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Effect of urban habitats on colony size of ants (Hymenoptera, Formicidae) In memory of Professor A. A. Zakharov (Russian Academy of Sciences, Moscow)

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Abstract: Urbanized ecosystems are suitable for the habitat of only a few species of ants, due to conditions caused by human activities. Invasive species of ants have adapted to urbanized ecosystems most successfully. The study of the ant colonies sizes started in Crimea in 2013–2014. In 2019–2021 it was carried out in Ukraine (the Carpathians, Kyiv city, and Kyiv region), in Russia (Rostov-on-Don city and region, and the Urals), and in Uzbekistan (Tashkent city, and tugai forests). The study covers natural (forest, meadow, steppe), suburban (alleys and tree planting) and urban habitats (tree planting along streets and roads, botanical gardens). Our study covers 21 species of ants with trails on forage areas. Nine species were sampled for interspecific comparison of colony sizes. They were collected in at least 2 habitat types within the same geographic region. According to the activity parameter on the trails, the number of foragers and the population of the colony were calculated (using the formula of A. Zakharov). According to our calculations, the maximum colony sizes are typical for invasive species (*Crematogaster subdentata, Lasius neglectus,* 100–7500 thousand workers) in the urban habitats. Some native species (*Dolichoderus quadripunctatus, Formica cinerea*) in the urban areas have colonies with 120–350 thousand workers. These values may exceed those for ant species inhabiting natural habitats (30–250 thousand workers). High rates of colony size in the urbanized habitats can be achieved due to availability of food, nesting resources, and the absence of competing ant species.

Key words: Colony size, urban ecology, invasive species, native species, *Crematogaster subdentata, Lasius neglectus, Dolichoderus quadripunctatus, Formica cinerea*

1. Introduction

Ant colonies are of various sizes, and, therefore, the infrastructure of the forage area is different in complexity. Some submissive ant species usually have a protected area only near the nest entrance; subdominant species can protect prey and forage trees, while in dominant ants, the entire forage area is protected (Savolainen and Vepsäläinen, 1989). The size of forage areas in dominant species, for example, red wood ants, can reach several hectares per one large anthill (Zakharov, 2015). The rest of the dominant ant forest species in the temperate zone of Europe (*Lasius fuliginosus* (Latreille, 1798), *Lasius emarginatus* (Olivier, 1792), *Formica cinerea* Mayr, 1853, *Liometopum microcephalum* (Panzer, 1798)) have smaller forage areas up to tens and hundreds of square meters (Zakharov, 2015; Radchenko, 2016; Stukalyuk and Radchenko, 2011; Stukalyuk, 2017). Sophisticated infrastructure helps distribute foragers throughout the entire forage area. Trails, an infrastructure element, are not jammed directly next to the nest as foragers quickly move to the periphery. Trails usually lead to forage trees where the ants hunt or visit aphid colonies. The renewal of trails to the same trees occurs every year after wintering, so the direction of the trails may remain constant over many years, as it was shown by the example of *Formica rufa* Linnaeus, 1761 (Zakharov, 1991). Foragers usually travel on each trail in two opposite directions, but there may be unidirectional trails, e.g., in L. *microcephalum* (Zakharov, 2015).

Foragers form permanent groups of worker ants, which tie to specific trails (Zakharov, 1991). Foragers share in a general population is quite constant and is within 13%

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(12.98%) in red wood ants (Zakharov, 2015) and 15% each in *L. fuliginosus* (Hennaut-Riche et al., 1980), *Lasius alienus* (Foerster, 1850) (Nielsen, 1974) that allows of calculation of the total population of a colony, for example, using a formula developed by A. Zakharov (Zakharov, 1978, 2015).

The population of nests of various species of ants can differ by 2–3 order of magnitude. For example, in ants of the genus *Temnothorax* Mayr, 1861, these are hundreds of individuals; the entire nest can be located in a separate acorn, under the bark of a tree, or in a stone's crack (Czechowski et al., 2012). On the other hand, populations of red wood ants can live in huge nests 3–4 m in diameter and up to 1.8 m in height (Seifert, 2018; Stukalyuk et al., 2021a). The population of a single anthill can reach 15 million individuals. At the same time, it is very difficult and time-consuming to calculate the exact population of an anthill; for this, the method of complete removal of all workers, alates, and in some cases, brood is usually used (Zakharov, 2015). A method of complete excavation of the nest developed by Dlussky (1965; 2009) is appliable mainly for ant species with a small population and a passage depth of up to 1 m. Therefore, the given population data for individual ant species are rather approximate, the authors usually report the order of magnitude, i.e. hundreds, thousands, etc. (Czechowski et al., 2012; Radchenko, 2016).

In ant ecology, the colony size is an important issue, since in the same species it varies across habitats. Thus, invasive ant species *Linepithema humile* (Mayr, 1868), *Lasius neglectus* Van Loon, Boomsma & Andrasfalvy, 1990, *Solenopsis invicta* Buren, 1972 have small colonies in the primary range and can form supercolonies in the secondary range having territory covered tens of hectares (McGlynn 1999; Holway et al. 2002). An exception is *Crematogaster subdentata* Mayr, 1877, which is able to form supercolonies in the primary range, although in cities only (Stukalyuk et al., 2021b, c). On the other hand, the fact that both invasive and aboriginal species can create supercolonies in urban habitats (Stukalyuk, 2018) imply that urban landscapes give an advantage of ants' species able to develop this social structure unusual for them in natural conditions. To test this hypothesize here we studied ants' activity on the trails to calculate the entire populations size and compare results in natural and urban habitats.

2. Materials and methods

2.1. Research region

As ants' activity on the trails reaches its maximum in July and August (Mabelis, 1979; Mershchiev, 2010) our study was performed in July–August 2013 on the Crimean Peninsula (Ukraine) and in July–August 2020–2021 in other locations in Kyiv's region and Carpathian Mountains in Ukraine, Tashkent city and tugai forests in Uzbekistan, Ural region and Rostov-on-Don city in Russian Federation (Figure 1). Studied sites were situated in natural, suburban (rural), and urban habitats (Table 1). In the Carpathian Mountains and Crimean Mountains data were obtained at the altitudes of 500 m and 700–900 m above sea level respectively.

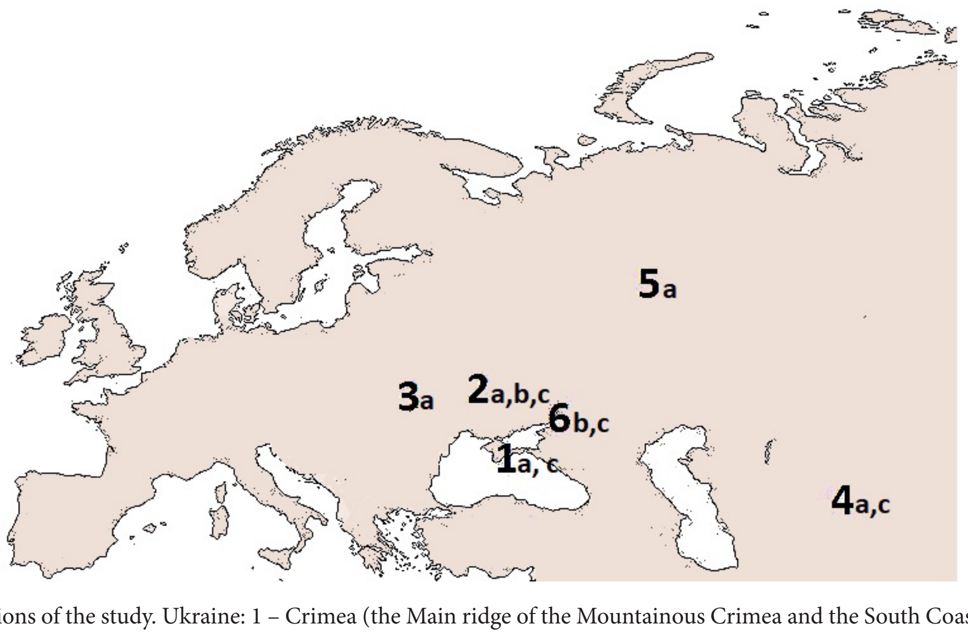

Figure 1. D Locations of the study. Ukraine: 1 – Crimea (the Main ridge of the Mountainous Crimea and the South Coast, Saki region), 2 – Kyiv and Kyiv region, 3 – Carpathians; Uzbekistan: 4 – Tashkent city, tugai forests; Russian Federation: 5 – Ural, 6 – Rostov-on-Don city and region. Habitats. a – natural, b – suburban, c – urban.

Table 1. Study regions, habitats and tree species.

Regions	Type of habitat	Habitat	Tree species
Kyiv and Kyiv region	Natural	Deciduous forests	*Quercus robur, Acer platanoides, Carpinus betulus**
		Coniferous forests	*Pinus sylvestris**
	Suburban	Single-species tree planting along roads in rural areas	*Salix fragilis, Populus nigra**
	Urban	Tree alleys along streets and highways, city squares	*Robinia pseudoacacia, A. platanoides, Tilia cordata, P. nigra**
Crimea	Natural	Mountain steppes and meadows (altitude of 700-900 m above sea level)	*Festuca pratensis (in steppes), Alchemilla taurica (in meadows)***
		Oak-pistachio-juniper forests	*Pistacia mutica, Quercus pubescens, Juniperus excelsa***
		Steppes in the flat areas	*Elytrigia nodosa***
	Urban	Territories of gardens and private houses	*Prunus armeniaca, Morus nigra, Malus domestica, Prunus domestica***
Carpathian Mountains	Natural	Mountain meadows (altitude of 500 m above sea level)	*Agrostis capillaris, Alopecurus pratensis*
Uzbekistan and Tashkent city	Natural	tugai forests	*Salix sp.****
	Urban	Tree alleys along streets and highways, city squares	*M. domestica, P. nigra, Cydonia oblonga, P. domestica****
Rostov-on-Don city and region	Suburban	Single-species tree planting along roads in rural areas	*Q. robur, A. platanoides, R. pseudoacacia****
	Urban	Tree alleys along streets and highways, city squares	*Ailanthus altissima, P. nigra, Acer sp.****
Urals	Natural	Taiga	*Picea obovata, Abies sibirica, Larix sibirica, Betula pendula*****

2.2. Study design

The study consists of three related parts. In the first part, the average activity of different ant species was determined on the trails. Our study covers 21 species of ants with trails on forage areas and partially or completely protected forage area (Table 2). The second part of the study is the calculation of the average population of the colony (according to A. Zakharov 1978, 2015). This method works well for ant species with protected forage areas and permanent trails. A limitation of the method is the presence in the considered colony of foraging tunnels, or those leading a secretive lifestyle (geobiont species). In addition, this method is not appliable to submissive ant species that do not have a protected forage area, since up to 40%–50% of the population can participate in foraging. An accurate assessment requires exposure to similar weather and time conditions (Zakharov, 2015). The final stage of our study was a comparison of the ant colonies population between natural, suburban and urbanized areas. For interspecific comparison of colony sizes were sampled 9 species, which were collected in at least 2 habitat types within the same geographic region.

Table 2. Number of measurements of activity on the trails in ants.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Formica cinerea							33	20	86						
Lasius neglectus					42				22			65		37	35
Lasius niger								18	210						
Camponotus vagus							130	141							
Dolichoderus quadripunctatus						3		2	50						
Formica polyctena						11	14						18		
Formica aquilonia													33		
Formica rufa						19	51						25		
Formica truncorum							6								
Lasius brunneus						31		6							
Lasius emarginatus						115			17						
Lasius fuliginosus						145	8	23							
Lasius platythorax						15									
Camponotus aethiops				35											
Messor structor				11											
Crematogaster schmidti			290												
Formica gagates			15												
Plagiolepis tauricus			45												
Formica pratensis	101	18								24					
Crematogaster subdentata					111						70	221			52
Plagiolepis pallescens												36			

2.3. Field research methods

To evaluate the population of nests Zakharov's framework (1978) was used, that includes series of 5-min long counts of ants' activity on trails, from which 10 trails were selected with traffic intensity from 14 to 140 workers per minute in one direction. The results of 5-min tests were recalculated by 1-min. Foragers were selected throughout the day of observation until their flow ceased. After that, their number was determined by the weight method.

In clear and cloudless days' ant activity was measured on the trails in the morning between 9:00 and 11:00, i.e. at the morning peak of ants' activity (Dlussky, 1967; Mershchiev, 2010; Peng et al., 2012; Zakharov, 2015). The air temperature was 20–25 °C that corresponds to optimal regime for the activity of ants in the temperate climatic zone (Dlussky, 1967). Ants moving in one direction along the forage trail (from the nest) was registered. The time of each accounting was 2 min; the number of ants per 1 min was calculated as an arithmetic mean. If the traffic was too lively and the number of ants cannot be counted, video filming was carried out. For ant species that can have part of the trails in the form of tunnels (*L. fuliginosus, Lasius niger* (Linnaeus, 1758)) their absence for each of the colonies was controlled, which were necessary for accurate calculation of activity on trails. For red wood ants, either anthills with one trail were chosen or if the anthill was large, the counts were carried out on all trails of one nest. The sum of the foragers of all trails was used for further calculations of anthills populations. If anthills had shared trails, the calculation of the population of an individual anthill was performed under absence of significant exchange between them (Zakharov, 2015). We considered the trail to be purposeful movement of ants in both directions, with an intensity of at least 10 individuals per 1 min.

2.4. Calculations

Formula 1.1 (Zakharov, 1978, 2015) gives the number of foragers in the colony:

$A = 36.82 - 2.127\, I + 0.112\, I^2 - 0.00047\, I^3$ (1.1),

where A is the number of foragers (in hundreds of individuals); I is the number of foragers who walked the trail in one direction during 1 min of count.

Formula 1.2 (Zakharov, 1978, 2015) was used to calculate the total number of workers N in a colony:

$N = 7.7A$ (1.2).

For the calculation, five 5-min long counts are sufficient, the calculation error is within 5%. The exact average number of foragers corresponded to the figure of 12.98% (13%) (Zakharov, 1978, 2015). These formulas have been used previously to calculate populations in mixed ant colonies (Stukalyuk et al., 2021d).

Formula 1.1 work is appropriate in the range of 10–140 foragers per minute due to the cubic degree of the polynomial adopted for the approximation of the experimental data. For traffic intensities over 140 foragers per minute, this expression was used (Figure 2, Equation 1.3):

$A = -0.0025\ I^2 + 1.4394\ I + 479.37$ (1.3).

The reliability of the approximation of the experimental data by the polynomial dependence is R = 0.9907.

2.5. Statistical analysis

Statistical calculations were performed using the Past v. 4.03. The data were checked for normality of distribution; in case of nonobservance of the normal distribution, methods of nonparametric analysis were used. Differences between groups (the number of workers in the nest) were checked using the Kruskal–Wallis (K-W) test for equal medians. In case of significant differences, the Mann–Whitney test (M-W) was used.

3. Results

3.1. Interspecific comparison of colony sizes within the same regions (for 21 species)

Colonies of dominant species in deciduous forests in Kyiv region have a similar size (Figure 3A, Table 3). Formica *rufa* has the largest colonies (on average 63 thousand, maximum - 365 thousand); *L. fuliginosus* (average value 33 thousand, maximum - 340 thousand, Figure 3A), the rest of the species have an average colony size in the range of 20–23 thousand workers. In the coniferous forests of the Kyiv region, colonies of different species differ in size (Figure 3A, Table 3). Formica *polyctena* Foerster, 1850 has the maximum colony size (average value 121 thousand, maximum 480 thousand), followed by *Formica cinerea* (average 100 thousand, maximum 390 thousand, Table 3), *L. fuliginosus* (average 60 thousand, maximum 140 thousand), *F. rufa* (average 50 thousand, maximum

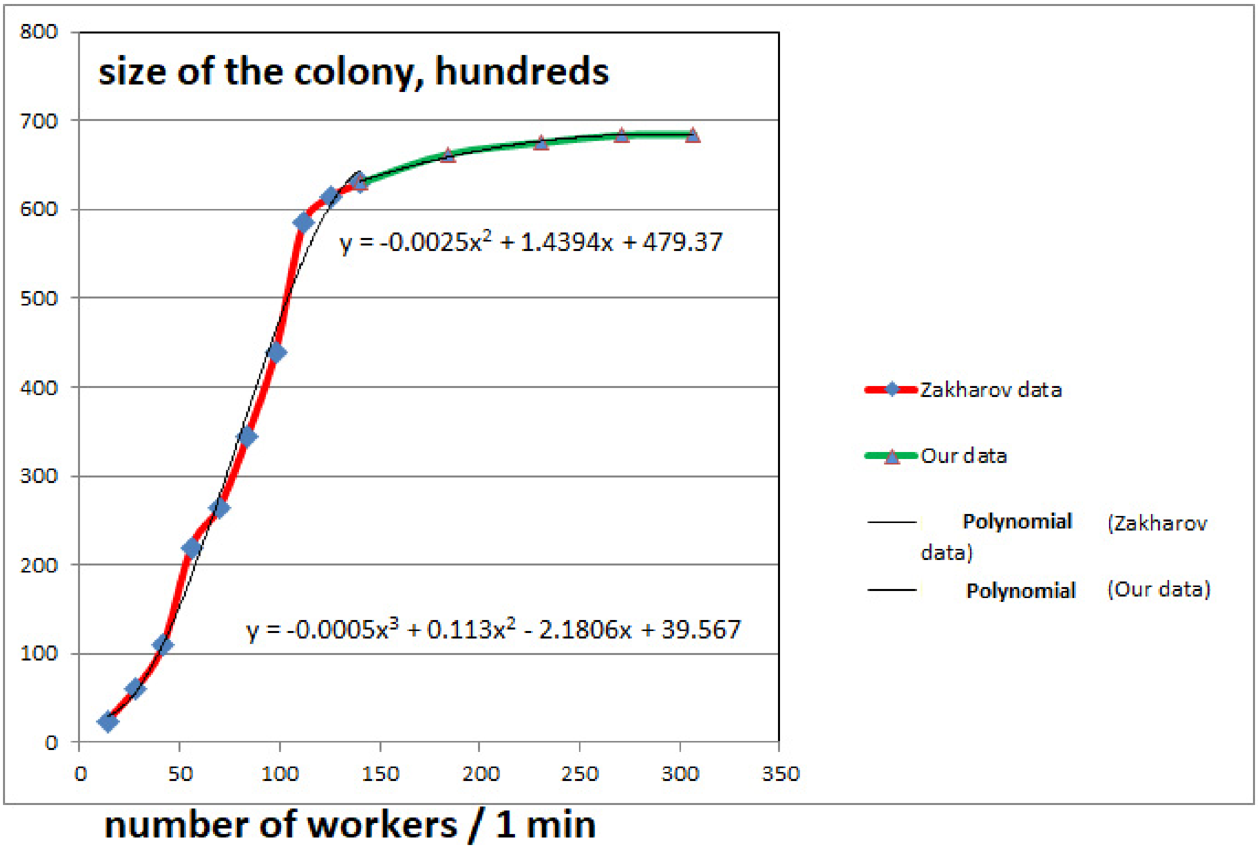

Figure 2. Calculated curve of the size of the ant colony by the intensity of movement of foragers per 1 min along the trail (counting only in one direction, Zakharov, 1979; 2015). Within 14–140 - according to A. Zakharov (1979), from 184 to 307 - our data, with an additional calculation formula in this range of values.

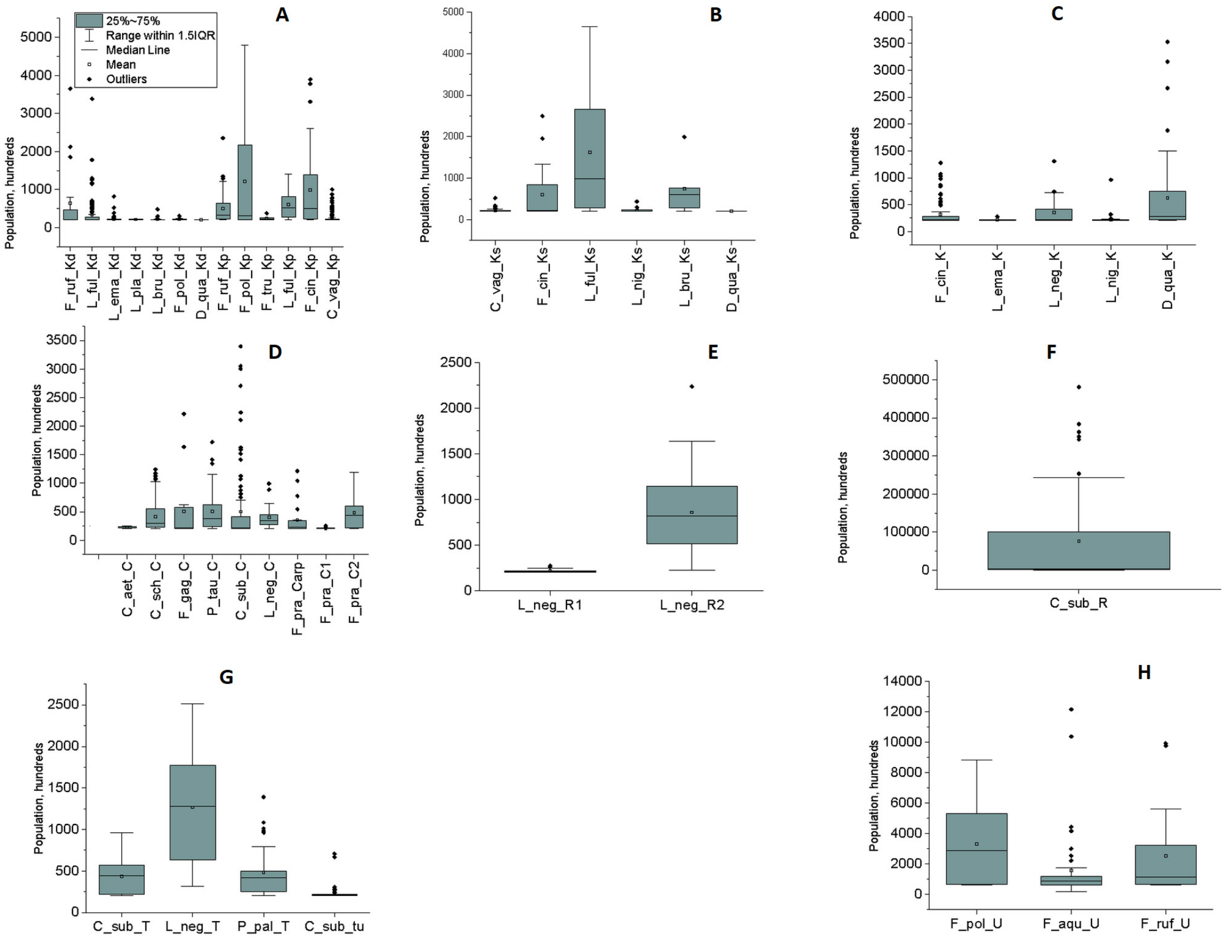

Figure 3. Colony size in 21 ant species, calculated by the formula of A. Zakharov (1979; 2015). Ukraine: A – Kyiv region, deciduous (Kd) and coniferous (Kp) forests, natural habitats; B – Kyiv, suburban habitats (Ks); C – Kyiv city, urban habitats; D – natural habitats in Crimea (C1 – mountain steppes, C2 – mountain meadows) and in the Carpathians (Carp, mountain meadows); Crimea, steppe areas, natural habitats (C_aet); suburban and urban habitats in Crimea (L_neg, C_sub); Crimea, oak-pistachio-juniper forests, natural habitats (P_tau; F_gag; C_sch); Russian Federation: E, F – Rostov-on-Don, suburban (L_neg_R2) and urban (L_neg_R1; C_sub_R1) habitats; Uzbekistan: G – natural (riparian forests, C_sub_tu) and urban (Tashkent city, everything else) habitats; Russian Federation: H – Ural, natural habitats (taiga).
Ant species: 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*; C_aet – *Camponotus aethiops*; F_tru – *Formica truncorum*; F_pol – *Formica polyctena*; L_neg – *Lasius neglectus*; F_pra – *Formica pratensis*; P_tau – *Plagiolepis tauricus*; F_gag – *Formica gagates*; C_sch – *Crematogaster schmidti*; C_sub – *Crematogaster subdentata*; M_ber – *Myrmica bergi*; P_pal – *Plagiolepis pallescens*; F_aqu – *Formica aquilonia*.

235 thousand), *Camponotus vagus* (Scopoli, 1763) (average 26 thousand, maximum 100 thousand, Table 3), *Formica truncorum Fabricius*, 1804 (average 25 thousand, maximum 37 thousand). For suburban habitats of the Kyiv region, the maximum colony size for *L. fuliginosus* (Figure 3B, average 162 thousand, maximum 464 thousand, Table 3) is followed by colonies of *Lasius brunneus* (Latreille, 1798) (74 thousand, maximum 200 thousand), *F. cinerea* (60 thousand, maximum 250 thousand, Table 3), other species - 20–25 thousand (Figure 3B). In the urbanized territories of Kyiv, the largest colonies are formed by *Dolichoderus quadripunctatus* (Linnaeus, 1771) (Figure 3C, 62 thousand, maximum 353 thousand), 2 times smaller the size of the colonies of F. *cinerea, Lasius neglectus* (35 thousand, maximum 130 thousand, Table 3), other species had colonies of 20–22 thousand workers.

In Crimea, in the steppe areas, the colonies of the only dominant species *Camponotus aethiops* (Latreille, 1798) did not exceed 23 thousand in size (maximum - 25 thousand, Figure 3D). In the oak-pistachio-juniper forest, the

Table 3. Results of statistical tests by colony size of different species in the same habitat.

Regions	Habitat	Type of habitat	K-W test for all species in one habitat	Species (larger size vs. smaller size of colony)	M-W test
Kyiv region	Deciduous forests	Natural	0.0969	-	-
			4.514E-09	*F. rufa vs. C. vagus*	1.76E-06
	Coniferous forests			*F. cinerea vs. C. vagus*	6.499E-06
	Single-species tree planting along roads in rural areas	Suburban	7.459E-10	*L. fuliginosus vs. F cinerea*	0.02683
				L. fuliginosus vs. C. vagus	8.272E-10
				L. fuliginosus vs. L. niger	7.38E-05
Kyiv	Tree alleys along streets and highways, city squares	*Urban*	1.367E-10	*D. quadripunctatus vs. F cinerea*	0.0135
				F. cinerea vs. L. niger	0.0004938
				D. quadripunctatus vs. L. niger	3.969E-10
Crimea	Mountain meadows and steppes	Natural	5.202E-07	*F. pratensis (Crimean mountain meadows) vs. F. pratensis (same, mountain steppes)*	1.911E-05
Carpathians	Mountain meadows	Natural	-	*F. pratensis (Carpathian mountain meadows) vs. F. pratensis (Crimean mountain steppes)*	1.876E-05
Rostov-on-Don	Tree alleys along streets and highways, city squares	Urban	1.281E-22	*C. subdentata vs. L. neglectus*	2.024E -12
Tashkent	Tree alleys along streets and highways, city squares	Urban	7.944E-36	*L. neglectus vs. P. pallescens*	1.15E-09
				L. neglectus vs. C. subdentata	1.879E-20

colonies of all three dominants are approximately the same, from 40 to 50 thousand workers per on average, although *Formica gagates Latreille*, 1798 has a larger maximum colony size than the other two species – *Crematogaster schmidti* (Mayr, 1853) and *Plagiolepis tauricus* Santschi, 1920 (up to 220 thousand, Figure 3D). The only dominant species of mountain meadows and steppes of Crimea and the Carpathians, *Formica pratensis* Retzius, 1783, has colonies of 20 to 48 thousand workers, depending on the habitat (Table 3). Colonies of *Crematogaster subdentata* in suburban and urban habitats of Crimea are larger than in *L. neglectus*. In *C. subdentata*, the average colony size is 50 thousand workers (maximum 340 thousand), in *Lasius neglectus* - 40 thousand (maximum 100 thousand).

In the suburban habitats of Rostov-on-Don, L. neglectus has colonies 4 times larger than in the city (Figure 3E, average 21 thousand (maximum 48 thousand) versus 85 thousand (maximum 275 thousand). This is due to the total dominance of another invasive species, *C. subdentata,* on the territory of the city, whose colonies have an average size of 7.5 million workers (Table 3, Figure 3F, maximum - 48 million workers).

In the tugai forests of Uzbekistan, the size of the colonies of *C. subdentata* is minimal (Figure 3G, 22 thousand, with a maximum of 70 thousand), in Tashkent city they are twice as large (average 43 thousand, maximum 96 thousand). Colonies of other ant species also have different sizes (Figure 3G), among them the maximum size is in *L. neglectus* (126 thousand, maximum 250 thousand), followed by colonies of *Plagiolepis pallescens* Forel, 1889 (48 thousand, maximum 138 thousand), *C. subdentata* (43 thousand, maximum 96 thousand).

In the Urals, colonies of red wood ants are approximately the same in size (Figure 3H, the M-W test showed no significant differences). *Formica polyctena,* on average, has slightly larger colonies than the other two species (333 thousand, maximum 885 thousand).

3.2. Colonies' size comparison between different habitats of same geographic regions of the same species (9 species)

The surveyed ant colonies in Kyiv and Kyiv region had different sizes, depending on the habitat. *L. fuliginosus* reaches its maximum colony size in suburban habitats (Figure 4A, Table 4). For C. *vagus,* there is no difference between the size of colonies in natural (coniferous forests) and suburban habitats (Figure 4B, Table 4), while *L. emarginatus* has minimal colony sizes under urban habitats, here it is replaced by another species (Figure 4C, Table 4), *L. niger. F. cinerea* tends to decrease the average colony size in urban territories compared to natural and suburban habitats (Figures 4D and 4E, Table 4). There was opposite trend for *D. quadripunctatus* in Kyiv and Kyiv region with maximal size of colonies in urban habitats (Figure 4F, Table 4). *L. brunneus* demonstrated the maximum size of colonies in suburban habitats compared to natural ones (Figure 4G, Table 4).

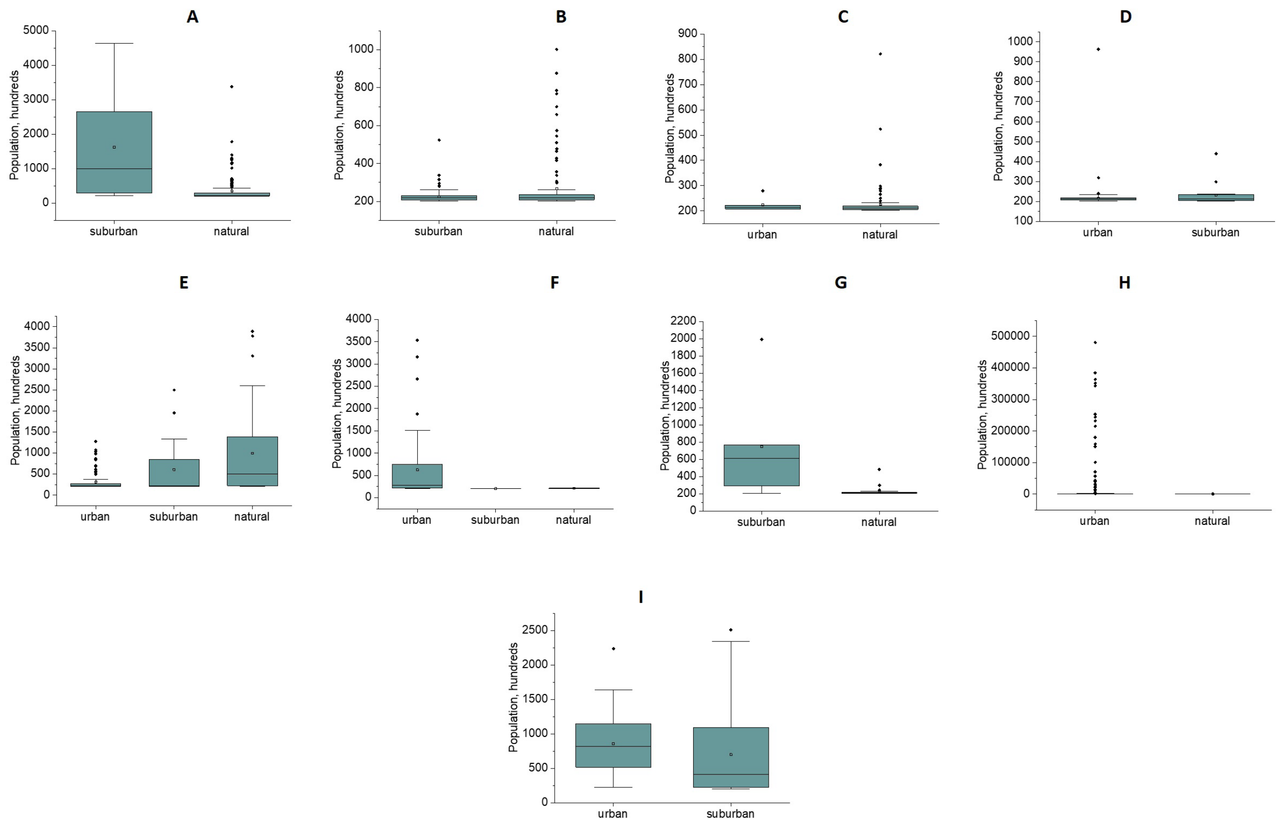

Figure 4. Colony size of 9 species of ants in several habitats of the same geographic area (calculated according to (A. Zakharov, 1978, 2015). A – *Lasius fuliginosus*; B – *Camponotus vagus*; C – *Lasius emarginatus*; D – *Lasius niger*; E – *Formica cinerea*; F - *Dolichoderus quadripunctatus*; G – *Lasius brunneus*; H – *Crematogaster subdentata*; I – *Lasius neglectus.*

C. subdentata had the largest colonies in urbanized habitats (Tashkent city) compared to natural ones (tugai forests, Table 4, Figure 4H). *L. neglectus* had the largest colonies in suburban areas (Rostov-on-Don region) compared to fully urbanized habitats (cities centers) (Figure 4I, Table 4).

Table 4. Results of statistical tests by colony size of the same species in different habitats of the same geographical region.

Region	Species	Habitats (larger size vs. smaller size of colony)	M-W test
Kyiv and Kyiv region	*Lasius fuliginosus*	Suburban vs. natural	3.141E-06
	Camponotus vagus	Suburban vs. natural	0.2846
	Lasius emarginatus	Natural vs. urban	0.04295
	Lasius niger	Suburban vs. urban	0.6345
	Formica cinerea	Natural vs. urban	1.09E-05
		Natural vs. suburban	0.04126
		Suburban vs. urban	0.6453
	Dolichoderus quadripunctatus	Urban vs. suburban	0.0253
		Suburban vs. natural	0.1489
		Urban vs. natural	0.07981
	Lasius brunneus	Suburban vs. natural	0.007842
Rostov-on-Don	*Lasius neglectus*	Suburban vs. natural	0.001584
Tashkent and Tashkent region	*Crematogaster subdentata*	Urban vs. natural	1.225E-15

3.3. Comparison of colony size between colonies in different regions.

C. subdentata has the maximum size of supercolonies in Rostov-on-Don city (secondary range of invasive species), smaller ones - in Crimean peninsula (secondary range) and Tashkent city (natural range), minimum - in natural habitats of Uzbekistan (Figure 5A, Table 5). *L. neglectus* has the largest colonies in Tashkent city (natural range - Uzbekistan), somewhat smaller - in suburban habitats of Rostov-on-Don region, even smaller - in Crimean peninsula and in Kyiv city (secondary range of invasive species) (Figure 5B, Table 5).

4. Discussion

There are few specific data on the size of ant colonies; separate data are provided for only a few species (Seifert, 2018). We have combined the data available in the literature on the approximate or exact size of ant colonies, based on the analysis of 4 monographs (Table 6). The colony sizes which were calculated are mostly in line with those indicated this authors. *Lasius neglectus* has the largest colony sizes in Tashkent and Rostov-on-Don, and smaller ones in Kyiv and Crimea. This may be due to various reasons - in Kyiv, the invasion of this species began relatively recently (Radchenko et al., 2019), and polycalic colonies have not yet managed to unite into a supercolony. In Crimea, the

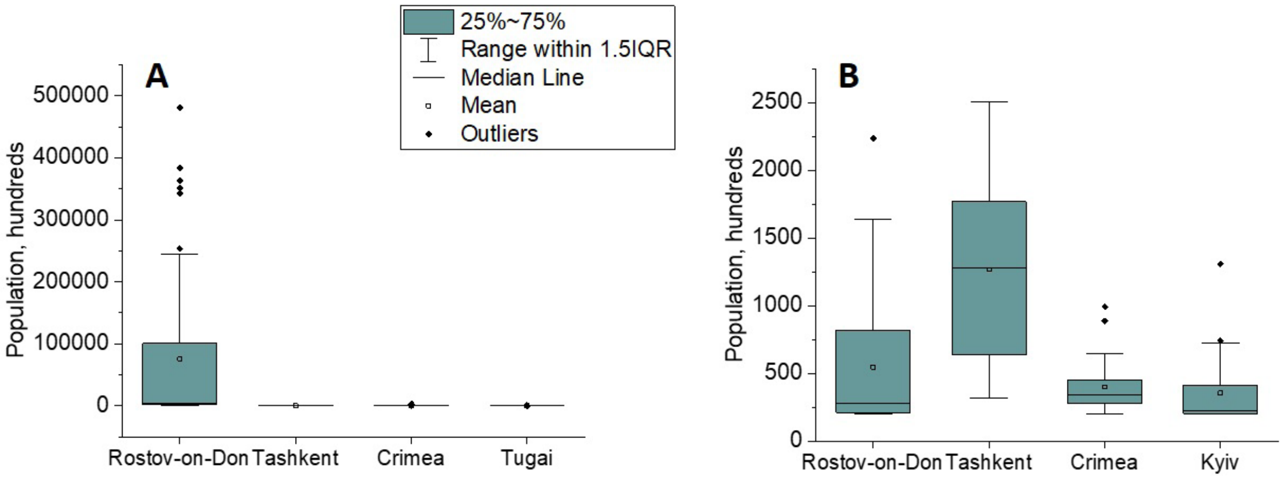

Figure 5. Colony size of species per different geographic area. A – Crematogaster subdentata; B – Lasius neglectus.

Table 5. Results of statistical tests by colony size of the same species in the same habitat in different geographical region.

Species	Region (larger colony size vs. smaller)	M-W test
Lasius neglectus	Tashkent vs. Rostov-on-Don	3.016E-12
	Tashkent vs. Crimea	6.863E-14
	Rostov-on-Don vs. Crimea	0.5688
	Tashkent vs. Kyiv	1.1E-09
	Rostov-on-Don vs. Kyiv	0.09665
	Crimea vs. Kyiv	0.01049
Crematogaster subdentata	Rostov-on-Don vs. Crimea	3.255E-21
	Rostov-on-Don vs. Tashkent	1.456E-27
	Crimea vs. Tashkent	2.401E-05

invasion began in the 70s of the 20th century (Stukalyuk and Radchenko, 2018), and its supercolonies have since fallen into decay, as in other points of Europe (Tartally et al., 2016). *Crematogaster subdentata,* on the other hand, appeared in Crimea in the early 2000s, and in Rostov-on-Don - back in the 1980s, and since then has shown a steady trend towards the growth of supercolonies (Stukalyuk et al., 2021b,c). Therefore, the largest colonies among all studied ant species in this species are in Rostov-on-Don. In Tashkent, quite large supercolonies of this species have also survived, although, on average, individual nests of *C. subdentata* here have a smaller population compared to nests of *L. neglectus,* which does not form supercolonies here (Stukalyuk et al., 2020a). The high rates of colony size for *C. subdentata* under the conditions of Rostov-on-Don may be a consequence of the active population exchange between different nests under the conditions of a supercolony (Stukalyuk et al., 2021b). At the same time, in the urban conditions of Rostov-on-Don, the colonies of L. neglectus are much smaller, which can be explained by the competition with supercolonies of *C. subdentata* that have already existed here for decades.

Table 6. Size of the colonies of ants (number of workers) by literature data (Czechowski et al., 2012; Zakharov, 2015; Radchenko, 2016; Seifert, 2018).

Species	Colony size
Lasius neglectus	Tens of thousands - hundreds of thousands (R); tens of millions (in a supercolony) (C); 112 million (in a supercolony) (S);
Lasius niger	Several hundred - ten thousand (R); several hundred – more than ten thousand (exceptionally tens of thousands) (C); 14000 (average) – 60000 (maximum size) (S); 50000 maximum size of a colony) (Z).
Lasius brunneus	Up to ten thousand (R); populous as L. niger (S);
Lasius emarginatus	Several thousand (R); very populous (C); populous or even populous than L. niger (S);
Lasius fuliginosus	Up to two million (R); up to 2 million (C); up to 1.3 million (S); 500000 (maximum size of a colony) (Z).
Lasius platythorax	Several hundred – ten thousand (R); several hundred – thousands (C); 20000 (S);
Formica cinerea	Tens of thousands – hundreds of thousands (R); very populous (C); several millions (in a supercolony) (S); 100000 (Z).
Formica gagates	Several hundred – 1500 (R); may develop supercolonies (S);
Formica polyctena	Hundreds of thousands - millions (R); over a million (C); hundreds of thousand – 17 million (maximum size of a colony) (S); ten million (maximum size of a colony) (Z).
Formica rufa	Hundreds of thousands - millions (R); up to several hundred thousand (C); 120000 – several millions (S); 5 million (maximum size of a colony) (Z).
Formica truncorum	Tens of thousands - hundreds of thousands (R); over a thousand – many tens of thousands (C); tens of thousands – hundreds of thousands (S); 100000 (maximum size of a colony) (Z).
Formica aquilonia	Hundreds of thousands – millions (R); over a million (C); hundreds of thousand – several millions (S); ten million (maximum size of a colony) (Z).
Formica pratensis	Tens of thousands – hundreds of thousands (R); many tens of thousands (C); hundreds of thousand – 3.1 million (maximum size of a colony) (S); 70000 (maximum size of a colony) (Z).
Camponotus aethiops	Several hundred – over a thousand (R); 1000 workers (S);
Camponotus vagus	Hundreds – one thousand (R); few thousand – up to ten thousand (C); 1000-4000 (average), 10300 (maximum size of a colony) (S); 10000 (Z).
Crematogaster schmidti	4500 – 5000 (R); 10000 or more workers (S); 50000 (maximum size of a colony) (Z).
Crematogaster subdentata	Several thousand (R)
Plagiolepis pallescens	-
Plagiolepis tauricus	Polygynous, polydomous (S)
Dolichoderus quadripunctatus	Up to several hundred (R); 200–300, rarely up to 1500 (small colonies – 0.5–2.0 million (supercolony) (S); 400-500 (Z).

Urban (urbanized) habitats are primarily associated with invasive species, they are capable of forming supercolonies here. For native species in Kyiv city, such cases are one; however, for the location of Kyiv, we managed to establish one species that form supercolonies under certain conditions. These are *D. quadripunctatus*. In this case, supercolonies of these species are found in orchards (walnut and apple orchards). The absence of potential competitors and the availability of resources (aphid colonies on trees, as well as trees as a nesting substrate) made it possible for *D. quadripunctatus* to form a supercolony (Stukalyuk, 2018). In natural and suburban habitats of Kyiv region, only 3–4 colonies of *D. quadripunctatus* were founded, which had a size of more than several hundred workers. Other native species, *C. subdentata*, form supercolonies in the urban conditions of Tashkent city (Stukalyuk et al., 2021b).

In suburban habitats of the Kyiv region, quite large colonies have native species *C. vagus*, *L. fuliginosus*. This is due to the fact that for these dendrobiont species, in addition to food resources, nesting sites (dry and withering trees, stumps and logs from old trees, 0.5–1.0 m in diameter) are available here, while in urban conditions they are regularly removed, which reduces the nesting limit for these species of ants. Some species in urbanized habitats of Kyiv have survived (*L. emarginatus*), but their colonies are much smaller than in natural habitats.

As for the red wood ants on the territory of the Kyiv region, small colonies of these species (on average 60–110 thousand workers) were studied, therefore, in no case was the population calculated at 1 million individuals or more. On average, the diameter of the anthill in the populations of *F. polyctena*, *F. rufa* in the Kyiv region is about 1 m, which corresponds to larger colonies, from 300 thousand individuals (Stukalyuk et al., 2021a). Red wood ants were observed only in natural conditions; they are absent in urbanized habitats.

Thus, only a part of native species can reach the same abundance values in urbanized habitats as in natural habitats. As a rule, the ecological niches of natural dominant species are occupied by invasive ant species. There is no doubt that urban conditions can be favorable for some native and invasive ant species, as favorable habitats are settled. These habitats can be characterized as an extensive food resource and the presence of a substrate for nesting. It is single-species tree plantations, on which ants visit aphid colonies, and whose wood is inhabited by ants (Stukalyuk et al., 2020b); b) the absence of natural dominant species that can compete - red wood ants and others. It is for this reason that such native species as *D. quadripunctatus* managed to develop to the level of supercolonies, which is not typical for them under natural conditions. Invasive species-dendrobionts (*C. subdentata*), in the conditions of the cities of the Crimea, Rostov-on-Don, adapted to the urban conditions even more.

5. Conclusion

Ant colony sizes vary with habitat. In the urban habitats, the largest colonies are made up of invasive (*Lasius neglectus*, *Crematogaster subdentata*) and some native species (*Dolichoderus quadripunctatus*, *Formica cinerea*). In the suburban habitats, *Camponotus vagus*, *Lasius fuliginosus* has the largest colonies.

In natural habitats colony sizes of these invasive species are usually limited up to 250 thousand of workers, while in urbanized habitats they can reach up to 7.5 million workers per colony. Invasive species *C. subdentata* have larger colonies in secondary range (Crimea, Rostov-on-Don) than in natural range (Tashkent, tugai forests of Uzbekistan). Urban habitats may have optimal conditions for the emergence of supercolonies of invasive and some natural species of ants.

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