization in the same ant species is played by the type of habitat (Table 5; Sanchez-Garcıa et al. 2022). In different habitats, the average distance to the nest and the area of the forage territory can vary greatly, 6 times for *L. niger*, 3 times for *T. caespitum*, and 1.5 times for *F. cinerea*. On the other hand, in some desert ant species, the sizes of forage areas are constant and do not depend on the type of habitat and season (Bernstein 1975). Perhaps, in the dominant species studied by us, the indicators of the size of the forage area are less variable than in the submissive species. This statement is supported by calculations of the size of colonies of dominants, which, although they differ in different habitats, in any case include tens of thousands of workers (Stukalyuk et al. 2022a). In urban habitats, the size of the colonies of some native and invasive species can be much larger than in natural ones. On the other hand, in red wood ants, the most favorable habitats are associated with natural ones: mature forests dominated by pine 80–140 years old (Berberich et al. 2020).

The large size of colonies makes it possible to quickly mobilize for a food resource. An interesting point is how flexible the mobilization, for example, from the same colony, can be for baits located at equal distances from the nest entrance. We found that for the majority of species from cluster 3, mobilization was for one pair of baits. However, this may be due to the fact that the forage areas of these species are small and the distances between pairs of baits (3 m) in most cases simply exceeded their size. Therefore, the study of simultaneous mobilization to baits located at equal distances from the nest in species of the third cluster remains topical.

Invasive species (*C. subdentata*, *L. neglectus*) showed different mobilization strategies. *L. neglectus* mobilized its workers only short distances from the nest, which may be due to its attachment to trees with aphid colonies, a major resource. *C. subdentata* successfully mobilized throughout the forage area. This is possible due to the "mesh" branching of its trails, when secondary trails branch off from the main trails throughout the territory (Stukalyuk et al. 2021). The success of invasive species is largely associated with an effective combination of mass mobilization and wide adaptive capacity, which allows them to outcompete native ant species and form supercolonies (Carpintero et al. 2007). The stability of polydomic systems can be determined by the presence of links between nests when a single nest is a subunit of a supercolony and there is no competition between nests for food resources (Buczkowski & Bennett 2008). In some cases, the foraging strategy of invasive species may be less efficient than that of native ant species (Cordonnier et al. 2020).

Such polydomic systems are quite flexible: in the absence of access to a source of food resources, a previously single colony can break up into a network of smaller ones (Burns et al. 2020a). In addition, the forage area can also be stable – in red wood ants with larger nests are more likely to remain in one place (Burns et al. 2020b). Species capable of forming supercolonies and polydomic settlements, such as *Formica paralugubris* Seifert, 1996, can form them even under completely new conditions (Seifert 2016). Apparently, they retain the predominant type of mobilization strategy. Ant mobilization is determined by many factors, but among them, in addition to the availability of the resource, the distance to the nest is of decisive importance.

Conclusions

Our work shows that the distance to the nest is the main factor influencing the efficiency of ant mobilization. We found that, depending on the habitat, ants of the same species can differ significantly in both the distance to the nest and the size of the forage area. In 15 species, significant differences were found in the choice of the type of bait. For some species, despite a large number of observations (*Lasius niger*), no such differences were found. This indicates a high adaptive potential of *L. niger* as a species that has mastered urban habitats everywhere. For the invasive species *Crematogaster subdentata* in the primary range, it was found that it can effectively mobilize at distances up to 50 m in urban conditions, which is comparable to the indicators of red forest ants. Another species, *L. neglectus*, did not move more than 1–1.5 m from the nest. Mass mobilization was present both in dominants (*L. fuliginosus*) and in submissive species with small forage areas (*Tetramorium caespitum*). Ants, therefore, show wide variability in the choice of the type of mobilization strategy, depending on a number of factors, such as habitat type, species. At the same time, the distance to the nest determines the effectiveness of mass mobilization in ants.

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