ACQUISITION OF INVASIVE TRAITS IN ANT, *Crematogaster subdentata* MAYR (HYMENOPTERA: FORMICIDAE) IN URBAN ENVIRONMENTS

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ABSTRACT

The native (primary) range of *Crematogaster subdentata* Mayr lies in Central Asia. Within the secondary range in Ukraine and Russia, it is invasive. The 1st objective of this work was to study the evolution of the biological and ecological features (habitats, queen number, colony structure, behavior, worker's activity on foraging trails) of *C. subdentata* in the urban environments (Tashkent) and secondary ranges (Crimea, Rostov-On-Don region). Whilst, the 2nd objective was to compared these parameters in the natural habitats in the native (Uzbekistan) range. Result showed that in the territory of the primary range in Kyzylkum, colonies of *C. subdentata* are strictly monogynous; in Zarafshan's oasis (riparian forests) they were polygynous (5.0±1.2 queens), but in cities of Uzbekistan *C. subdentata* forms supercolonies with hundreds of nests, and in total with hundreds of queens (on average 17.7±4.4 queens per one nest in supercolony). In the secondary range, *C. subdentata* forms even larger supercolonies with thousands of nests, containing 53.0±8.7 queens per nest. *C. subdentata* avoids contacts with another invasive ant species, *Lasius neglectus*, in the foraging territories both in the primary and secondary ranges, but other ant species avoid *C. subdentata*. Workers of *C. subdentata* are aggressive toward conspecific ones from other nests in the natural habitats, but are tolerance to those in both the secondary range and in the cities in the primary range. In conclusion, our results show that some ants may acquire invasive species traits in the urban habitats in the primary range.

Key words: Invasive ants, *Crematogaster subdentata*, monogyny, polygyny, polycaly, urban environment, Central Asia

ABSTRAK

Taburan natif (primer) *Crematogaster subdentata* Mayr terletak di Asia Tengah. Di antara kawasan sekunder, Ukraine dan Rusia adalah invasif. Tujuan utama kajian ini adalah untuk melihat evolusi, ciri biologi dan ekologi (habitat, bilangan ratu, struktur koloni, kelakuan, aktiviti pekerja di sepanjang laluan mencari makan) spesies *C. subdentata* di kawasan urban (Tashkent) dan kawasan sekunder (Crimea, Rostov-On-Don). Objektif kedua kajian ini adalah untuk membandingkan parameter tersebut di habitat semulajadi di kawasan natif (Uzbekistan). Di teritori kawasan primer di Kyzylkum, koloni *C. subdentata* adalah *monogynous*, manakala di oasis Zarafshan (hutan riparian) adalah *polygynous* (5.0±1.2 ratu), tetapi di bandar Uzbekistan *C. subdentata* membentuk superkoloni dengan ratusan sarang dengan jumlah (purata 17.7±4.4 individu per sarang dalam superkoloni). Di kawasan sekunder, *C. subdentata* membentuk superkoloni lebih besar dengan ribuan sarang yang mengandungi 53.0±8.7 ratu per sarang. *Crematogaster subdentata* mengelak dari berhubung dengan spesies semut invasif, *Lasius neglectus* di teritori mencari makanan di kawasan primer dan sekunder, tetapi spesies semut lain juga mengelak dari berhubung dengan *C. subdentata*. Pekerja *C. subdentata* adalah sangat agresif dan konspesifik untuk sarang yang lain di habitat semulajadi, tetapi bertoleransi di kawasan sekunder dan primer. Hasil kajian ini menunjukkan spesies semut memerlukan ciri spesies invasif di habitat urban di kawasan primer.

Kata kunci: Semut invasif, *Crematogaster subdentata*, *monogyny*, *polygyny*, *polycaly*, kawasan urban, Asia Tengah

INTRODUCTION

Invasive species of ants can monopolize vast territories, negatively affecting native species. Invasive ants are often polygynous and polydomous, with some becoming “unicolonial” in the sense of a complete lack of aggression between individuals from colonies even 1000’s of km distant (Giraud et al. 2002). In some instances, changes in social structures have been observed between native and introduced populations (*Solenopsis invicta* Buren 1972 from monogynous to either monogynous or polygynous) (Chen et al. 2006). Urban environments can also alter social structures, as has been observed in *Tapinoma sessile* (Say 1836), which is monogynous (or weakly polygynous) and monodomous in non-urban settings, but becomes supercolonial in urban locations (Buczkowsky 2010). Two invasive ant species are the most common in Europe, *Linepithema humile* (Mayr 1868) and *Lasius neglectus* Van Loon, Boomsma et Andrásfalvy 1990. Both form huge supercolonies with the foraging territories of many hectares. In secondary habitats, invasive ants establish supercolonies, but in extreme cases, they can exhibit unicoloniality (i.e. whereby individuals mix freely in both natural and laboratory conditions). A supercolony comprises all nests where workers are able to mix freely and exchange resources in nature; it is an extreme (i.e. with large numbers of connected nests) form of polydomous colony.

Linepithema humile in invasive range (Southern Europe) is also characterized by unicolonality, when foraging area of the supercolony continuously extends for hundreds of kilometers, and workers from different nests are not aggressive towards each other (Helanterä et al. 2009). Invasive species of ants have several common traits, e.g. the high level of polygyny and polycaly, tolerance between workers from different nests, and aggressiveness to native ant species (McGlynn 1999; Holway et al. 2002).

Despite *Crematogaster* Lund, 1831 is one of the most speciose ant genera, in contains a very few invasive species. Fifty-two *Crematogaster* species are known from Malaysia (Bakhtiar & Maryati 2009; List of ant species from Malaysia). *Crematogaster subdentata* Mayr 1877 originates from Central Asia, and its range covers Turkmenistan, Uzbekistan, Kyrgyzstan, southern Kazakhstan, Transcaucasia, northern Iran, Afghanistan, western China, Mongolia, the Hindu Kush, Karakorum, and the northern Himalayas (Radchenko 2016). *C. subdentata* has not yet penetrated into Western Europe, but inhabits many places in Eastern Europe, including Crimea (Stukalyuk 2015), Kherson and Nikolaev (Radchenko 2016), and Rostov-On-Don, where it seems to be an invasive species. These regions are the secondary range of *C. subdentata*, where it forms supercolonies occupying up to 250 hectares in Crimea (Stukalyuk & Netsvetov 2018). *C. subdentata* may displace *L. neglectus*, which is also originated from Central Asia (Stukalyuk et al. 2020) when their colonies came into contact (Stukalyuk et al. 2021).

In the secondary range, *Crematogaster subdentata* possesses all the characteristics of invasive species, such as high level of polygyny, tolerance to workers of its own species and aggressiveness towards other ant species, and enable to form supercolonies (Stukalyuk 2015; Stukalyuk & Netsvetov 2018). Moreover, supercolonies of this species are quite resistant to various external negative influences, since there are permanent trails between the nests and brood and queens can be carried from nest to nest. Unlike *L. neglectus*, *C. subdentata* has a true nuptial flight in both native and secondary ranges, which allow its gynes disperse far away and found new nests on the periphery of maternal supercolony, which subsequently becomes a part of the supercolony. *Crematogaster subdentata* is aggressive towards the local dominant ant species, for example, *Myrmica bergi* Ruzsky, 1902 in Crimea, and is able completely eliminates its polycalic colonies (Stukalyuk & Netsvetov 2018). In contrary, *L. neglectus* prefers to surround the foraging areas of native dominant species (Paris & Espadaler 2012). Moreover, unlike other European invasive ants, *C. subdentata* is an arboreal species and may inhabit gardens and fruit orchards, where its workers actively use honeydew and protect colonies of aphids and coccids (Stukalyuk 2015).

Assessing the biology of introduced species in their natural distribution range is crucial to understand how they acquire their "invasive traits" in the secondary range. Such data are known for many ant species that have become invasive in the Old and New Worlds, e.g. *Myrmica rubra* (Linnaeus, 1758), *Linepithema humile*, *Solenopsis* species from the *invicta* species-group and others (Radchenko & Elmes 2010; Suarez et al. 2010; Wetterer 2008; 2013; Wetterer & Radchenko, 2011). Some of these species, for example, *Solenopsis invicta* live in the primary ranges in separate nests, aggressive to conspecific workers from other colonies (Calcaterra et al. 2008). At the same time, many biological features of *C. subdentata* in the primary range are still understudied (Dlussky 1981; Dlussky et al. 1990), though its biology in some parts of the secondary range is relatively known (Stukalyuk 2015; Stukalyuk & Netsvetov 2018).

The purposes of this work were to study the evolution of the biological and ecological features (habitats, queen number, colony structure, behavior, worker’s activity on foraging trails etc.) of *C. subdentata* in the urban environments (Tashkent) and secondary ranges (Crimea, Rostov-On-Don region), and to compare these features in the natural habitats in the native (Uzbekistan) range.

MATERIALS AND METHODS

Species Identification

Besides *C. subdentata*, three more *Crematogaster* species occur in Central Asia: *C. bogojawlenskii* Ruzsky, 1905, *C. sorokini* Ruzsky, 1905 and *C. schmidti* (Mayr, 1852); the latter is known in this region only from the Kopetdagh Mts., but is common in the Caucasus and Crimea. Only one species of the *Crematogaster* genus, *C. subdentata* is present in Rostov-On-Don. Key to species identification (Dlussky et al. 1990): *Crematogaster subdentata*: Propodeum without spines or teeth, at most with blunt teeth. *C. schmidti*: propodeal spines straight and long. *C. sorokini* additionally has a narrow petiole with parallel sides. *C. bogojawlenskii*: propodeum with spines. Thus, these three species differ well from *C. subdentata*. A stereomicroscope (Olympus SZX12) and a camera (Canon EOS 5DSL) were used to identify the ant species and for taking the photo. All collected workers found in all locations were of the same species, the *Crematogaster subdentata* (Figure 1A-C).

Figure 1. Workers of *Crematogaster subdentata* from Uzbekistan (A), Rostov-On-Don (B), Crimea (C)

Study Sites

Investigations on *C. subdentata* in its native range were performed in Uzbekistan–from July 2018 to august 2019 and comprised of six sites in natural habitats of the Kyzylkum desert and an oasis in the Zerafshan State Reserve, and eight sites in urban landscapes (Table1). Besides natural habitats, *C. subdentata* was studied in urban landscapes in Rostov-On-Don (Russia) in July-August 2018-2019, and Mykhailivka village in Crimea in June-August 2013-2014. The city of Rostov-On-Don has 14 parks and 31 public gardens with a total area of about 185 hectares. Urban forests cover an area of 3440 hectares, and the green zone occupy an area of 6160 hectares (Kozlovsky et al. 2013). The examined territory of Crimea (Mykhailivka village in Saky District, Crimea) is a residential area with gardens surrounding the buildings and trees planted along the streets (Stukalyuk & Netsvetov 2018). In Tashkent, the green area is 15.2 thousand hectares, or 35% of the total area of the city (Radkevich & Shipilova 2018). There are 20 large parks and about 100 public gardens in Tashkent. The study sites in Kyzylkum desert were oases dominated by plants of the genus *Haloxylon* and *Calligonum*. Tugai forests in Uzbekistan are floodplain gallery forests, the tree layer of which is dominated by willows (*Salix* sp.) growing along the banks of perennial rivers (Stukalyuk et al. 2021).

Calculation of Number of Queens in Nests

To calculate the number of queens in colonies, 10 nests of *C. subdentata* were excavated for each study site, inside and outside of their native distribution. In the Kyzylkum desert and an oasis, nests occurred naturally near saxaul's root collar on sandy soil, which allow the queens to be unearthed and counted *in-situ* easily. In urban areas, where *C. subdentata* resided in dead trees and outbuildings between the woody construction and insulation, a nest-containing substrate was extracted and placed in a wooden container (three liters, 260 x 190 x 100 mm) and transferred in a laboratory (all ants from Crimea – in the laboratory of the department of ecological monitoring (Institute for Evolutionary Ecology of the National Academy of Sciences of Ukraine, Kyiv, Ukraine); ants, collecting in the Rostov-on-Don – in the laboratory of the Rostov Research Institute of Microbiology and Parasitology; ants, collecting in the Uzbekistan – in the laboratory of the Institute of Zoology of the Academy of Sciences of the Republic of Uzbekistan). Ants collected to the container with nests' material during on the same 1-2 days are relocated to a formicarium joined by pipes with container (pipe length 20 cm, diameter 2 cm).

Observation of Workers' Activity on Foraging Trails

A total of 10 *in situ* trails in each the desert, oasis, Tashkent, Rostov-On-Don, and 30 in Crimea were investigated. Each colony was tested on one trail, and all workers on the trail were counted within two minutes of the survey. A gate was installed over the trail. The number of ants passing in both directions under the gate was counted.

Table 1. Collection sites of *Crematogaster subdentata* in Uzbekistan (sites 1-14), Rostov-On-Don (15) and Crimea (16)

	Collection sites + (habitat)	**Coordinates**		**Altitude above sea level, m**	**Size of the colony (number of workers per nest)**	**July average and maximum temperatures (°C), Precipitation level (mm) ****
		Northern latitude	**Eastern longitude**			
1	Namangan (gardens, houses)	41° 0’5.87"	71°39’55.55"	447	> 1000	Average t: 30.1 C Maximum t: 37.0 C Precipitation: 10 mm
2	Fergana (gardens, houses)	40°22’54.05"	71°47’12.44"	585	> 1000	Average t: 29.0 C Maximum t: 35.5 C Precipitation: 10 mm
3	Tashkent (gardens, houses)	41°17’7.34"	69°15’46.43"	430	> 1000	Average t: 27.9 C Maximum t: 34.6 C Precipitation: 11 mm
4	confluence of the rivers Syr Darya and Chirchik* (floodplain forests)	40°54’15.66"	68°42’57.45"	253	500-600	Average t: 25.6 C Maximum t: 32.0 C Precipitation: 10 mm
5	Jizzakh (gardens, houses)	40° 7’35.95"	67°50’18.74"	371	> 1000	Average t: 27.4 C Maximum t: 33.1 C Precipitation: 4 mm
6	Zarafshan’s oasis	39°39’57.20"	67°05’23.29"	718	> 1000	Average t: 30.5 C Maximum t: 35.7 C Precipitation: 2 mm
7	Karshi (gardens, houses)	38°52’47.59"	65°47’53.88"	378	> 1000	Average t: 29.8 C Maximum t: 36.8 C Precipitation: 1 mm
8	Guzar (gardens, houses)	38°52’47.59"	65°47’53.88"	524	> 1000:	Average t : 27.7 C Maximum t: 34.5 C Precipitation: 1 mm
9	Baysun* (woods in the foothills)	38°12’17.20"	67°12’1.23"	1237	500	Average t: 24.5 C Maximum t: 30.0 C Precipitation: 11 mm
10	Termez (gardens, houses)	37°13’5.29"	67°17’1.58"	300	> 1000	Average t: 33.6 C Maximum t: 40.2 C Precipitation: 0 mm
11	Zarafshan* (woods in the foothills)	41°34’24.60"	64°10’58.79"	395	100-200	Average t: 26.4 C Maximum t: 33.3 C Precipitation: 4 mm

12	Shalkar* (desert, near the artificial lake)	41°57’41.64"	63°32’25.19"	20	100-200	Average t: 29.6 C Maximum t: 34.8 C Precipitation: 2 mm
13	Mullaly (desert Kyzylkum)*	41°55’54.34"	64°35’10.87"	202	100-200	Average t: 29.6 C Maximum t: 34.8 C Precipitation: 2 mm
14	Urgench (gardens, houses)	41°36’7.76"	60°32’4.18"	97	>1000	Average t: 30.2 C Maximum t: 36.1 C Precipitation: 1 mm
15	Rostov-On-Don (gardens, houses)	47°08’15.8"	39°44’31.48"	10	>10000	Average t: 25.0 C Maximum t: 29.7 C Precipitation: 40 mm
16	Mykhailivka (gardens, houses)	45°06’43"	33°37’00"	7	>10000	Average t: 24.9 C Maximum t: 28.9 C Precipitation: 25 mm

* Natural habitats;
** - data from www.climate-data.org

Density Examination of Workers on Plots and Baits
The *C. subdentata* workers' density, i.e., the mean number of individual ants per carbohydrate and protein baits was examined. Observation on baits started 30 minutes after their installation. In Central Asia, 130 examinations of each type of habitat were carried out: in the desert (10 baits), oasis (60 baits), and Tashkent Botanical Garden (60 baits). Outside the native range in Rostov-On-Don, ants were counted only on 21 protein baits (in parks). We also used earlier published data collected in Crimea (Stukalyuk & Netsvetov 2018) on 288 protein baits and 192 carbohydrate baits (Mykhailivka village, Saky district). In each site, workers of other ant species we also counted.

Behavior Tests
The behavioral tests using a framework developed in earlier studies have been performed (Le Moli & Parmigiani 1981; Stukalyuk & Netsvetov 2018) to estimate intraspecific and interspecific aggression of *C. subdentata* in its natural and secondary distribution ranges. One week before trials, workers of *C. subdentata* from neighboring colonies and rival species *L. neglectus* from Tashkent and Rostov-On-Don or *M. bergi* in Crimea were collected. Authors avoid using the ants from inside colonies by collecting individuals on foraging trails or tree trunks more than one meter away from nests' entrances. Each group of workers was kept in separate containers with their original nesting materials. The conditions for maintenance and experiments were 23-25°C and 70–80% of relative humidity and corresponded to that in natural habitats in July. Prior to this trails, experimental ants were kept for a day in Petri dishes (110 x 100 x 20 mm) with a thin layer of sand and sprayed once with water to prevent drying. Five hours before the start of experiments, we fed ants with honey syrup. To enable group identification during investigations, we marked ants with a color dot of paint. The fighting boxes were made from glass and measured 9×9×3 cm and 22×18×21 cm for contests between two individuals (1:1) and two groups (5:5 and 10:10), respectively. Before the experiment, the arena was wiped with ethanol. Two groups of ants were placed on the opposite sides of a box divided by a moving barrier. Contests started after 30 min of ants' acclimation in the box and lasted for 2 min. Each worker participated in only one battle. All tests were repeated three to five times in each combination (1:1, 5:5, and 10:10 worker).

In Uzbekistan, 15 tests each were conducted in the Kyzylkum and in the Zarafshan reserve (Zarafshan's oasis) and in Tashkent. At each point 5 out of 15 tests were conducted in categories 1 to 1 worker (category A), 5 to 5 (category B), and 10 to 10 workers (category C). To compare the intraspecific aggression of *C. subdentata* from different colonies and interspecific aggression between *C. subdentata* and *L. neglectus*, authors conducted nine similar tests with the same ratio of workers. *L. neglectus* is another native species in Uzbekistan (Stukalyuk et al. 2020). In each category, 3 tests were performed.

In the secondary range (Rostov-On-Don), five tests were conducted: one test on category A, three in category B and C between workers of *C. subdentata*. For the pair *L. neglectus* vs *C. subdentata*, three tests for category A, B and C of workers of each species were carried out. For Crimea, data on interspecific aggressiveness of *C. subdentata* and the native dominant *M. bergi* are present by 30 tests, 10 in each category. Contests were recorded using video that was further examined to evaluate ants' aggression intensity. Recording began five seconds before the survey start. A video camera was placed on a tripod to capture the entire fighting box's area.

Following earlier behavioral assays (Batchelor & Brifa 2011; Wallis 1962), authors classified ants' responses into six categories: i) peaceful contact, i.e., antennation and licking,

ii) swoops and bounces, iii) threaten poses, i.e., mandibles opening or gaster flexion, iv) seizing or clenching an enemy's appendages using mandibles, v) digging or the attack with seizing and a locomotive behavioral element, vi) and attack using secret spraying. Additionally, counted the number of workers killed during contests. To quantify aggressive behavior, scored obtained responses and calculated Total Agonistic Index (TAI) (Batchelor & Brifa 2011). Swoops, bounces, and threats were scored 1, seizing was scored 2, attacks with or without poison secret spraying scored 3, and other responses scored zero.

Statistical Analysis

Given the non-normal data distribution, we used Kruskal–Wallis test (Kruskal & Wallis 1952), a non-parametric analog of one-way analysis of variance (ANOVA), to test whether there was a difference between i) species in a number of workers on baits, ii) locations in a number of *C. subdentata* queens in nests and workers on trails, and iii) locations in TAI. The number of workers on baits was analyzed separately for each site. Kruskal–Wallis tests with significant differences followed by multiple pairwise comparisons test (Dunn 1961) with a Bonferroni adjustment. Both analyses were performed in R statistical software using the 'rstatix' package in R statistical software (R Core team 2020).

RESULTS

Habitats of *C. subdentata* in the Primary Range

Crematogaster subdentata occurs in Uzbekistan in various habitats at the altitudes from 20 to 1237 m above sea level (a.s.l.) (on average – 425.5±79.6 m) (Table 1, Figure 2).

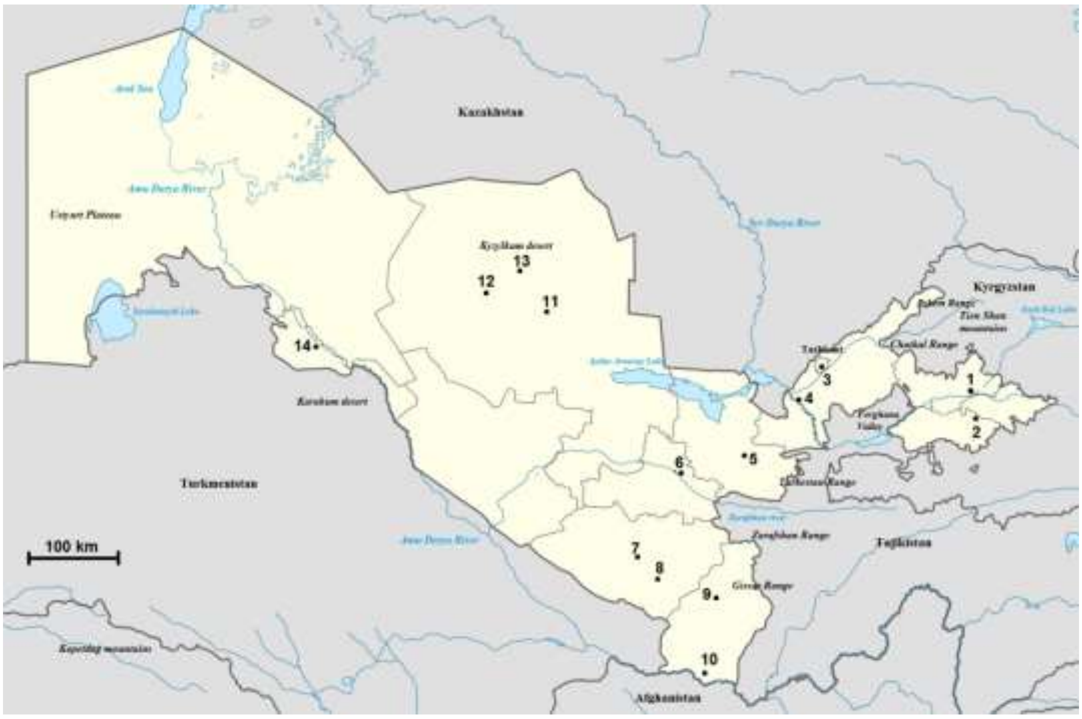

Figure 2. Collection sites of *Crematogaster subdentata* in Uzbekistan. 1. Namangan city; 2. Fergana city; 3. Tashkent city; 4. Confluence of the rivers Syr Darya and Chirchik; 5. Jizzakh city; 6. Zarafshan reserve (oases); 7. Karshi city; 8. Guzar city; 9. Baysun; 10. Termez city; 11. Zarafshan city; 12. The surroundings of the Shalkar village; 13. Mullaly village; 14. Urgench city

In the foothills and in the Kyzylkum desert, it inhabits saxaul's thickets (*Haloxylon* sp.). Colonies of this species here are small and do not exceed 100-200 workers (Table 1). Workers do not forage on the soil surface, at most move no further than 0.2 m from the trunk of the saxaul shrub. One monocalic colony of *C. subdentata* usually occupies one plant. Authors did not observe the protective behavior of *C. subdentata* on the foraging territory towards other ant species; for example, the workers of *Tetramorium* sp. which foraged at the base of the shrub near the entrance to the *C. subdentata* nest.

The other natural habitat of *C. subdentata* was Zarafshan's oasis that stretches along the non-drying rivers of Central Asia (Amu-Darya, Ili, Syr-Darya). The colonies of *C. subdentata* here are much bigger and contain up to 1000 workers (Table 1). Foraging trails can pass on the soil surface, and workers of *C. subdentata* are aggressive both towards other ant species and conspecific workers from other colonies. Moreover, its colonies in these habitats are polycalic, with one central and several auxiliary nests (so-called level of simple polycaly).

Crematogaster subdentata reaches its maximum level of sociality in Uzbekistan cities (Tashkent, Urgench, etc.), where number of workers in colonies starts from 10 thousand in single nest. It forms here supercolonies of hundreds of nests connected by a developed network of trails. Supercolonies comprise from hundreds of thousands to millions of workers and use foraging territories occupying areas of up to 800 m^2. From data in Table 1, it can be seen that *C. subdentata* forms larger colonies (with more than 1000 workers per nest) in urban conditions, regardless of the level of precipitation or temperature. In addition, the July average and maximum temperatures recorded in the secondary habitats (in the Crimea and in the Rostov-on-Don) are slightly lower than in Uzbekistan, but the level of precipitation is higher. Such conditions along with an abundance of trees in Rostov-On-Don and Crimea facilitated the successful spatial expansion of the *C. subdentata* colonies.

The main eight supercolonies of *C. subdentata* found in Crimea cover an area of 34.2 hectares, the remaining single monocalic and small polycalic colonies occupy an area of more than 200 hectares in Mykhailivka village, Crimea (Figure 3).

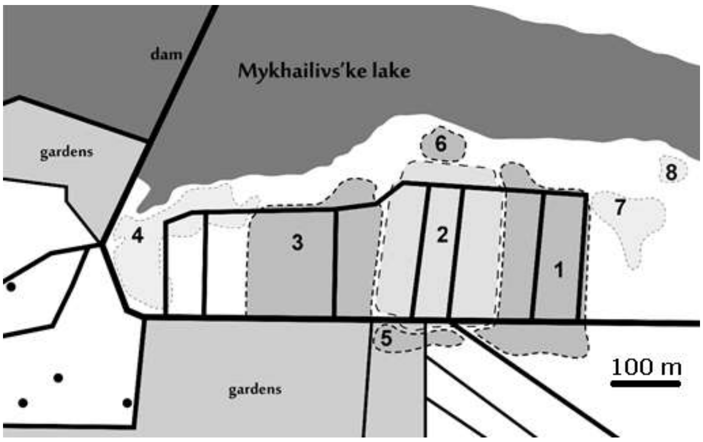

Figure 3. Locations and area (in hectares, ha) covered by 8 supercolonies of *C. subdentata* in Crimea (Mykhailivka village, Saky District): 1. 66.920 m^2 (6.6 ha); 2. 105.900 m^2 (10.6 ha); 3. 95.025 m^2 (9.5 ha); 4. 48.500 m^2 (4.8 ha); 5. 10.800 m^2 (1 ha); 6. 8810 m^2 (0.8 ha); 7. 6500 m^2 (0.6 ha); 8. 3000 m^2 (0.34 ha). Total area covered was 342.455 m^2 (34.2 ha)

Supercolonies cover areas of variable sizes (from 0.3 hectares to 10.6 hectares) depending on the possibility that polycalic colonies can build connections within the area. Typically, these connections are roads that run along gas pipelines and adjoining tree branches over natural obstacles (such as highways, streets, and ditches). After 14 years of invasion (which began in early 2000s), *C. subdentata* has occupied vast areas of more than 270 hectares.

The situation in the primary area (Tashkent) and in the secondary area (Rostov-on-Don), where the invasion of *C. subdentata* has been taking place for a relatively long time (more than 40 years), is fundamentally different from that in Crimea. In Tashkent, for instance, there were 4 supercolonies detected, which occupied areas from 1 to 3.3 km^2, ten times larger than those in Crimea (Figure 4).

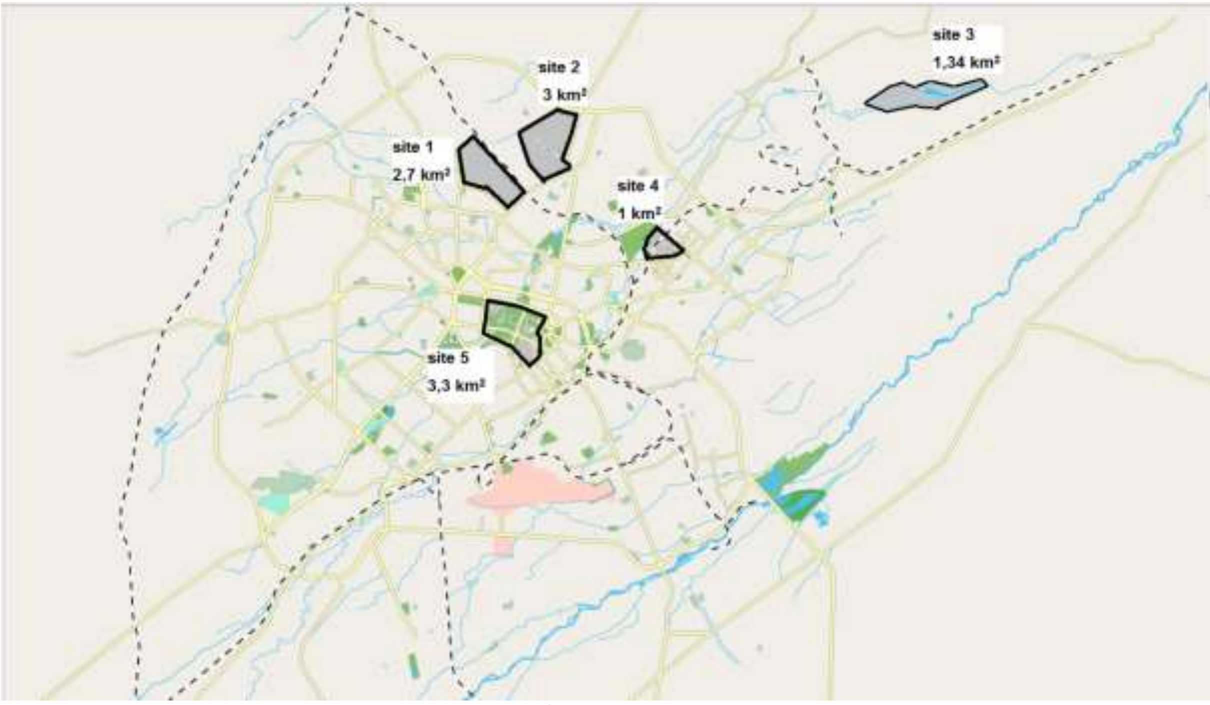

Figure 4. Locations and area (in km^2) covered by 4 supercolonies of *C. subdentata* in Tashkent. Total area covered was 11.34 km^2

Perhaps, such supercolonies resulted from the merger of several smaller supercolonies that were able to build trails between the colonies. The cities of Tashkent and Rostov-On-Don have dozens of parks and gardens, the conditions in which are similar to those in oases and Tugai forests, where *C. subdentata* colonies reach their maximum sizes possible. Apparently, the natural conditions in Rostov-On-Don turned out to be more favorable for the *C. subdentata* supercolonies to grow than those in Tashkent, as evidenced by their 7-10 times larger sizes. The nests and trails built by ants of this species were seen along the entire length of the traversed routes. Moreover, they were interconnected (Figure 5).

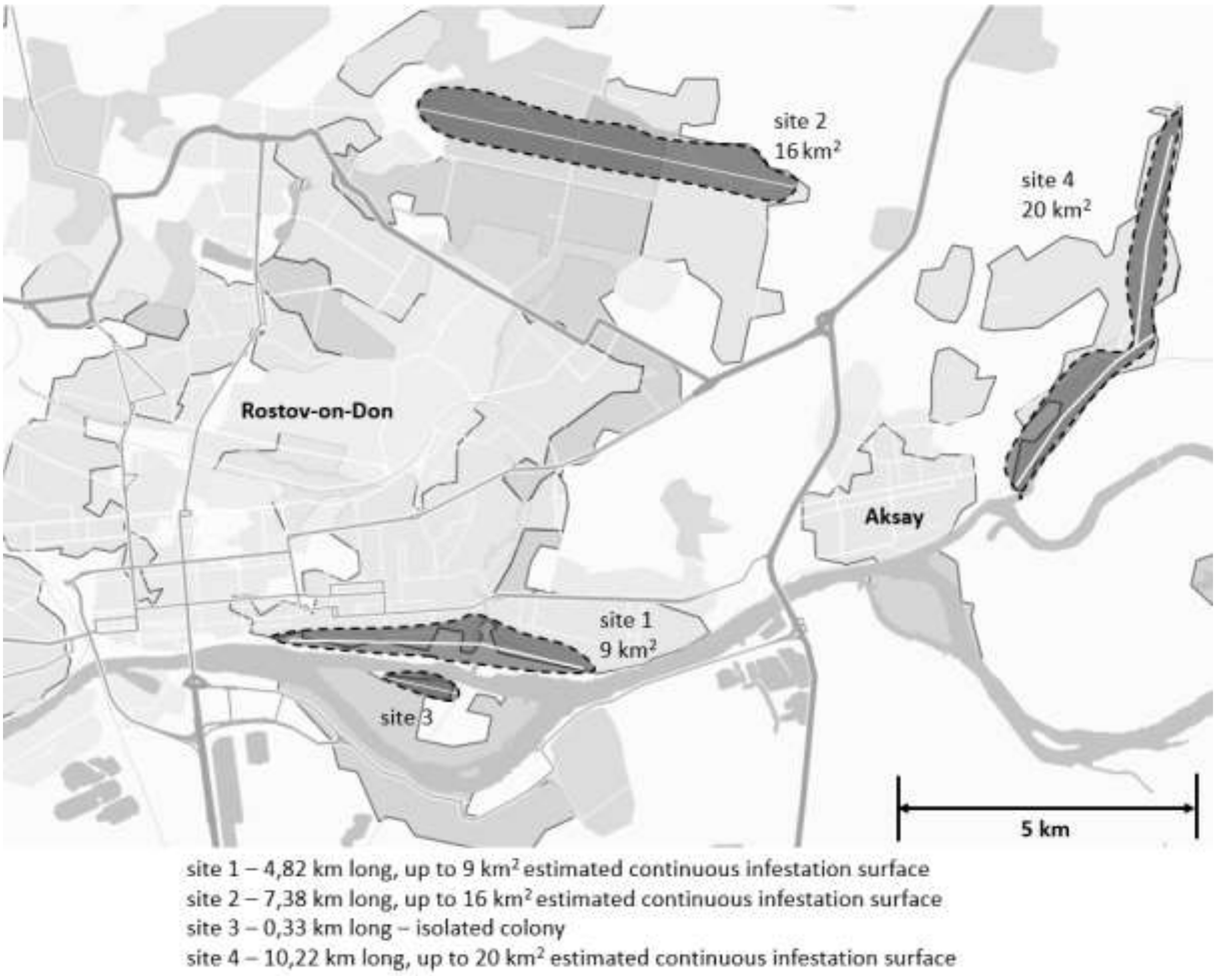

Figure 5. Locations and area (in km^2) covered by 4 supercolonies of *C. subdentata* in Rostov-On-Don. Total area covered was 45.6 km^2

Number of Queens per Nest and Workers on Foraging Trails

As mentioned above, the colonies of *C. subdentata* in the Kyzylkum desert are monocalic and strictly monogynous, and the activity of workers on the trails is also minimal due to the small size of the colonies (Table 2). Kruskal-Wallis test revealed a significant difference in both the number of queens in nests and foragers' activity, i.e., the number of foragers on a trail per 2 minutes for studied locations (Figure 6; Table 3).

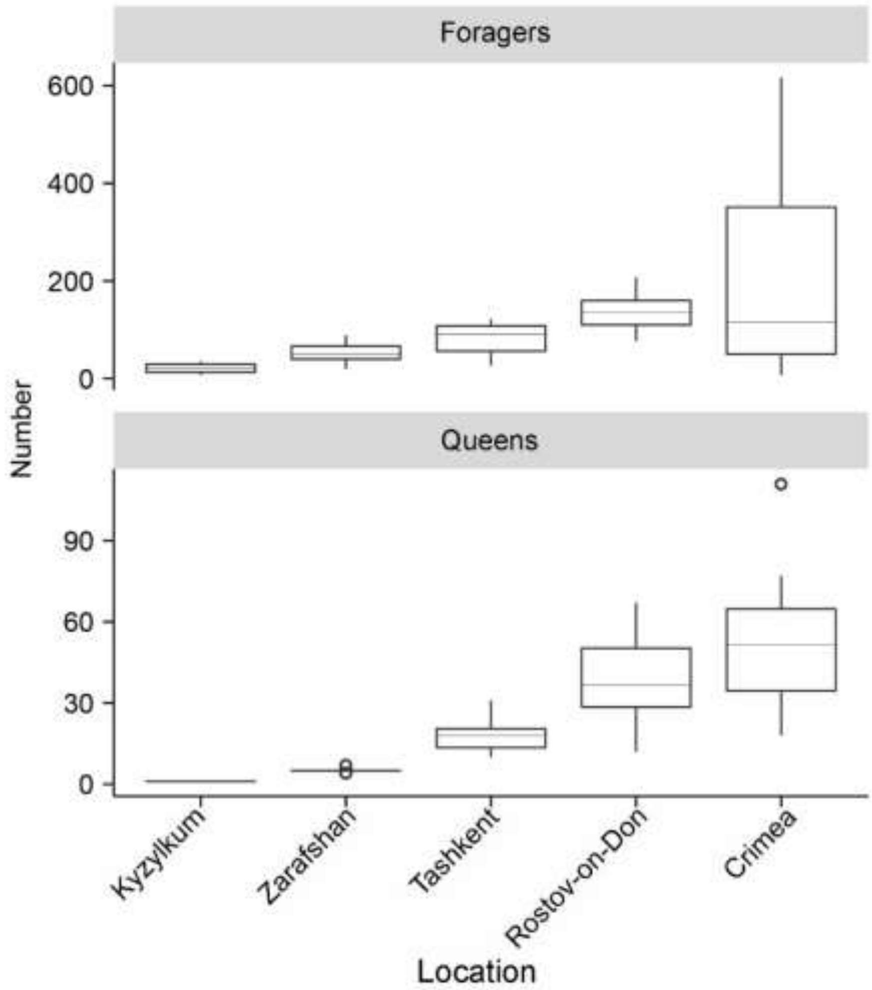

Figure 6. Mean number (±SE) of queens of *C. subdentata* per nest (total 10 nests per location) and average number of foragers on trails (n/2 min) in different collection sites of primary and secondary range

In the Kyzylkum desert, colonies of *C. subdentata* were monocalic, strictly monogynous, and small-sized with the low foragers' activity on trails (20.0±5.4). In Zarafshan's oasis, providing benign local conditions for *C. subdentata*, polycalic and polygynous colonies had 5±1.2 queens per colony and 52.0±6.6 foragers' activity on average, although these did not differ significantly from those in the Kyzylkum in the pairwise test (Table 4). In Tashkent city, polycalic colonies joined in supercolonies with 17.7±4.4 queens per nest and 81.0±6.1 foragers on trails per 2 minutes on average that were significantly higher than those detected in the Kyzylkum. In secondary range in urban city of Rostov-on Don and in Crimea, supercolonies had 39.8±13.4 and 53.0±8.7 queens per nest with 136.2±11.7 and 260.2±27.9 foragers on trails per 2 minutes, respectively.

Density of Workers of *C. subdentata* on Baits

The most numerous ants' species coexisting with *C. subdentata* were *M. bergi* and *Tetramorium caespitum* (Linnaeus, 1758) in Crimea, *T. caespitum* and *L. neglectus* in Rostov-On-Don and Tashkent, and *Tetramorium armatum* Santschi, 1927 and *Plagiolepis pallescens* Forel, 1889 in Kyzylkum desert (Figure 7).

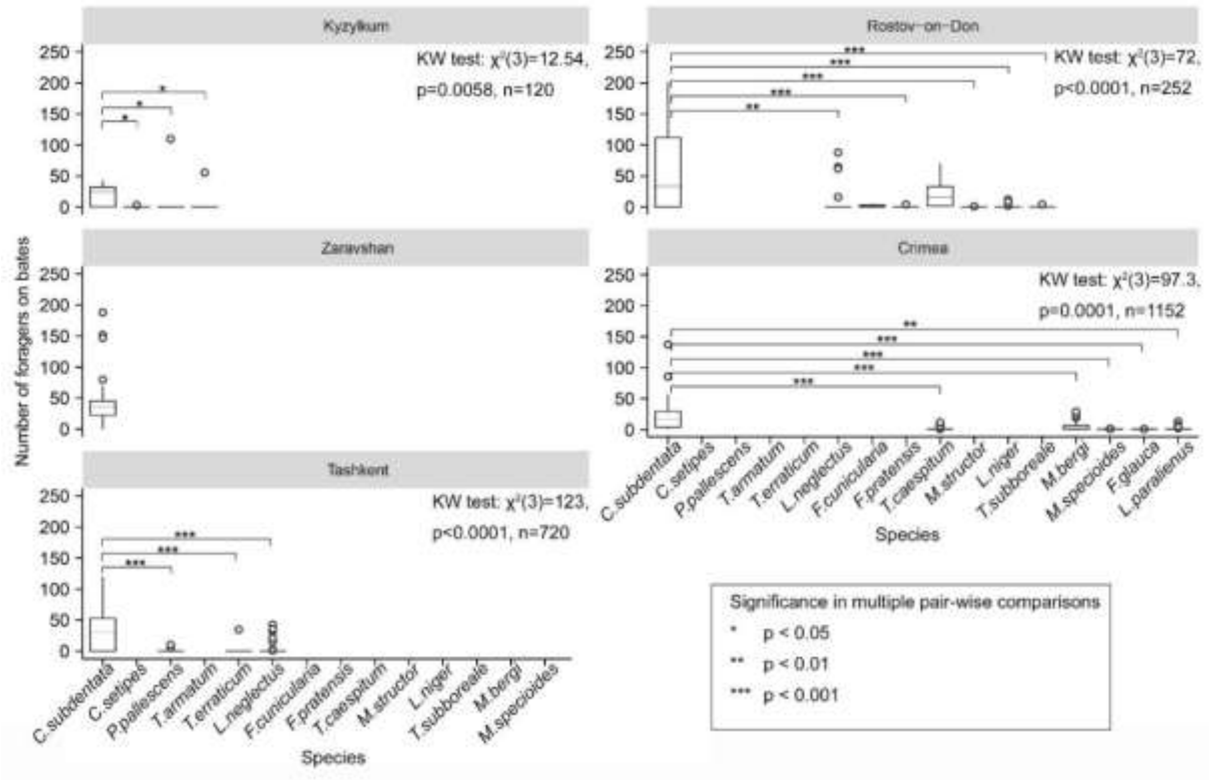

Figure 7. Mean number (±SE) of foragers on the protein baits in the Kyzylkum and the Zarafshan oases, Tashkent city, Rostov-On-Don city, and the Crimean Peninsula*. In the box-and-whisker plots, the lower and upper hinges indicate the 25th and 75th percentiles, the horizontal lines denote the median values, the whiskers extend from the hinges to the largest and smallest values within the 1.5 inter-quartile range, and the points indicate outliers. The short results of Kruskal-Wallis (KW) test is present in annotations. The significant results of Dunn's pair-wise test for *C. subdentata* are presented by horizontal brackets with asterisks

In total, four ant species coexisted with *C. subdentata*, were found in the Kyzylkum desert in Uzbekistan (Table 4). In the Zarafshan's oasis we found only *C. subdentata* as other species of ants avoided its foraging territory. Three species occurred with *C. subdentata* in Tashkent, seven species – in Rostov-On-Don, and 12 species – in Crimea (Table 5; Figure 7).

Table 2. Attendance of baits by ants in the primary and secondary ranges of *C. subdentata* (average number of workers per bait/two minutes)

Location	**Habitat**	**Species of ants and average number of workers on protein baits**
Uzbekistan	Desert Kyzylkum	*Crematogaster subdentata* (27.5±5.2) *Plagiolepis pallescens* (10.0±10.0) *Tetramorium armatum* (5.1±5.1) *Tetramorium shneideri* (1.4±1.4) *Cataglyphis setipes* (0.3±0.3).
	Tugai forests, Zarafshan's oasis	*Crematogaster subdentata* (38.4±4.4)

	Tashkent, Botanical garden	*Crematogastersubdentata* (32.5±3.9) *Lasius neglectus* (3.1±1.2) *Plagiolepis pallescens* (0.25±0.18) *Tapinoma erraticum* (0.58±0.58).
Rostov-on-Don	Parks, forest belt	*Crematogaster subdentata* (60.5±14.1) *Lasius neglectus* (11.0±5.6) *Formica cunicularia* (1.7±0.4) *Formica pratensis* (0.2±0.2) *Tetramorium caespitum* (20.8±4.5) *Messor structor* (0.04±0.04) *Lasius niger* (1.6 ± 0.8) *Tapinoma subboreale* (0.2±0.2).
Crimea, Mykhailivka *	Gardens, alleys	*Crematogaster subdentata* (28.9±2.1) *Myrmica bergi* (12.3±1.6) *Tetramorium caespitum* (5.9±3.2).

Table 3. Results of Kruskal-Wallis tests for number of foragers on trails per 2 minute and number of queens per nests (significant results are bolded)

Feature	**Observations**	***Chi-square***	**DF**	***P*-value**
Number of foragers	70	25.8	4	**<0.001**
Number of queens	50	43.3	4	**<0.001**

Table 4. Results of the multiple pairwise comparisons using Dunn's test for number of foragers on trails per 2 minute and number of queens per nest among studied sites

Group1	**Group2**	**Number of foragers**		**Number of queens**	
		Z	***P-value***	***Z***	***P-value***
Kyzylkum	Zaravshan	1.69	0.917	1.54	1
Kyzylkum	Tashkent	2.83	0.047	3.34	0.0084
Kyzylkum	Rostov-on-Don	4.30	<0.001	5.01	<0.001
Kyzylkum	Crimea	4.32	<0.001	5.53	<0.001
Zaravshan	Tashkent	1.14	1	1.80	0.725
Zaravshan	Rostov-on-Don	2.61	0.091	3.47	0.0052
Zaravshan	Crimea	2.25	0.245	3.99	0.0007
Tashkent	Rostov-on-Don	1.47	1	1.67	0.944
Tashkent	Crimea	0.85	1	2.19	0.286
Rostov-on-Don	Crimea	-0.94	1	051	1

Table 5. Mean number (±SE) of behavioral responses of *C. subdentata* in intraspecific and interspecific aggressiveness assays

Location	**Response scores**							
	1	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Assay 1×1, *intraspecific*								
Kyzylkum	0.4±0.24	0.8±0.37	1±0.32	0.2±0.2	0.2±0.2	0.4±0.24	NA	0.2±0.2
Zarafshan	1.2±0.2	1.4±0.24	1.6±0.24	0.6±0.24	0.4±0.24	1.0±0.32	NA	1.2±0.2
Tashkent	0.2±0.2	0	0	0	0	0	0	0.6±0.24
Rostov-on-Don	0	0	0	0	0	0	NA	1.4±0.24
Crimea	0	0	0	0	0	0	NA	1.2±0.2
Assay 5X5, *intraspecific*								
Kyzylkum	1.6±0.51	5.6±0.68	1.8±0.37	0.2±0.2	0.2±0.2	4.8±0.37	NA	1.6±0.51
Zarafshan	3.4±0.4	5±0.55	3.6±0.4	1.4±0.4	7.2±0.37	7.2±0.8	NA	3.8±0.66
Tashkent	1.2±0.2	0	0	0	0	0	0	3.6±0.68
Rostov-on-Don	0.3±0.33	0	0	0	0	0	NA	5±1.15
Crimea	0	0	0	0	0	0	NA	6.4±0.51
Assay 10X10, *intraspecific*								
Kyzylkum	4.4±0.4	11±0.84	4.2±0.49	2.4±0.24	2.6±0.24	8.4±0.4	NA	5.6±0.75
Zarafshan	6.4±0.4	13±1.3	6.4±0.68	2.4±0.51	9±0.71	10.4±0.93	NA	7.8±1.07
Tashkent	2±0.55	0	0	0	0	0	0	10.6±0.68
Rostov-on-Don	1.7±0.33	0	0	0	0	0	NA	11.3±2.91
Crimea	0	0	0	0	0	0	NA	9.8±0.66
Assay 1×1, *interspecific*								
Tashkent	0.2±0.2	0.2±0.2	0.2±0.2	0.2±0.2	0	0	NA	0.2±0.2
Rostov-on-Don	3.7±0.33	0.3±0.33	0.3±0.33	0	0.3±0.33	0	0.3±0.33	0.3±0.33
Crimea	0.2±0.13	0	0	0	0	0	0	0.6±0.22
Assay 5×5, *interspecific*								
Tashkent	0.8±0.37	6±0.77	5.6±0.4	1.8±0.37	1±0.32	0	NA	0.4±0.24
Rostov-on-Don	12.7±2.03	4.7±0.33	4.3±0.33	1±0.58	6.0±1.15	0	4.7±0.33	0.7±0.33
Assay 10×10, *interspecific*								
Tashkent	4.6±0.51	13.4±1.36	9.8±0.58	3.4±0.51	3±0.45	0.6±0.24	NA	0.4±0.4
Rostov-on-Don	24.3±2.4	9.3±0.67	9.7±0.33	4.3±0.67	18±2.31	1±0.58	9.7±0.33	3±0.58

Crimea	3.3±0.47	0.6±0.22	0.5±0.22	0.1±0.1	0.3±0.15	0.2±0.13	0	2.9±0.46

Killed enemy are *Lasius neglectus* and *Myrmica bergi* workers in Rostov-On-Don and the Crimea peninsula respectively. Responses scores: 1. Swoops and bounces. 2. Threatened poses, i.e., openings of the mandibles or gaster flexions. 3. Attack the enemy's appendages. 4. Attack the head and waist followed locomotive elements. 5. Attack using mandibles and poisonous secrets. 6. The number of killed *Crematogaster subdentata* workers. 7. The number of killed enemies. 8. Peaceful responses, i.e., antennation or licking.

Crematogaster subdentata mobilized on baits two to five times more workers than other ant species in all habitats (Figure 7). The number of *C. subdentata* workers on protein baits was similar in the Kyzylkum and Zarafshan's oasis and the city in Uzbekistan, and in Crimea which are respectively from 27.5±5.2 to 38.4±4.4, but this number was significantly larger in Rostov-On-Don (60.5±14.1) (Table 2; Figure 7). Foragers of *C. subdentata* were found in smaller numbers on carbohydrate baits: 19.0±2.7 in the Kyzylkum, 15.6±1.8 in Zarafshan's oasis, 10.9±1.4 in Tashkent, 5.3±0.7 in Crimea (data from Rostov-On-Don are absent). Further analysis of the structure of species complexes is carried out for protein baits.

The low level of competition between *C. subdentata* and other species in the Kyzylkum was confirmed by the proximity of their nests with those of *Tetramorium* spp. and small sizes of colonies (Figure 7). *C. subdentata* completely dominated on protein baits in Zarafshan's oasis and does not allow other species to penetrate on its territory (Figure 7).

Interspecific and Intraspecific Aggressiveness

Total Agonistic Index (TAI) values for intraspecific aggressiveness of *C. subdentata* significantly differed for Kyzylkum and Zarafshan's oasis on the one hand, and Tashkent, Rostov-on-Don, and Crimea on the other ($P \leq 0.001$) (Figure 8).

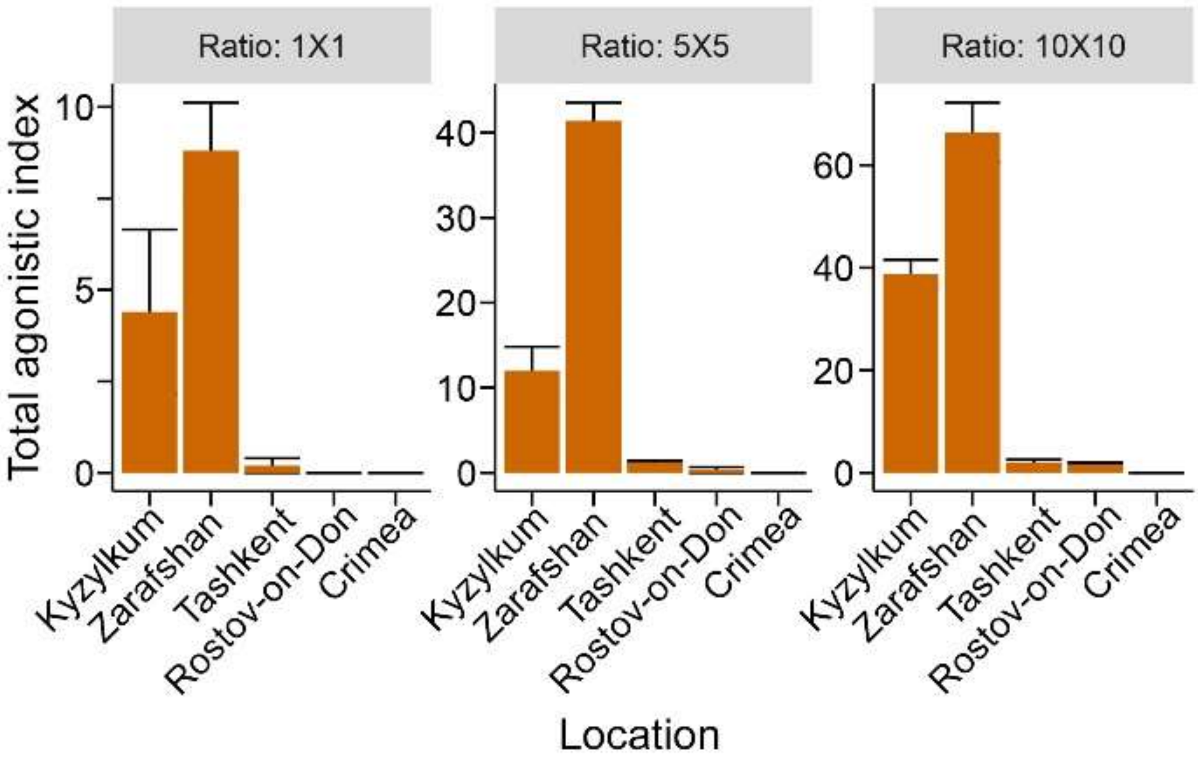

Figure 8. Total agonistic index's (TAI) mean (+SE). expressed intraspecific aggressive behavior of *C. subdentata* in its primary range (the Kyzylkum, the Zarafshan oasis, and Tashkent city) and secondary range (Rostov-On-Don city and Crimean Peninsula). The contests were performed between groups pairs with size ratios 1×1, 5×5, and 10×10

Differences in TAI between these regions were significant between A, B, C categories (P≤0.001) (Figure 8). With an increase in the number of participants in the fight in the Zarafshan's oasis, TAI also rose from 11 in category A to 42 and 66 in categories B and C respectively (*P*≤0.001). In Kyzylkum TAI 3, 15 and 41 in categories A, B, C respectively (*P*≤0.001), but the differences between Kyzylkum and Zarafshan are non-significant. Hence, *C. subdentata* demonstrated similar aggressiveness in intraspecific tests in natural habitats, but in Tashkent and in the secondary range (Rostov-On-Don, Crimea), intraspecific aggressiveness was not observed that was confirmed by a low value of TAI (Figure 8). Interspecific aggressiveness was fiercer than intraspecific (*P≤0.001*) (Figure 8 & 9).

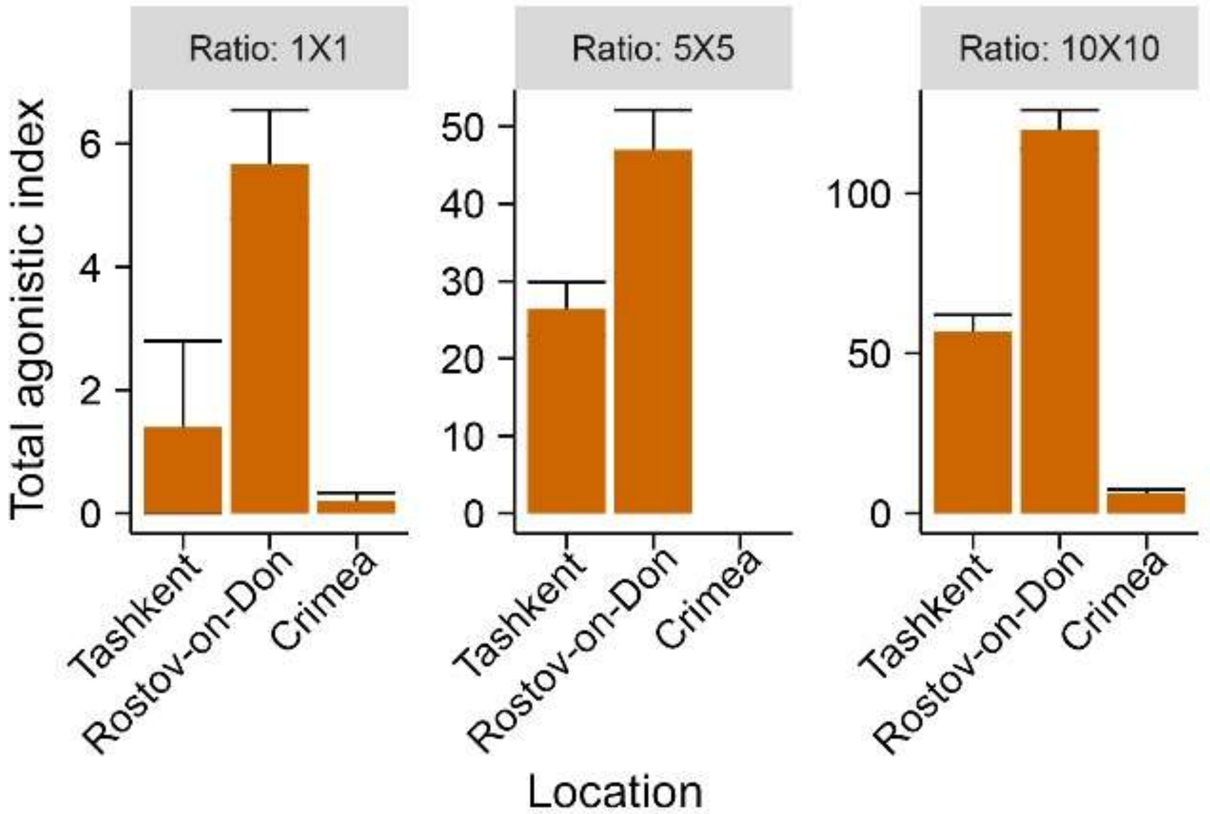

Figure 9. Total agonistic index's (TAI) mean and s.e. expressed interspecific aggressive behavior of *C. subdentata* in its primary range (Tashkent city) and secondary range (Rostov-on-Don city and Crimea). The contests were performed between groups pairs with size ratios 1×1, 5×5, and 10×10

Thus, in the interspecific tests of *C. subdentata* vs *L. neglectus* in Tashkent, the index value was higher and ranged from 3 (category A) to 30 (category B) and 60 (category C). The differences in TAI values between ants in single and group interspecies tests, as well as between intra and interspecies tests were significant (*P≤0.001*; Figure 9). Higher values of TAI were fixed in tests between *C. subdentata* vs *L. neglectus* in Rostov-On-Don which are 7 (in category A), 52 (category B), and 130 (category C) (*P≤0.001*) (Figure 9). Hence, the interspecific relations of *C. subdentata* vs *L. neglectus* in the secondary range were more intense than in the natural one.

In Crimea, in *C. subdentata* vs *M. bergi* (local species) contests in A and C categories were less fierce when compared to *C. subdentata* vs *L. neglectus*. The TAI index in Crimea values are significantly lower than in Rostov-On-Don and Tashkent which are 0.6 (category A) and 11 (category C) ($P \leq 0.001$) (Figure 9). This shows that *C. subdentata* was more aggressive towards the species with which it lives together in the primary and secondary ranges (*L. neglectus*) as compared to *M. bergi*, which it encounters only in one of the localities in the secondary range.

Crematogaster subdentata showed various behaviors in the primary and secondary ranges. Its workers are aggressive toward workers from other colonies it the natural habitats (Kyzylkum and Zarafshan's oasis) in Uzbekistan (Table 5). In contrary, workers of *C. subdentata* from different nests are tolerant of each other in Tashkent. So, this species here acquired most of the important traits of invasive species which includes tolerance between workers from different nests, exchange trails, polygyny and polycaly (up to the forming of supercolonies).

The number of *C. subdentata* workers killed in intraspecific conflicts was maximum in the natural habitats (Kyzylkum and Zarafshan's oasis) of Uzbekistan (Table 5). *L. neglectus* workers were always killed during fights with *C. subdentata*, and the total loss of ants in fights in the secondary range (Rostov-On-Don) was higher than in intraspecific fights of *C. subdentata* ($P \leq 0.05$) in the natural range (Table 5).

Both *C. subdentata* and *L. neglectus* are invasive species in the secondary ranges, but in the native range they are also territorial dominants in the multispecies ant assemblages, that lead to the aggressiveness of their conflicts. Furthermore, interspecific competition in the secondary range is more aggressive.

The results of these tests demonstrated that the intraspecific aggressiveness in *C. subdentata* is in the native range, but *C. subdentata* acquired tolerance between workers from different nests in the secondary range, as well as in the primary range in the cities, where polycalic colonies unite to the supercolony. In general, interspecific aggressiveness of *C. subdentata* is higher with respect to the species that coexists with it both in the natural and in the secondary ranges, i.e., *L. neglectus*, compared to the native *M. bergi* (in Crimea).

DISCUSSION

The biology, taxonomy, and zoogeography of *C. subdentata* may be the key factors in determining its characteristics as an invasive species (Stukalyuk 2015). The *Crematogaster subdentata* assign to the species-group *C. inermis* Mayr, 1862 of the subgenus *Crematogaster* s. str., the main distinguishing feature of which is the absence of propodeal spines. In particular, *C. inermis* and related species are widespread in the North Africa, the Iberian Peninsula, Cyprus, Israel, Syria and Lebanon, easternmost reaching Iran, but are absent in Asia Minor Afrotropical species are distributed from Sudan, Mozambique and Madagascar to South Africa, and are also recorded to Yemen (Collingwood & Agosti 1996).

Crematogaster subdentata distributed in the eastern part of the range of this group. Tarbinsky (1976) recorded this species from Kyrgyzstan (Tuya-Muyun desert) and Tajikistan (sandy desert in the western part of the Ferghana Valley), and from the vicinity of Balkhash Lake and the Muyun-Kum desert in Kazakhstan. Finally, *C. subdentata* was also found in Afghanistan (Collingwood 1961; Pisarski 1967a,b; 1970) and Mongolia (Pfeiffer et al. 2003;

2007; Pisarski 1969; Pisarski & Krzysztofiak 1981). The data about distribution of this species were supplemented in the more recent papers for Transcaucasia (Arakelyan 1994; Gratiashvili & Barjadze 2008), Kyrgyzstan (Borowiec et al. 2009; Schultz et al. 2006), Western China (Collingwood & Heatwole 2000), and Iran (Paknia et al. 2008; 2010).

Distribution and biological features of *C. subdentata* in the Central Asia were studied in detail by (Dlussky 1981; Dlussky et al. 1990). He pointed out that this species lives everywhere, including various types of deserts, where there is woody vegetation (mainly saxaul), and is also common inhabitant of urban landscapes. *C. subdentata* inhabits both lowlands and midlands, rising to altitude of just over 2000m (Pisarski 1967a).

Thus, it is suggested that the primary range of *C. subdentata* is the lowlands and partly mountainous regions of Central Asia, where it most commonly occur and widespread in various habitats. To the east, it penetrates the mountain systems of the Hindu Kush, Karakoram and the northern Himalayas, and to the west into the Transcaucasia, with the penetration route passed most probably through northern Iran. This is confirmed by the fact that to the north of the Caspian Sea, *C. subdentata* reaches only the Ural River (Guryev, now Atyrau). On the other hand, in the south of the European part of Russia, in the North Caucasus and in Crimea, *C. subdentata* is found sporadically and only in the anthropogenic habitats, i.e. here is its secondary range and invasion zone (Dubovikov & Yusupov 2017; Stukalyuk 2015).

Place of origin of *C. subdentata* probably were also in semiarid and arid regions of Central Asia. This territory started to form after the closure of Tethys Ocean from the east at the end of the Eocene and beginning of the Oligocene, when the Indian plate collided with Asia. The complete closure of Tethys and its transformation into a complex of isolated seas and lakes occurred at the beginning of the Miocene, when Arabian plate merged with Asia. Herewith, the ancestor (or chain of ancestors) of *C. subdentata* acquired a number of biological and behavioral adaptations making them successfully exist as a modern species in the desert zone. Thus, *C. subdentata* can be considered an autochthonous species in its modern primary range.

Some features of the colony structure of *C. subdentata* can be considered as the kind of preadaptation to the acquisition of the traits of invasive species. Despite that in the primary range (in the Kyzylkum) this species is monogynous, one colony consists of several isolated nests (main nest with queen and brood and auxiliary nests on the same plant) connected by trails. Similar permanent trails connect nests and brood-free feeding buds with aphid colonies. Such a system resembles that of *Lasius fuliginosus* (Latreille, 1798) or of the red wood ants (Dlussky 1981; Zakharov 2018). The biological features that are a wide range of habitats, nesting manners, and close relation with aphids providing the colonies with an almost inexhaustible source of food indicate a great adaptive potential of *C. subdentata*.

Crematogaster subdentata, similarly to arboreal tropical ants (Camarota et al. 2018), organizes mobilization to the discovered food sources and protects them from other ant species. Due to the vast majority of its workers, *C. subdentata* monopolizes almost all baits in the territory of supercolony. Besides, workers of *C. subdentata*, like those of other species of the genus, actively use chemical protective agents from the Dufour's glands (Daloze et al. 1991) that gives them additional advantages over other ants in conflicts. The tolerance to conspecific workers in the secondary ranges is inherent to invasive ants, for example, *M. rubra* in Canada. This species' workers completely displace local ants, numerically making up to 99% of all ants and outnumbering other species by 10–1300 times (Naumann et al. 2017). Like *M. rubra* in Canada, *C. subdentata* dominates its secondary range and outnumbering local species, especially on the area of supe colonies. On the other hand, *M. rubra* in the primary distribution area (e.g., Europe) is also capable of building supercolonies (Seifert 2018). In Ukraine, such supercolonies were found in the Carpathians, along the rivers flowing through the meadows (Radchenko 2016).

According to our data, *C. subdentata* also dominates in the primary range (except for Kyzylkum), and especially in the cities of Uzbekistan, where it acquired traits of invasive species. *M. rubra* has a normal nuptial flight in the native range (in Eurasia), but lost it in the secondary range (in the North America), where fertilized gynes move away from the nest for the short distances together with groups of workers, i.e., they establish new nests by budding (Hicks 2012; Radchenko & Elmes 2010). Similar pattern occurs in another invasive species, *L. neglectus* that has normal nuptial flight in the native area (Uzbekistan), and lost it in the secondary range (Espadaler & Rey 2001; Espadaler et al. 2004; Stukalyuk et al. 2020). In contrary, *C. subdentata* has a normal nuptial flight in both the primary and secondary ranges. In our opinion, this contributes to its faster spread, since newly founded colonies are able to unite with the supercolony where their protected territories meet each other (Stukalyuk & Netsvetov 2018) that makes *C. subdentata* even become highly invasive than some other invasive species. Many invasive species, for example, *L. humile*, hurt the species richness of local ant communities, crowding out even the dominant species (Cammell et al. 1996; Lach & Thomas 2008), or surrounding their foraging areas by the territories of their own supercolonies, as do *L. neglectus* (Paris & Espadaler 2012). In the case of *C. subdentata* in Crimea, we observed the crowding out of the local dominant (*M. bergi*), but the remaining species preserved and some of them (e.g. *T. caespitum*) even increased their density (Stukalyuk & Netsvetov 2018). Beyond ants, invasive species, for example, *Anoplolepis gracilipe*s Smith, 1857 can make the negative impact to other invertebrates, as was demonstrated for red endemic land crabs in tropical islands (Abbott 2005).

Colonies of the *Crematogaster* species are generally mono- or oligogynous, containing up to 2-5 queens (Dlussky et al. 1990; Radchenko 2016). Nonetheless, polygyny (and polydomy) is not uncommon for this genus, some species can form large colonies with hundreds of queens in the primary range, for example, *C. pygmaea* Forel, 1904 in Brazil (Quinet et al. 2009). The emergence of polygyny may be due to environmental factors, such as patchy distribution of habitats or high instability of nesting sites (Hölldobler & Wilson 1977), and queen number has been interpreted as an ecologically responsive trait, explainable by a combination of kin selection and ecological elements (Nonacs 1988). Perhaps this mechanism also worked for *C. subdentata* upon relocation from the Kyzylkum to Zarafshan's oasis, and then to cities.

Most probably, *C. subdentata* originally monogynous and has small-sized colonies as it was observed in Kyzylkum and mountainous regions of Central Asia. It is also noteworthy that in Kyzylkum a colony of *C. subdentata* may occupy several non-connected chambers on the same saxaul plant suggesting the colony is monogynous and polydomous (Dlussky 1981; Dlussky et al. 1990). In the Zarafshan's oasis *C. subdentata* forms large colonies with hundreds of thousands of workers and several queens (Marikovsky 1979). At last, *C. subdentata* acquired the traits of an invasive species in the urban environments, i.e., tolerance between workers from different colonies and forming of the supercolonies, while they are not as large as in the secondary range. In Yerevan (Armenia) this species also inhabits parks, but there are no data on the size of colonies (Arakelyan 1994).

Thus, the transition from monogyny to polygyny and from monocaly to supercoloniality, and as a result, acquiring the traits of an invasive species occurred in *C. subdentata* on the territory of the primary range at more favorable conditions in the anthropogenically modified landscapes. The conditions of the cities are similar to those in oases, where there is a higher level of humidity, a large number of trees and no strong competition with other species. Ant species that routinely alternate between monogyny and polygyny are numerous in Europe. This is also similar for *Myrmica* sp., *Tapinoma* sp. and *Formica* sp. including its subgenera, *Serviformica* sp. (Seifert 2018). The behaviour that these species have in common is partial independent colony founding. If the environments are favourable these species will form secondary polygyny and which sometimes will further lead to supercoloniality. Different social forms of *C. subdentata* may have possibly has the situation is similar behaviour to these species. However, the major difference of *C. subdentata* to other species is that it finds environments with trees especially in cities to be more favorable.

Crematogaster subdentata is not the only invasive species of ants that forms super colonies in urban environments. Similar behavior was previously demonstrated by *Tapinoma sessile*, which had monogynous, monodomous small colonies in natural habitats and formed polygynous supercolonies in urban areas (Buczkowski 2010). Consequently, this ability is inherent in only a small number of invasive ant species. Monogynous and polygynous ant colonies have opposite characteristics, as was shown by the example of *Pseudomyrmex ferruginea* Smith 1877 (monogyny) and *P. veneficus* (Wheeler, 1942) (polygyny) (Janzen 1973). Workers from monogynous colonies are hostile to workers, queens, and winged individuals from other nests thus resulted that their colonies usually do not exceed several thousand workers. In polygynous colony there is tolerance towards workers from other colonies; thus, colony sizes can reach up to several million individuals. After the nuptial flight, the queens establish new colonies away from their nest, or a part of an existing colony. All these characteristics were also observed in mono- and polygynous *C. subdentata* colonies.

The coexistence of mono and polygynous colonies in one species of ants is a common phenomenon. For example, such colonies are known in *Solenopsis invicta* Buren 1972 in the secondary range, in the USA (Greenberg et al. 1985). Queens from monogynous colonies may be larger in mass and have more developed ovaries compared to queens from polygynous colonies, for example, in *L. humile*) (Keller 1988). This is also observed in *C. subdentata* within the primary range. In ants, the monogyny is probably a primitive condition and polygyny is a derived condition (Brian 1983). Monogynous colonies of *C. subdentata* demonstrate a primitive social organization with a simpler structure of the foraging area compared to polygynous colonies. This indicates that the monogyny in *C. subdentata* was likely to be primary. For palaearctic species of the genus *Crematogaster*, monogyny is considered as primary, but when advancing to polygyny, representatives of the genus acquire the features of dominant species (Boulay et al. 2014).

The main reason for *C. subdentata* to acquire the behavior of an invasive species maybe due to its relocation to more favorable habitats with abundant food sources. The parameters for determining the size of colonies are the number of queens per nest and the activity of workers on the foraging trails. For example, one colony of *C. subdentata* in Kyzylkum is monogynous, there are already several queens per colony in Zarafshan's oasis, and many tens or even hundreds queens per colony in cities (Tashkent, Rostov-on-Don and Mykhailivka in Crimea). In the absence of the native Central Asian ant species-competitors in the secondary range, *C. subdentata* was able to form huge supercolonies there. The supercolonies of *C. subdentata* in Rostov-on-Don were even bigger than in Crimea. They occupy practically all the city and interrupted by only roads, ponds and large areas of trees (longer than 200 m) without heated buildings, where the nests of *C. subdentata* can survive in winter. Likely, this is due to the fact that invasion of *C. subdentata* in Rostov-on-Don started at least in early 1980th (Stukalyuk et al. 2021), but it appeared in Crimea in 2003 (Stukalyuk 2015).

The nuptial flight in *C. subdentata* was observed in the primary and secondary ranges at the end of August-September. Additionally, workers from different nests were found to be tolerant to one another, which may be due to the common set of cuticular hydrocarbons presence in all members of the supercolony, as was shown for the polygynous colonies of *Formica exsecta* Nylander, 1846 (Martin et al. 2009). *Crematogaster subdentata*, like *L. neglectus*, penetrated into the secondary range from the same region Central Asia (Stukalyuk et al. 2020). However, unlike *C. subdentata*, the colonies of *L. neglectus* are polygynous in the natural habitats in the primary range. Perhaps, the process for acquiring the invasive traits of *C. subdentata* was longer than that of *L. neglectus.*

CONCLUSION

In the primary habitat (Uzbekistan), *Crematogaster subdentata* acquires traits of an invasive species, getting into the cities (Tashkent), where there is a sufficient amount of resources – planting and tree alleys, parks, gardens. Here this species forms real supercolonies for the first time, with population hundreds of thousands of workers and several tens to hundreds of queens. In the secondary range, in Rostov-On-Don and Crimea, *Crematogaster subdentata* is capable to form much larger supercolonies (on the territory of hundreds of hectares or more) than in Tashkent. The population of such supercolonies reaches up to tens of millions of workers and thousands of queens. This is achieved due to a milder climate (lower temperature drops, higher air humidity), as well as due to successful competition with local ant species. The results show that *C. subdentata* acquires the traits or behavior of invasive species in urban territories even in its natural range. This suggests the high ecological plasticity of this species and the potential threat of the formation of invasive traits not only in native ants, but also in other components of biota that can become dangerous pests as a result of human activity.

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