# TRAIL ACTIVITY OF ANTS (HYMENOPTERA, FORMICIDAE) AT DIFFERENT HABITAT STRUCTURE

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## ABSTRACT

The study was conducted in two stages, in 2013-2014, on the territory of the Crimea, Ukraine, and in 2019-2021 at the city of Kyiv in the region of Carpathians, Ukraine and in the city of Tashkent in Uzbekistan. The study covered natural (forest, meadow, steppe), suburban (alleys and tree planting) and urban habitats (tree planting along streets and roads, botanical gardens). The average number of workers on the trails per 2 minutes (activity) are obtained for each of the 21 dominant species of ants. Urbanized habitats are favorable for some ant species (*Crematogaster subdentata* and *Lasius neglectus* - invasive or native species, depending on the region, *Dolichoderus quadripunctatus* - native species), it is reflected in the maximum rates of activity on the trails. In urbanized habitat there are about 200-800 individuals of ants that can be observed on the trails, it is equal to or greater than the activity for other ant species in natural habitats (100-400 individuals per 2 minutes). In the primary range (Uzbekistan), activity indicators on trails in native species *C. subdentata* and *L. neglectus* are equal or lower than those in the secondary range (Crimea, Kyiv city, Ukraine). The maximum activity of *L. neglectus* on trails in urbanized habitats is in Tashkent city, less in Crimea (M-W test, Tashkent vs Crimea, $P \leq 0.001$), and in Kyiv city (Tashkent vs Kyiv, $P \leq 0.001$). For *C. subdentata*, the maximum activity in the conditions of Tashkent, less activity - in natural habitats (tugai forests) (Tashkent vs tugai, $P \leq 0.001$). The presence of permanent foraging trails indicates the dominant status of the ant species. The amount of traffic on the trails can vary greatly in different habitats.

**Keywords**: activity, workers, trails, dominants, invasive species

## ABSTRAK

Kajian ini telah dijalankan pada dua peringkat, iaitu pada 2013-2014 di jajahan Crimea, Ukraine dan pada 2019-2021 di bandar Kyiv dalam kawasan Carpathians, Ukraine dan bandar Tashkent di Uzbekistan. Kajian ini meliputi kawasan semulajadi (hutan, padang rumput, padang rumput lapang), tepian bandar (laluan dan kawasan penanaman pokok) dan habitat luar bandar (penanaman pokok sepanjang jalan dan laluan, tanam botani). Bilangan purata pekerja pada laluan per minit (aktiviti) didapati dari setiap 21 spesies semut dominan. Habitat urban dipilih oleh beberapa spesies (*Crematogaster subdentata* dan *Lasius neglectus* – spesies invasif atau natif bergantung kepada kawasan, *Dolichoderus quadripunctatus* – spesies natif), ia dipengaruhi oleh kadar maksimum aktiviti pada laluan. Habitat luar bandar melibatkan kira-kira 200-800 individu semut telah diperhatikan pada laluan, menyamai ke lebih besar dari aktiviti spesies tersebut pada habitat semulajadi (100-400 individu per 2 minit). Pada julat primer (Uzbekistan), indikator aktiviti pada laluan pada spesies natif *C. subdentata* dan *L. neglectus* adalah sama atau kurang dari julat sekunder (Crimea, bandar Kyiv, Ukraine). Aktiviti maksimum *L. neglectus* pada laluan di kawasan habitat urban di bandar Tashkent, kurang dari Crimea (ujian M-W, Tashkent vs Crimea, $P \leq 0.001$), dan bandar Kyiv (Tashkent vs Kyiv, $P \leq 0.001$). Untuk *C. subdentata*, aktiviti maksimum pada keadaan di Tashkent, kurang aktiviti – di habitat semulajadi (hutan tugai) (Tashkent vs tugai, $P \leq 0.001$). Kehadiran laluan tetap mencari makan menyatakan status dominan spesies semut. Jumlah kesesakan pada laluan akan bervariasi tinggi pada habitat berbeza.

**Kata kunci**: Aktiviti, pekerja, laluan, dominan, spesies invasif

## INTRODUCTION

Ant colonies have different sizes, and, consequently, the infrastructure of the forage area is different in complexity. Some of the species of ants belonging to submissive ones usually have a protected area only next to the entrance, subdominant species can protect prey and forage trees, whereas in dominant ants, the entire forage area is protected (Pisarski & Vepsalainen 1989). The size of forage areas in dominant species, for example, red wood ants, can reach a hectare per large anthill (Zakharov 2015). The remaining dominant species of temperate forests in Europe (e.g., *Lasius fuliginosus* (Latreille 1798), *Lasius emarginatus* (Olivier 1792), *Formica cinerea* (Mayr 1853) and *Liometopum microcephalum* (Panzer 1798) have smaller forage areas – tens and hundreds of square meters (Radchenko 2016; Stukalyuk & Radchenko 2011; Zakharov 2015). In order to distribute foragers throughout the forage area, a complex infrastructure is needed. Trails are one of the elements of infrastructure. Moving along the trails, foragers do not create areas of high density directly next to the nest but can quickly get to the periphery. Trails, as a rule, lead to forage trees on which ants hunt or visit aphid colonies. The resumption of trails to the same trees occurs every year after wintering, so the direction of the trails remains constant for many years, as was shown by the example of *Formica rufa* (Linnaeus 1761) (Zakharov 1991). The movement of foragers along trails is usually in two opposite directions, but there may also be unidirectional trails, for example, such may occur in *L. microcephalum* (Zakharov 2015). Foragers make up a permanent group of worker ants, usually tied to a certain trail (Zakharov 1991).

The more trails per anthill the red wood ants have, the larger the population of this nest (Dyachenko 2017). An increase in the number of trails is associated with both an increase in the linear sizes of the nest and with a complication of the infrastructure of the forage area in red wood ants (Stukalyuk et al. 2021a). With the increasing impact of the anthropogenic factor, red wood ants experience shortening the length of the trails (Soboleva 2010).

The issue of terminology for the classification of ant trails is most fully disclosed by Zakharov (1978). There are the following types of trails: *Forage trails*: These include: One-time trails along which foragers are mobilized to a food source; vector trails - indicate to the forager stream the place where the forage resource is collected, as is observed in *Messor* workers. Another type of forage trails is *temporary*, usually existing for up to several weeks. In temporary trails, workers are mobilized to the zone of successful foraging (e.g. *Tapinoma*). There are also permanent forage trails laid either to the place where aphids are collected (on trees), or to a part of the forage area where invertebrates are hunted. In some species of ants, these trails run along the surface of the earth (red forest ants), in some trails can be sunk into the soil in the form of grooves (e.g. *Formica pratensis* (Retzius 1783) and *Messor intermedius* (Santschi 1927)) and finally, they can be in the form of tunnels (e.g. *Lasius fuliginosus*).

*Resettlement trails* – one-time flows of workers during the relocation of the entire colony to another place. *Hiking trails* - for slave-owning ants (e.g. *Polyergus rufescens* (Latreille 1798)). *Exchange trails* – they are used for population exchange between different nests, can also be temporary and permanent. *Multifunctional trails* - used both for the direction of forage collection and for communication between nests as part of a polycalic colony or a supercolony. We studied only permanent trails, forage trails, as well as multifunctional ones (in red wood ants). The only exception was the vector forage trails that we studied in the *Messor muticus* (Nylander 1849) foragers. The same species is not included in the interspecific hierarchy, since it is a carpophages, while the other species are zoonecrophages (Stukalyuk & Radchenko 2011). We considered the dominant species capable of forming permanent forage trails. The remaining species (without trails) are classified as subordinates.

The aim of the work is to analyze the effect of urban conditions on the activity on trails of native and invasive ant species. The objectives of the study included: a) to study the activity of ants on the trails; b) to compare the activity on trails of different ant species between different habitats.

## MATERIALS AND METHODS

### Region of Research

Survey was conducted in July-August 2013 on the territory of the Crimean Peninsula (Ukraine). In July-August 2020-2021, the research was continued in other locations: Kyiv city and the Kyiv region, the Carpathian Mountains (Ukraine), Tashkent city and tugai forests (Uzbekistan) (Figure 1). July and August are the inclusive months as the activity of ants on the trails is maximum (Mershchiev 2010). In Crimea, studies were conducted in the following habitats: a) mountain steppes and meadows (the main ridge of the Mountainous Crimea); b) The southern coast of Crimea (oak-pistachio-juniper forests); c) steppe areas in the flat part (a-c – natural habitats; total 10 study sites); d) Saky district (territories of gardens and private houses, urban habitats, 3 study sites). Kyiv and the Kyiv region included the following habitats: a) deciduous forests; b) coniferous forests (natural habitats, total 10 study sites); c) single-species tree plantings along trails in rural areas (suburban habitats, total 10 study sites); d) urban habitats (alleys of trees along streets and highways, city squares, 7 study sites). Meadow habitats at an altitude of 500 m above sea level (natural habitats) have been studied in the Carpathian Mountains (2 study sites). Natural (tugai forests, 2 study sites) and urban habitats (Tashkent city, 6 study sites) have been studied in Uzbekistan.


Figure 1. Locations of the study

(Source: Google Map 2022)

**Description of Plant Communities**

In the Crimea, *Festuca pratensis* dominates in the mountain steppes (altitude of 700-900 m above sea level). *Alchemilla taurica* dominates in mountain meadows. The forests located on the southern slope of the Main Ridge are dominated by *Pistacia mutica*, *Quercus pubescens*, and *Juniperus excelsa*. In steppe areas on the flat part, the dominant herb is *Elytrigia nodosa* (Stukalyuk & Radchenko 2011). In the Saky district, gardens are dominated by *Prunus armeniaca*, *Morus nigra*, *Malus domestica*, and *Prunus domestica* (Stukalyuk et al. 2020a). The deciduous forests of the Kyiv region are dominated by *Quercus robur*, *Acer platanoides*, and *Carpinus betulus*, while in coniferous, it being dominated by *Pinus sylvestris*. Tree plantings in suburban habitats of the Kyiv region consist of *Salix fragilis*, and *Populus nigra*. *Robinia pseudoacacia*, *A. platanoides*, and *Tilia cordata*, predominate in the alleys of trees on the territory of Kyiv city (Stukalyuk et al. 2020b). In the Carpathians, meadow communities are represented by *Agrostis capillaris*, and *Alopecurus pratensis*. In the tugai forests of Uzbekistan, *Salix* sp. dominates, in the territory of Tashkent city, *M. domestica*, *P. nigra*, *Cydonia oblonga*, and *P. domestica* predominate in the alleys (Stukalyuk et al. 2020a).

**Study Design**

The study consists of three related parts. In the first part, the average activity on the trails of ants for each of the species is determined. In order to show the differences in the traffic of ants on the trails and on the territory of the forage area, we also took into account the parameter of the density of ants per unit of time per unit of territory (n/2 min, 0.250 $m^2$ each plot). The time of 2 minutes was chosen by us because 1 minute may not reflect the dynamics of the movement of ants along the trails or in the plots. In 1 minute, a different number of ants can pass along the trail or in the plots. A longer time interval allow to get more reliable data.

This data will show the difference in the number of ants on the trails and on the forage area. It will be able to confirm the assumption that the trails are a place of increased density of ants compared to the rest of the forage area. In addition, we will be able to show that in submissive species that do not have permanent trails, the density of workers in the forage areas can be comparable to that of the dominant ones. Finally, the final stage of our research is to compare the activity of ants on the trails at natural, suburban, and urbanized territories.

**Field Research Methods**
The identification of ant species was carried out according to Czechowski et al. (2012) and Radchenko (2016). The activity of ants on the trails at 09:00 to 11:00h is being recorded. This time corresponding to the morning peak of ant activity (Dlussky 1967; Mershchiev 2010; Peng et al. 2012; Zakharov 2015). Samplings were conducted during the sunny day. The temperature was range between 20-25°C corresponds to the optimum for the activity of ants of the temperate climatic zone (Dlussky 1967).

The period of each recording of ant activity on the trails was 2 minutes; and ants moving in both directions were taken into account. Wire gates were installed over the trail, and all the ants passing under them were counted. If the traffic is too lively and the number of ants cannot be counted, video filming is carried out (by video camera Canon Ivy Rec, Japan). In total, 2460 measurements on the trails were carried out for 21 species of ants (Table 1).

Table 1. Number of observations of the ant trails in different habitats

| **Species** | **Region** | **Habitat** | **Number of observations** |
|---|---|---|---|
| *Formica cinerea* | | coniferous forests | 33 |
| | | suburban habitats | 20 |
| | | urban habitats | 86 |
| *Lasius niger* | | suburban habitats | 18 |
| | | urban habitats | 210 |
| *Camponotus vagus* | | suburban habitats | 130 |
| | | urban habitats | 140 |
| *Dolichoderus quadripunctatus* | | deciduous forests | 3 |
| | | suburban habitats | 2 |
| | | urban habitats | 50 |
| *Formica polyctena* | | deciduous forests | 11 |
| | Kyiv city and | coniferous forests | 14 |
| *Formica rufa* | region | deciduous forests | 19 |
| | | coniferous forests | 51 |
| *Formica truncorum* | | coniferous forests | 6 |
| *Lasius brunneus* | | deciduous forests | 31 |
| | | suburban habitats | 6 |
| *Lasius emarginatus* | | deciduous forests | 115 |
| | | urban habitats | 17 |
| *Lasius fuliginosus* | | deciduous forests | 145 |
| | | coniferous forests | 8 |
| | | suburban habitats | 23 |
| *Lasius platythorax* | | deciduous forests | 15 |
| *Lasius neglectus* | | urban habitats | 22 |
| *Lasius neglectus* | Crimea | urban habitats | 42 |
| *Lasius neglectus* | Tashkent city | urban habitats | 65 |
| *Camponotus aethiops* | | steppe areas | 35 |
| *Messor muticus* | | | 11 |
| *Crematogaster schmidti* | | oak-pistachio-juniper | 290 |
| *Formica gagates* | Crimea | forest | 15 |
| *Plagiolepis tauricus* | | | 45 |
| *Formica pratensis* | | mountain steppes | 101 |
| *Formica pratensis* | | mountain meadows | 18 |
| *Formica pratensis* | Carpathians | mountain meadows | 24 |
| *Crematogaster subdentata* | Crimea | urban habitats | 111 |

| | | | |
|---|---|---|---|
| | Tashkent city | tugai forests | 70 |
| | | urban habitats | 221 |
| *Plagiolepis pallescens* | | urban habitats | 36 |

For the locations of the Crimea (all habitats) and Kyiv city and Kyiv region (deciduous forests and urban ecosystems), measurements of the activity of ants were carried out at the plots (on the territory of the forage area). The counts of density of workers were carried out on plots of 0.250 $m^2$, set in the forage area (except for zones adjacent to the nest). If an ant species had trails in the forage area, then the activity of ants on the trails was considered in parallel. The counts were carried out at the same time of the day as the counts on the trails. All ants within the plot were counted for 2 minutes. Detailed data on the number of counts on the plots are presented in Table 2.

Table 2. Number of observations on plots of worker density in ant species

| **Species** | **Region** | **Habitat** | **Number of Observations** |
|---|---|---|---|
| *Camponotus piceus* | Crimea | Steppes | 25 |
| *Cataglyphis aenescens* | | | 25 |
| *Camponotus aethiops* | | | 10 |
| *Lasius paralienus* | | | 5 |
| *Plagiolepis tauricus* | | | 5 |
| *Tapinoma erraticum* | | | 5 |
| *Tetramorium caespitum* | | | 15 |
| *Formica cunicularia* | | Mountain meadows | 5 |
| *Myrmica specioides* | | | 23 |
| *Formica pratensis* | | | 7 |
| *Tapinoma erraticum* | | | 6 |
| *Formica cunicularia* | | Mountain steppes | 14 |
| *Lasius paralienus* | | | 15 |
| *Formica pratensis* | | | 5 |
| *Tapinoma erraticum* | | | 49 |
| *Tetramorium caespitum* | | | 12 |
| *Camponotus lateralis* | | oak-pistachio-juniper forests | 20 |
| *Temnothorax parvulus* | | | 138 |
| *Aphaenogaster subterranea* | | | 14 |
| *Crematogaster schmidti* | | | 17 |
| *Formica gagates* | | | 47 |
| *Plagiolepis tauricus* | | | 15 |
| *Formica cunicularia* | | Urban | 33 |
| *Lasius paralienus* | | | 37 |
| *Crematogaster subdentata* | | | 350 |
| *Messor muticus* | | | 26 |
| *Myrmica bergi* | | | 155 |
| *Myrmica specioides* | | | 36 |
| *Tapinoma erraticum* | | | 28 |
| *Tetramorium caespitum* | | | 93 |
| *Myrmica spp.* | Kyiv region | Natural (Deciduous forests) | 337 |
| *Leptothorax spp.* | | | 9 |
| *Camponotus fallax* | | | 64 |
| *Temnothorax spp.* | | | 418 |
| *Dolichoderus quadripunctatus* | | | 220 |

| | | | |
|---|---|---|---|
| *Formica polyctena* | | | 15 |
| *Formica rufa* | | | 65 |
| *Lasius brunneus* | | | 80 |
| *Lasius emarginatus* | | | 835 |
| *Lasius fuliginosus* | | | 90 |
| *Lasius platythorax* | | | 110 |
| *Formica cinerea* | | | 480 |
| *Lasius niger* | Kyiv city | Urban habitats | 810 |
| *Dolichoderus quadripunctatus* | | | 20 |

**Statistical Analysis**

Statistical calculations were performed using the Paleontological Statistics Software Package for Education and Data Analysis (PAST) software (version 4.03). The data were checked for normality of distribution; in case of non-observance of the normal distribution, methods of nonparametric analysis were used. Differences between groups (the number of individuals on the trails in 2 minutes of counting) were checked using the Kruskal-Wallis (KW) test for equal medians. In case of significant differences, the Mann-Whitney test (M-W, with a corrected Bonferroni p-value) was used. Average parameter values are shown as a histogram (performed in OriginPro 2021), box and jitter mode.

## RESULTS

**Density of Workers of Dominant and Submissive Ant Species in The Forage Areas**

For broadleaf forests of Kyiv region, there are significant differences between the average density of different ant species in the forage areas (Figure 2A; Table 3). The most numerous are workers of the genus *Lasius*: *L. fuliginosus, L. brunneus,* and *L. emarginatus*; their average number is 1.5 times higher than that of *F. rufa* and *F. polyctena* (Figure 2A; Table 3). Submissive species, *D. quadripunctatus*, *Myrmica* spp., *Temnothorax* spp., and *Leptothorax* spp. on average, 1.5-2.0 times less abundant than red wood ants (Figure 2A; Table 3). The minimum falls on *C. fallax* and *F. fusca* as their number is almost 2 times less than submissive species (Figure 2A; Table 3).

Three dominant ant species in forage areas in urbanized and suburban areas of Kyiv are *D. quadripunctatus, L. niger* and *F. cinerea* (Figure 2C). These species have different average densities (Table 3). The most abundant are *D. quadripunctatus* (territory of the supercolony). Species of *L. niger* is more abundant than *F. cinerea* (Table 3). Species of *D. quadripunctatus* in deciduous forests is one of the submissive species, but in urban territories under certain conditions it's become dominant species (in the gardens, where other dominant species of ants are absent).

In the steppe habitats of Crimea, ant species also show different density of workers (Table 3), the most numerous are two species - *C. aenescens* and *T. erraticum* (Figure 2B). *Cataglyphis aenescens*, inhabiting areas without grass cover. The dominant *C. aethiops* has the same number of workers on plots, as the submissive species *T. caespitum, L. paralienus* (Figure 2B). In the Crimean mountain steppes, the most abundant *L. paralienus,* which significantly exceeds the other submissive species, *T. erraticum*, in abundance (Figure 2D; Table 3). The abundance advantage of the dominant *F. pratensis* over the submissive species has not been established. In mountain meadows, there are significant differences in abundance (Figure 2E; Table 3): Dominant species *F. pratensis* is more numerous than *F. cunicularia* and *T. erraticum*. In another natural habitat of Crimea, oak-pistachio-juniper forests, ants of different species are approximately the same in abundance (Figure 2F; Table 3). The only exception is *C. lateralis*, it is less abundant than *F. gagates*. In urbanized and suburban habitats of Crimea, ant species differ in abundance (Figure 2G; Table 3). Two dominant species are the most abundant - the native species *M. bergi* (near the estuaries) and the invasive *C. subdentata*. The rest, subordinate species, are 2-5 times smaller in number (Table 3).

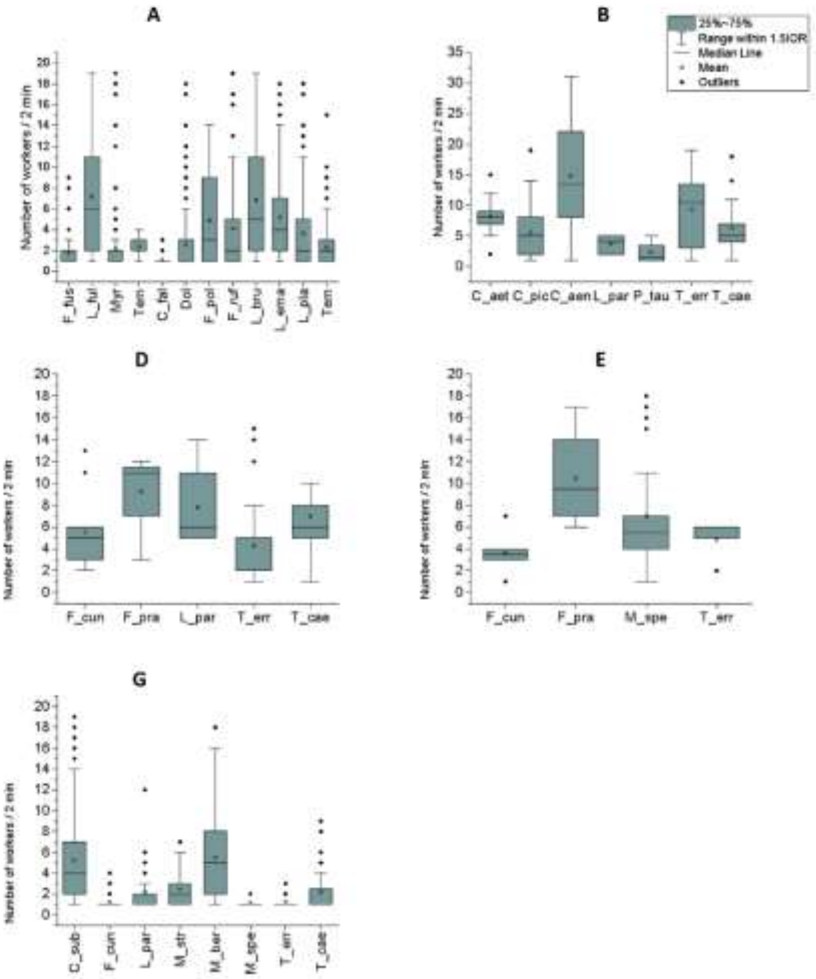


Figure 2. Average density of ants in the forage area. A - natural habitats of Kyiv and Kyiv region, deciduous forests; B - Crimea, steppe areas (natural habitats); C - Kyiv city, suburban and urbanized habitats; D - Crimea, mountain steppes, natural habitats, E - Crimea, mountain meadows, natural habitats; F - Crimea, oak-pistachio-juniper forests, natural habitats; G - Crimea, suburban and urbanized habitats

**Abbreviations;**

**Submissive species:** Tem – *Temnothorax* spp.; Lep – *Leptothorax* spp.; Myr – *Myrmica* spp.; F_fus – *Formica fusca* (Linnaeus 1758); T_cae – *Tetramorium caespitum* (Linnaeus 1758); T_err – *Tapinoma erraticum* (Latreille 1798); L_par – *Lasius paralienus* Seifert 1992; C_aen – *Cataglyphis aenescens* (Nylander 1849); C_pic – *Camponotus piceus* (Leach 1825); F_cun – *Formica cunicularia* (Latreille 1798); M_spe – *Myrmica specioides* (Bondroit 1918); A_sub – *Aphaenogaster subterranea* (Latreille 1798); T_par – *Temnothorax parvulus* (Schenck 1852); C_lat – *Camponotus lateralis* (Olivier 1792).

**Dominants:** L_pla – *Lasius platythorax* (Seifert 1991); Dol – *Dolichoderus quadripunctatus* (Linnaeus 1771); L_ful – *Lasius fuliginosus* (Latreille 1798); L_ema – *Lasius emarginatus* (Olivier, 1792); L_bru – *Lasius brunneus* (Latreille, 1798); F_ruf – *Formica rufa* (Linnaeus 1761); L_nig – *Lasius niger* (Linnaeus, 1758); F_cin – *Formica cinerea* (Mayr 1853); C_vag –

*Camponotus vagus* (Scopoli 1763); C_aet – *Camponotus aethiops* (Latreille 1798); F_tru – *Formica truncorum* (Fabricius 1804); F_pol – *Formica polyctena* (Foerster 1850); L_neg – *Lasius neglectus* Van Loon, Boomsma & Andrasfalvy 1990; F_pra – *Formica pratensis* (Retzius 1783); P_tau – *Plagiolepis tauricus* (Santschi 1920); F_gag – *Formica gagates* (Latreille 1798); C_sch – *Crematogaster schmidti* (Mayr 1853); C_sub – *Crematogaster subdentata* Mayr, 1877; M_ber – *Myrmica bergi* (Ruzsky 1902); P_pal – *Plagiolepis pallescens* (Forel 1889).
**Out-of-hierarchy species:** M_str – *Messor muticus* (Nylander 1849).

Table 3. Results of statistical tests on density in the plots of ants of different species in one habitat

| Region | Habitat | Type of Habitat | K-W Test for all Ant Species in One Habitat | Pair of Compared Ant Species (Higher Density Vs. Lower) | M-W Test |
|---|---|---|---|---|---|
| Kyiv region | Deciduous forests | Natural | ≤0.001 | *L. fuliginosus* vs *F. rufa* | 0.006221 |
| | | | | *L. brunneus* vs *F. rufa* | 0.03173 |
| | | | | *F. rufa* vs *Myrmica* spp. | ≤0.001 |
| | | | | *F. rufa* vs *D. quadripunctatus* | 0.01211 |
| | | | | *D. quadripunctatus* vs *C. fallax* | ≤0.001 |
| | | | | *Leptothorax* spp. vs *F. fusca* | 0.01737 |
| Kyiv city | Tree alleys along streets and highways, city squares | Urban | ≤0.001 | *D. quadripunctatus* vs *F. cinerea* | ≤0.001 |
| | | | | *D. quadripunctatus* vs *L. niger* | 0.01738 |
| | | | | *L. niger* vs *F. cinerea* | ≤0.001 |
| Crimea | Steppes | Natural | ≤0.001 | *C. aenescens* vs *C. piceus* | 0.002413 |
| | mountain steppes | | ≤0.001 | *L. paralienus* vs *T. erraticum* | 0.002799 |
| | mountain meadows | | 0.02651 | *F. pratensis* vs *F. cunicularia* | 0.01 |
| | | | | *F. pratensis* vs *T. erraticum* | 0.01 |
| | oak-pistachio-juniper forests | | 0.08961 | *F. gagates* vs *C. lateralis* | 0.03777 |
| | Tree alleys along streets and highways, city squares, gardens near estuaries | Urban | ≤0.001 | *C. subdentata* vs *F. cunicularia* | ≤0.001 |
| | | | | *C. subdentata* vs *T. caespitum* | ≤0.001 |
| | | | | *C. subdentata* vs *T. erraticum* | ≤0.001 |
| | | | | *M. bergi* vs *F. cunicularia* | ≤0.001 |
| | | | | *M. bergi* vs *T. caespitum* | ≤0.001 |
| | | | | *M. bergi* vs *T. erraticum* | ≤0.001 |

**Worker Activity on Trails**

In the deciduous forests of the Kyiv region, ant species have different forage trails by level of activity (Figure 3A; Table 4). The highest activity on the trails were *F. rufa*, *L. fuliginosus*, *L. emarginatus*, *L. brunneus*, and *F. polyctena* (Table 4). Minimum trail activity was recorded by *L. platythorax*. In the coniferous forests of the Kyiv region, there are also differences in activity between different species of ants (Figure 3B; Table 4): the highest activity on the trails was shown by *F. cinerea* in the surveyed, the Crimean steppe habitats have only one species, *C. aethiops* that forms the permanent trails; however, the *Messor* ants is much more active on temporary (vector) trails (Figure 3D).

In three dominant species (*C. schmidti*, *P. tauricus*, and *F. gagates*) in the oak-pistachio-juniper forests of the Crimea, the activity on the trails is approximately the same (Figure 3F). In suburban habitats of the Kyiv region, the activity on the trails of dominant species differs (Figure 3B; Table 4). The highest activity was noted in *L. fuliginosus*, the lowest activity on trails was observed in *C. vagus* and *L. niger*. In the urban habitats of Kyiv city, different activity of species on the trails was noted (Figure 3C; Table 4). The most active on trails are *D. quadripunctatus*, *L. neglectus*, and *F. cinerea* compared with other ant species (Table 4). In urban habitats of Crimea, two invasive species dominate, differing in activity on the trails (Figure 3G), and *C. subdentata* has a higher activity compared to *L. neglectus* (Table 4).

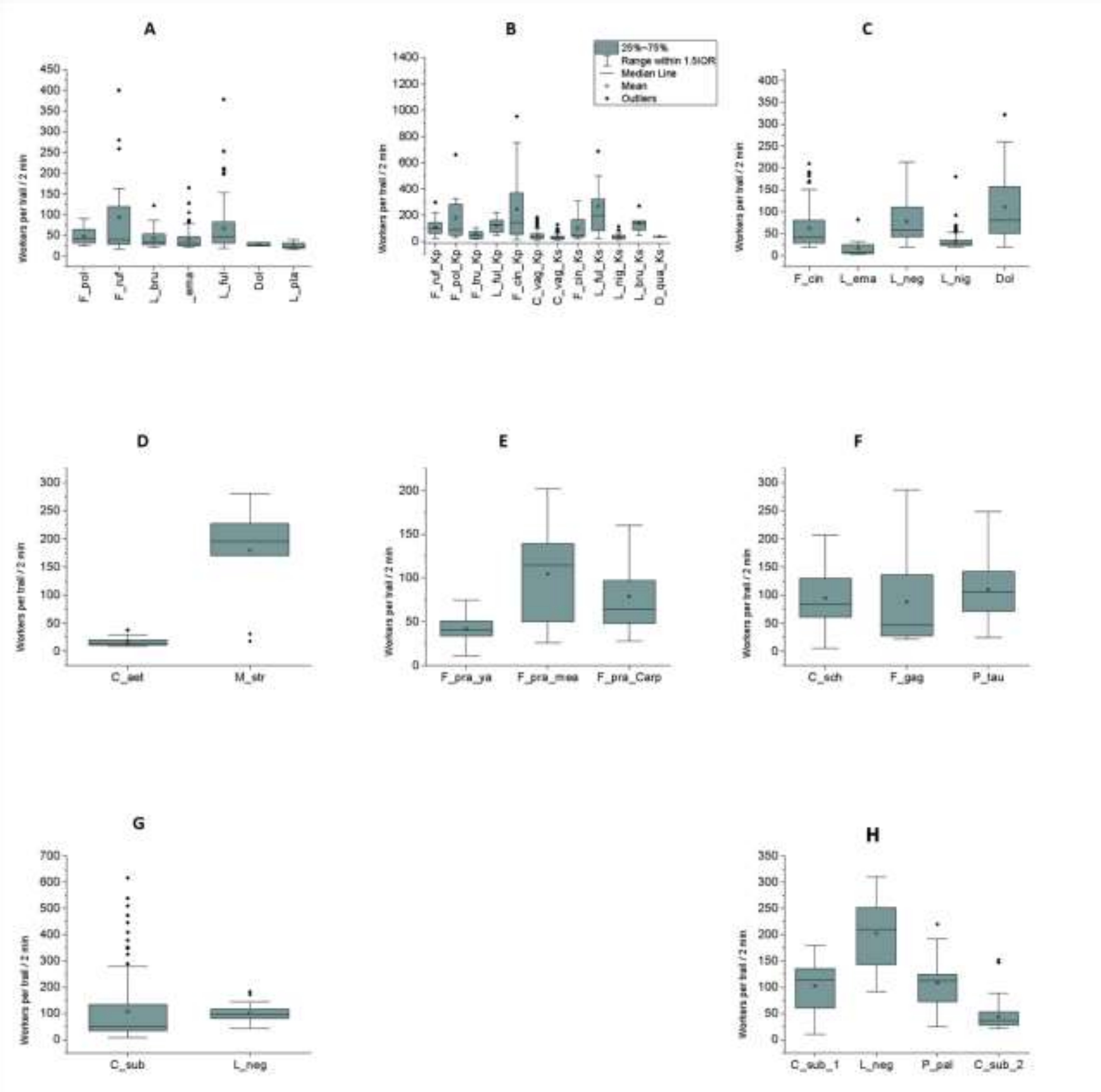


Figure 3. Average activity of ants on the trails (n / 2 min). A - Kyiv and Kyiv region, deciduous forests, natural habitats; B - Kyiv and Kyiv region, coniferous forests (Kp), natural habitats and suburban habitats (Ks); C - Kyiv, urbanized habitats; D - Crimea, steppe, natural habitats; E - natural habitats in Crimea (C1 - mountain steppes, C2 - mountain meadows) and in the Carpathians (Carp, mountain meadows); F - Crimea, oak-pistachio-juniper forests, natural habitats; G - Crimea, urban habitats; H - Uzbekistan, natural (tugai forests, C_sub_2) and urban (Tashkent city, everything else) habitats.

**Abbreviations:** L_pla - *Lasius platythorax*; Dol - *Dolichoderus quadripunctatus*; L_ful - *Lasius fuliginosus*; L_ema - *Lasius emarginatus*; L_bru - *Lasius brunneus*; F_ruf - *Formica rufa*; L_nig - *Lasius niger*; F_cin - *Formica cinerea*; C_vag - *Camponotus vagus*; F_tru – *Formica truncorum*; F_pol - *Formica polyctena*; L_neg - *Lasius neglectus*; M_str - *Messor muticus*; C_aet - *Camponotus aethiops*; F_pra - *Formica pratensis*; P_tau - *Plagiolepis tauricus*; F_gag - *Formica gagates*; C_sch - *Crematogaster schmidti*; C_sub - *Crematogaster subdentata*; P_pal - *Plagiolepis pallescens*.

Table 4. Results of statistical tests on the activity of ants of different species on the trails in one habitat

| Region | Habitat | Type of Habitat | K-W test For All Ant Species in One Habitat | Pair of Compared Ant Species (Higher Density vs. Lower) | M-W test |
|---|---|---|---|---|---|
| Kyiv region | Deciduous forests | Natural | ≤0.001 | *L. fuliginosus* vs *L. emarginatus* | ≤0.001 |
| | | | | *L. fuliginosus* vs *L. brunneus* | 0.01645 |
| | | | | *F. rufa* vs *L. emarginatus* | 0.03746 |
| | | | | *F. rufa* vs *L. platythorax* | 0.03511 |
| | | | | *L. fuliginosus* vs *L. platythorax* | ≤0.001 |
| | | | | *L. emarginatus* vs *L. platythorax* | 0.02523 |
| | Coniferous forests | | ≤0.001 | *F. cinerea* vs *C. vagus* | ≤0.001 |
| | | | | *F. polyctena* vs *C vagus* | 0.001005 |
| | | | | *L. fuliginosus* vs *C. vagus* | 0.006981 |
| | Alleys of trees along roads | Suburban | ≤0.001 | *L. fuliginosus* vs *F. cinerea* | 0.02975 |
| | | | | *L. fuliginosus* vs *C. vagus* | ≤0.001 |
| | | | | *F. cinerea* vs *C. vagus* | 0.0007833 |
| | | | | *L. fuliginosus* vs *L. niger* | ≤0.001 |
| Kyiv city | Tree alleys along streets and highways, city squares | Urban | ≤0.001 | *D. quadripunctatus* vs *F. cinerea* | 0.002891 |
| | | | | *D. quadripunctatus* vs *L. emarginatus* | ≤0.001 |
| | | | | *D. quadripunctatus* vs *L. niger* | ≤0.001 |
| | | | | *L. neglectus* vs *L. niger* | ≤0.001 |
| | | | | *L. neglectus* vs *L. emarginatus* | ≤0.001 |
| | | | | *F. cinerea* vs *L. emarginatus* | ≤0.001 |
| | | | | *F. cinerea* vs *L. niger* | ≤0.001 |
| Crimea | Steppes oak-pistachio-juniper forests | Natural | ≤0.001- 0.03534 | *M. muticus* vs *C. aethiops* | ≤0.001 |
| | | | | differences between species are not significant- | -≥0.05 |
| | Tree alleys along streets and highways, city squares, gardens near estuaries | Urban | ≤0.001 | *C. subdentata* vs *L. neglectus* | ≤0.001 |
| Tashkent | Tree alleys along streets and highways, city squares | Urban | ≤0.001 | *L. neglectus* vs *C. subdentata* | ≤0.001 |
| | | | | *L. neglectus* vs *P. pallescens* | ≤0.001 |

When comparing the activity on the trails of the dominant species inhabiting different habitats of Kyiv and the region, significant differences were obtained (Table 5). Thus, for *F. cinerea*, the most favorable habitat is coniferous forests, followed by suburban and urban habitats. *L. emarginatus* is more abundant in deciduous forests than in urbanized areas. *Lasius fuliginosus*, on the other hand, is more abundant in suburban habitats than in natural habitats. *Dolichoderus quadripunctatus* has the highest activity on the trails in urban habitats. Finally, *L. niger* is equally represented in suburban and urban habitats.

For the habitats of Uzbekistan, different activity of ants on the trails was also recorded (Table 5; Figure 3H). In tugai forests of Uzbekistan, the activity of *C. subdentata* was less than in urbanized habitats of Tashkent. (Table 5). In the mountainous habitats of the Crimea and in the Carpathians, dominant species *F. pratensis* demonstrate the different activity on trails. In mountain meadows of the Crimea, there is more activity of workers on the trails compared to Crimean mountain steppes and Carpathian mountain meadows (Figure 3E; Table 6). In different habitats, invasive species *L. neglectus* and *C. subdentata* demonstrate similar trends. *Crematogaster subdentata* has different trail activity: In urban territories of Crimea the activity is maximum, and less in the Tashkent city and in natural habitats (tugai forests) (Table 6). Thus, *C. subdentata* is characterized by the maximum activity on the trails in urban habitats, both in the primary and in the secondary ranges. The activity of *L. neglectus* also differs in different habitats (Table 6). The highest activity of the *L. neglectus* in urbanized habitats is in Tashkent city, 2 times less in Crimea, 3 times - in Kyiv city (Table 6).

Table 5. Results of statistical tests for activity on trails of ant species in different types of habitats in each geographical location

| Region | Species | Comparable Habitat Types (Higher Trail Activity vs Less) | M-W Test |
|---|---|---|---|
| Kyiv city and Kyiv region | *Formica cinerea* | Natural vs urban | 0.006082 |
| | *L. emarginatus* | Natural vs urban | ≤0.001 |
| | *L. fuliginosus* | Suburban vs natural | ≤0.001 |
| | *D. quadripunctatus* | Urban vs natural | 0.02197 |
| | *L. niger* | Urban vs suburban | 0.1776 |
| Crimea | *F. pratensis* | Natural (mountain meadows) vs natural (mountain steppes) | ≤0.001 |
| Tashkent city and Tashkent region | *C. subdentata* | Urban vs natural | ≤0.001 |

Table 6. Results of statistical tests for trail activity of ant species in each type of habitat in different geographic locations

| Species | Region (More Traffic Activity vs Less) | M-W Test |
|---|---|---|
| *Formica pratensis* | Carpathians vs Crimea (mountain steppes) | ≤0.001 |
| *Lasius neglectus* | Tashkent vs Crimea | ≤0.001 |
| | Tashkent vs Kyiv | ≤0.001 |

## DISCUSSION

For some species of ants with large colonies, trails exist for a short time (several hours or a day) and are associated with the mass mobilization of foragers. These species include nomadic ants (Franks 1989), *Carebara diversa* (Jerdon 1851) (Moffett 1988), and according to some reports, the pharaoh ant *Monomorium pharaonis* (Linnaeus 1758) (Jeanson et al. 2003).

Several other species, such as red wood ants (Rosengren & Sundström 1987), leaf cutter ants (Vasconcellos 1990), and *Messor* ants (Azcarate & Peco 2003; Dlussky 1981) have permanent trails that cleared of debris. Such trails remain constant for many years, as they lead to the same resources - forage trees with aphids' colonies or areas with cereals (in the case of *Messor* ants). This is known both for the *Formica rufa* and for other dominants species of the forests of the temperate zone of Eurasia, for example, *L. fuliginosus* (Quinet & Pasteels 1987). In the end of the forage trail is situated a forage tree, as was shown on example of *F. aquilonia* (Yarrow 1955) (Buhl et al. 2009). In some cases, if the trail is a hunting trail, then its end is the foraging zone (Zakharov 2015). Also, among the permanent forage trails, there are express trails (usually in the form of grooves buried in the ground), in which there are always a large number of foragers ready to mobilize from here to a site with a trophic resource. Such trails are typical for *F. pratensis*, *F. cinerea*, *Messor intermedius*; tunnels in *L. fuliginosus* perform similar functions. Dominant species are able to quickly seize the forage resource in any part of their forage territory. Submissive species are characterized by the absence of permanent trails; they can form only temporary trails with foragers mobilized to the source of resources. This was found for the species *Tapinoma*, *Tetramorium*, *Lasius* (Zakharov 2015).

According to Zakharov (1991), it is the high dynamic density of ants in the territory that leads to a number of significant rearrangements in the organization of the territory and in the behavior of ants. With a high density of individuals, the number of their contacts on the territory first of all increases (Zakharov 1991; 2015). This leads to the formation of trails. Trails is to direct to movement by foragers from places with high density near the nest to territories of forage area with lower density of workers.

In our work, it is shown that both in natural (mountain steppes, Crimean meadows, broad-leaved forests of the Kyiv region) and in urbanized territories (Crimea, Kyiv), submissive species can create a high density of foragers in the territory. The forage areas of submissive ant species are small, usually up to 15 $m^2$ (Stukalyuk & Radchenko 2011), and the creation of a high density of foragers in a small area can be effective in the development of a trophic resource. On the other hand, on the forage areas of dominants ranging in size from 100 $m^2$ to several hectares (per anthill taken separately), efficient distribution of foragers is possible only if there are permanent trails that distribute their flows. It is noteworthy that the density of foragers of dominant species in urbanized habitats significantly exceeds that of submissive species. Perhaps this is due to the large size of dominant colonies and limited resources. The maximum recorded case of high dynamic density is known for the invasive ant species *Anoplolepis gracilipes* (Smith 1857), in Christmas Island, 948-2254 ants / 1 $m^2$ (Abbott 2005).

When a nest of red wood ants is artificially relocated to another habitat, the same number of trails is preserved (Zakharov 1991). It follows from this that permanent trails are a very important element of the structure of the forage area. The nest is the center of the intersection of the trails. For invasive species, for example, *Linepithema humile* (Mayr 1868) (Heller & Gordon 2006) and *C. subdentata* (Stukalyuk & Netsvetov 2018; Stukalyuk et al. 2021b, 2021c), the forage area is a network of trails and nests.

The activity on the trails for different species of dominants can vary greatly. The largest number of workers per unit of time on the trails was noted by us for red wood ants, *L. fuliginosus*, *F. cinerea*, and *D. quadripunctatus*, as well as for invasive species *C. subdentata*, and *L. neglectus* (in the primary and secondary ranges). The maximum ant activity on the trails among all habitats was found in cities - Kyiv (*L. neglectus*, *D. quadripunctatus*, and *F. cinerea*), Tashkent (*L. neglectus*), and in urbanized territories of Crimea (*C. subdentata*, and *L. neglectus*).

One of the reasons for the successful development of new habitats by invasive ant species (including urbanized territories) is their abundance and longer foraging during the day (Human & Gordon 1996). But not necessarily the maximum activity in the studied habitats was only in invasive species. Under certain conditions, in urbanized landscapes have very busy trails from native species, which can occupy a submissive position in the hierarchy of ants in natural areas (*D. quadripunctatus*) (Stukalyuk 2018). Habitat type in urban conditions plays a very important role - for example, *L. niger* and *Myrmica rubra* (Linnaeus 1758) are most abundant in botanical gardens in Warsaw, while *T. caespitum* is more abundant in urban woodlands (Trigos-Peral et al. 2020). *L. niger* is also the dominant species in Kyiv, occurring in most habitats (Radchenko et al. 2019). According to our data, *L. niger* had permanent trails in suburban and urbanized landscapes, i.e., these conditions were most favourable for this species. In general, the presence of only *L. niger* and the absence of dominants species are the signs of degradation of multispecies ant assemblages (Ihnatiuk & Stukalyuk 2015). Therefore, not all species of ants can successfully exist in urban conditions. Most often this is due to the presence of suitable tree species and colonies of myrmecophilous aphids on the urbanized territories (Stukalyuk et al. 2020a). Botanical gardens (Trigos-Peral et al. 2020) and urban forests (Radchenko et al. 2019) turned out to be the most optimal for ants in the conditions of Warsaw and Kyiv.

Our data on trail activity (Figure 5) are consistent with those already known. For *Liometopum microcephalum* in the Lower Dnieper region, Ukraine, trail activity ranges from 50 to 100 workers per minute (Makarevich 2003). For the forest zone of Russia, Mershchiev (2010) found that *F. polyctena* is the most active among the red wood ants (the maximum value is 250 workers per minute, the average is 180 workers); *F. rufa* (max 180 per minute, average 90), *F. aquilonia* (max 85 per minute, average 73), *F. lugubris* (Zetterstedt 1838) (max 65 per minute, average 30), minimal - in *F. truncorum* (max 45 per minute, average 15). Among other ant species, only *L. fuliginosus* can be compared with red wood ants (max 140 workers per minute, average 52). Apparently, the value of activity on the trails has a direct relationship with the length of the trail - in *F. polyctena*, the trails are on average longer (24 m) than in other species (15-19 m), except for *F. aquilonia* (36 m). These two species have an average of 37-38 trees per colony, while the rest have only 6 to 23 (Mershchiev 2010). For comparison, some forage trails in *Atta* ants can be up to 200 m long (Lewis et al. 1974); the longest trails in the temperate zone were recorded in large nests of red wood ants - up to 150 m (Zakharov 1991).

Our data by activity on trails of native species *F. cinerea*, *D. quadripunctatus* (100-170 workers per 1 minute, Figure 5), *L. fuliginosus* (80-150 per 1 minute) and *F. rufa*, *F. polyctena* (30-150 per minute in Kyiv region) are comparable with data of other researchers (Mershchiev, 2010). Movement of workers of *C. subdentata* on such trails is formed not by one nest, but by many nests that are part of the supercolony. Other ant species in natural and urbanized habitats (*L. niger*, *L. emarginatus*, *L. brunneus*, *C. vagus*, and *F. truncorum*) have less activity - from 30 to 100 ants per minute.

Consequently, urban conditions can provide opportunities for both natural and invasive species to form supercolonies, whose population exceeds that even in supercolonies of red wood ants. It should be noted that the values of the activity of ants on the trails indicated by us are not the limit; in leaf-cutting ants *Atta colombica* Guérin-Méneville, 1844, activity on the trails can reach 2300 ants per minute (Dussutour et al. 2009), *L. humile* - from 200 to 800 individuals per minute (Rust et al. 2000). Other species of tropical ants have activity comparable to the ants of forest habitats studied by us (*Oecophylla smaragdina* (Fabricius 1775), 200-280 individuals per minute (Peng et al. 2012), *Anoplolepis gracilipes*, 160-220 ants per minute (Abbott & Green 2007); up to 250 in *Atta cephalotes* (Linnaeus 1758) (Lewis et al. 1974); in *Messor intermedius*, from 100 to 200 workers can pass along the trail in 1 minute in one direction (Dlussky 1981) or lower activity (*Solenopsis geminata* Fabricius 1804), 40-70 per minute (Perfecto 1994); *Acromyrmex lobicornis* (Emery 1888), 20-90 per minute, (Elizalde & Farji-Brener 2012); 60-400 *Dinomyrmex gigas* (Latreille 1802) workers per 5-20 min (Orr & Charles 1994).

According to the literature data, high activity can also be on temporary trails, for example, in *Messor barbarus* (Linnaeus 1767), 20-50 per minute (Detrain et al. 2000); *Pogonomyrmex barbatus* (Smith 1858), 40-100 per minute (Gordon 2002); *Pheidole pallidula* (Nylander 1849), 25-85 per 5 minutes (Detrain 1990). We obtained similar results for *M. muticus* in Crimea. *Carebara diversa* may have the highest activity on temporary trails (250-750 per minute, Moffett 1988).

Based on the literature and data obtained by us, it can be assumed that the activity of ants on the trails in the temperate climatic zone most often fits into values from 30 to 150 workers per minute. In exceptional cases, when supercolonies are formed by ants (in native and invasive species, most often in urbanized habitats), activity indicators can increase to 200-700 workers per minute. For some tropical ant species, activity indicators can reach 800 - 2300 individuals per minute. The intensity of the movement of ants on the trails has a direct relationship with the size of the ant colony.

## CONCLUSION

The high density of workers in the forage area is characteristic of submissive ant species, in which forage area is small. In large forage areas, efficient functioning of the infrastructure requires forage trails to distribute forage flows. For dominant ant species, the density of workers in the forage area is on average higher than that of subordinate species. Urbanized habitats are favorable for some species of ants, which have the highest rates of activity on the trails here. These are invasive species (*C. subdentata*, *L. neglectus*), as well as some native ones (*D. quadripunctatus*), whose activity indicators are in the range of 200-800 workers per 2 minutes, which is equal to or significantly exceeds the same parameters for ants in natural habitats (100 - 400 workers in 2 minutes). In the primary geographical range, activity indicators on trails in native species *C. subdentata* and *L. neglectus* are equal or lower than those in the secondary range. The presence of permanent foraging trails indicates the dominant status of the ant species. The amount of traffic on the trails can vary greatly in different habitats.

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## CONFLICT OF INTEREST

The authors declare no conflict of interest.

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