

Lasius neglectus Van Loon et al. (Hymenoptera, Formicidae), an Invasive Ant Species in Crimea

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Abstract—Data on distribution of *Lasius neglectus* Van Loon et al. in Crimea are reported. The structure of foraging areas of 111 monocalic and polycalic colonies, the daily activity rhythm, and the visiting of 26 species of trees by *L. neglectus* workers were studied; over a third of the visited tree species were conifers. Most colonies of *L. neglectus* in Crimea are monocalic. No replacement of the 12 native ant species present in the territories of the monocalic and polycalic colonies of *L. neglectus* was observed. Invasion of *L. neglectus* to Crimea probably started in the early 1970s.

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Invasive species of plants and animals, including ants, can drastically change the structure of ecosystems and even cause their degradation in the new areas of distribution (Holway et al., 2002). At present, over 200 ant species introduced by man into new territories are known; 5 of them are regarded as dangerous invaders (Lowe, 2004).

Invasive ant species share a number of features: a high level of polygyny; the ability to form polycalic colonies and federations (in the terminology of Zakharov, 2015); fertilization of gynes inside the nest; formation of new nests by budding, etc. This considerably reduces the level of aggression between the neighboring colonies and gives the invasive ants competitive advantage over the native species.

Only two species of the subgenus *Lasius* Fabricius, 1804 are polygynous with a high level of social organization and with fertilization of gynes within the nest: *L. neglectus* Van Loon, Boomsma et Andrásfalvy, 1990 and *L. sakagamii* Yamauchi et Hayashida, 1970, the latter distributed in Japan.

Colonies of *L. neglectus* were for the first time found in Budapest in 1974 (Seifert, 2000), but the species was described as new to science much later (Van Loon et al., 1990). *Lasius neglectus* is morphologically similar to *L. turcicus* Santschi, 1921, and Seifert (1992) at first regarded these names as synonyms and assumed that *L. neglectus* referred to the

polygynous form of the species. Later, Seifert (2000) reconsidered his opinion and restored the name *L. neglectus* from synonym.

The species is believed to have originated in Asia Minor and subsequently spread over wide territories both to the west and east. It is presently known from nearly 200 localities in 21 countries, and its range stretches from the Canary Islands to Uzbekistan and Kyrgyzstan, including South and Central Europe, the north and south of Ukraine (Kiev, Kherson Province), the south of European Russia (Rostov-on-Don, Bataisk), Israel, the Transcaucasia, and Iran (Schultz and Seifert, 2005; Schultz et al., 2006; Espadaler et al., 2007; Czechowski et al., 2012; Artokhin et al., 2013; Stukalyuk, 2017) (Fig. 1).

The dispersal of this species was most probably determined by human activity, i.e., it was accidentally imported into new localities together with introduced plants. This fact explains its presence almost solely in parks and public gardens in cities and towns. *Lasius neglectus* was found in Kherson Province (Askania-Nova arboretum) and in Crimea as early as at the end of the 1970s but these data were only recently published (Radchenko et al., 2012).

The goal of this work was to study the distribution of *L. neglectus* in Crimea and such features of its biology as (a) the structure of the foraging territories of the different categories of its colonies, (b) its diurnal

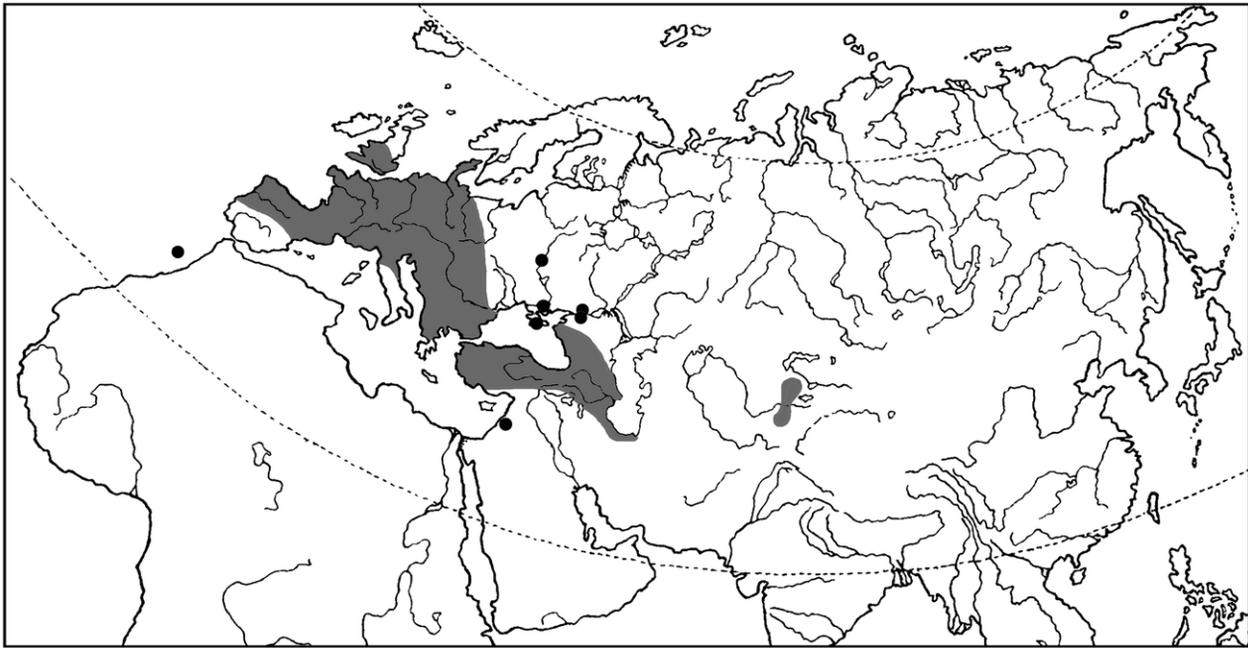


Fig. 1. Range of *Lasius neglectus* Van Loon et al.

activity pattern, (c) visitation of various tree species by *L. neglectus* workers, and (d) co-occurrence of *L. neglectus* with native ant species and its influence on these species in myrmecocomplexes.

MATERIALS AND METHODS

The study area and material. Stationary research was performed in 10 localities in Crimea, in June and July 2013 (Table 1); the foraging territories of *L. neglectus* colonies were mapped in detail in 5 of them: Yevpatoria, Sudak, Kurortnoe, Novy Svet, and the Biological research station of Karadag Nature Reserve. Altogether, the structure of the foraging territories, trails, and nests of 111 colonies of this species was analyzed. In Simferopol, where in 1998 and 1999 we found a federation of *L. neglectus*, detailed mapping was not carried out but the boundaries of territories of polycalic colonies were determined; these boundaries were assumed to be marked by the peripheral trees visited by foragers. Repeated monitoring of this population was performed in 2013. Collections made in 1978–1981 (Radchenko et al., 2012) were also used in this work.

Terminology. The colony-level and higher structures in *L. neglectus* are described here using the terms “monocalic” and “polycalic” colony (with different types of polycaly), and also “federation” (according to Zakharov, 2015). The monocalic colony inhabits one

nest; the polycalic colony inhabits several nests simultaneously. The following types of polycaly can be distinguished. Simple polycaly (PLC₁) is the type characterized by the presence of temporary (usually foraging) nests besides the central nest, with all the brood concentrated in the latter. Polycaly with separate brood nests (PLC₂) is the type of polycaly with three types of nests: central, brood, and foraging. Federation is a permanent polydominant supercolonial structure consisting of several polycalic colonies united by a network of connections. The primary federation is the result of development of a single colony, whereas the secondary federation, also referred to as “supercolony,” arises by merging of existing polycalic colonies.

Methods of study. Workers of *L. neglectus* were collected in each Crimean locality for subsequent identification. The density of *L. neglectus* colonies per unit area was determined by the route survey method; mapping of foraging territories was done according to Dlussky (1965) and Zakharov and Goryunov (2009). Since the main food source for *L. neglectus* is sugary secretion of aphids living on shoots and leaves of trees and shrubs, we suppose that the mean number of trees used by a colony reflects its size more precisely than the total area of its foraging territory. In assessing the species and age composition of trees visited by *L. neglectus*, the diameter of each trunk was measured by standard methods of forest resource management

Table 1. Finding localities of *Lasius neglectus* and places of stationary research in Crimea from 1978 to 2013

Place of finding	Latitude (N)	Longitude (E)	Altitude, m above sea level	Dates	Number of workers collected
Simferopol	44°56'53"	34°06'15"	300	VI.1998	10
				VI.1999	15
				VI.2013	50
Yevpatoria	45°12'00"	33°21'30"	3–22	VI.2013	100
Yalta (Nikitsky botanical garden)	44°30'34"	34°13'58"	54	VI.2013	15
Sudak	44°51'05"	34°58'21"	50	VI.2013	157
Novy Svet	44°49'45"	34°54'45"	33	VI.2013	23
Kurortnoe	44°54'45"	35°11'30"	12	VI.2013	18
Karadag (Biological research station)	44°55'55"	35°13'44"	20	VI.2013	9
Sovetskoe	44°32'05"	34°11'15"	458	VI.2013	5
Mikhailovka	45°06'45"	33°36'50"	17	VI.2013	7
Saki	45°08'01"	33°34'38"	10	VI.2013	10
Alushta	44°40'02"	34°23'52"	50	VIII.1978	8
Privetnoe	44°49'20"	34°40'40"	72	VIII.1981	50
Popovka	45°17'50"	33°02'15"	5	VIII.1981	30
Ivanovka	45°04'20"	33°39'35"	7	VIII.1981	15
Karasevka	44°59'45"	34°36'20"	256	VIII.1981	3
Mys Martyan Nature Reserve	44°30'38"	34°15'25"	50	VI.1979	5

(Anuchin, 1982). Altogether, 304 trees of 26 species visited by *L. neglectus* workers were recorded. The size of colonies of *L. neglectus* was calculated by determining the intensity of movement of workers along the forage trails and comparing the results with similar data obtained earlier for other ant species (Stukalyuk and Ivanov, 2013; Stukalyuk, 2015). Co-occurrence of *L. neglectus* with other ants was also recorded.

Assessment of ant activity outside the nest was made by the method of Zakharov and Goryunov (2009). The model colony of *L. neglectus* in Sudak (the Sokol health resort) consisted of 20 nests connected by 25 trails. This was the second largest colony found by us in Crimea (after the one in Simferopol), and the largest of those mapped in detail. There were 23 white poplars *Populus alba* within the foraging territory of the model colony; 17 nests were located at the tree bases, and others, in cracks of asphalt pavement not far away.

Since workers of *L. neglectus*, when outside the nests, move mainly along the forage trails, their foraging activity was assessed on trails leading up the tree trunks to the aphid colonies. For this purpose, a gate-shaped limiter raised over the surface so as not to im-

pede the moving of ants was installed on each of the three chosen trails of the model colony. Every hour of daylight (from 7 a.m. to 9 p.m. Kiev time), the workers of *L. neglectus* moving in both directions (down the trunk towards the main nest, and up the trunk towards the aphid colonies in the tree) were recorded for 2 minutes. The shade soil temperature was measured concurrently with ant activity assessment.

Data were statistically processed using Origin 8.0 software. Distribution of such characters as the number of nests, the number of trees, and the level of social organization (with monocalic colonies coded as 1, and polycalic colonies with two or more nests, as 2), did not deviate from the normal by the Shapiro-Wilk test; this permitted the use of Pearson coefficient of correlation. The significance of differences between the mean numbers of visited trees for *L. neglectus* colonies with different levels of social organization was determined by the *t* test at $p < 0.05$.

Since the distribution of ants on all the three forage trails of the model colony differed from the normal, we used nonparametric methods of analysis: Spearman correlations between characters, Wilcoxon *T* test at $p < 0.05$.

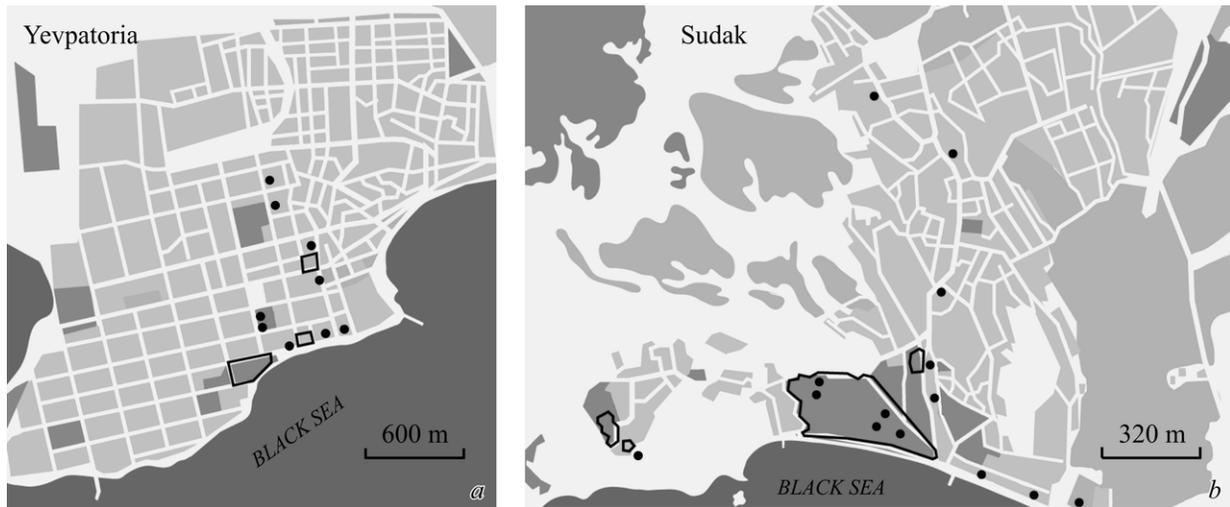


Fig. 2. Distribution of monocalic and polycalic colonies of *Lasius neglectus* in Yevpatoria (a) and Sudak (b), Crimea. Monocalic colonies are shown as black dots; the areas of polycalic colonies are outlined in black.

RESULTS

Specific biological features of *Lasius neglectus* in Crimea. *Lasius neglectus* was found in different climatic zones within the territory of Crimea (temperate continental in Steppe Crimea and subtropical on the Southern coast) and at different altitudes (from 3 to 458 m above sea level; see Table 1). At the same time, the species occurred almost exclusively in urbanized territories of the whole central and south Crimea and was found outside human settlements only in Kanakskaya Balka, in the environs of Privetnoe. *Lasius neglectus* was a common species in Simferopol and more southern localities (Yevpatoria, Sudak); this indicates either a longer history of its invasion or the more favorable conditions in this part of the peninsula.

In Yevpatoria and Sudak, all the polycalic colonies of *L. neglectus* were found in public gardens and parks within 100–300 m of the coast, whereas monocalic colonies were usually associated with single trees and occurred up to 3 km from the coast (Fig. 2). In the latter case, colony growth was probably limited by lack of place for nesting, since the trees were surrounded with asphalt pavement or stone tiles.

Nests of *L. neglectus* are built in the soil, mainly close to the bases of the foraged trees; the nest entrance is a small hole by the trunk. Besides central nests, polycalic colonies may have a network of small, probably foraging nests located, as a rule, among the undergrowth up to 1 m high housing aphid colonies.

Nests in polycalic colonies of *L. neglectus* are mainly connected by rather shallow soil tunnels. Sur-

face trails may also exist but most often they are absent and only single workers are to be seen in the foraging area. Forage trails on tree trunks are conspicuous due to the great numbers of workers. There is usually only one forage trail, sometimes several trails per trunk.

Although this species has no nuptial flight and copulation takes place within the nest, in early June, after rains, we observed numerous males on the soil near nest entrances. Fertilized gynes remain in the maternal nest, which results in a high level of polygyny. We found single wingless gynes (probably fertilized) on tree trunks or close to them on the ground, near nest entrances.

Monocalic colonies of *L. neglectus* may be divided into two groups: those controlling one tree and those controlling several trees. The former are quite small and comprise 1–2 thousand workers, whereas the population of the latter may amount to 5–10 thousand. Polycalic colonies may have tens of nests. Federations of *L. neglectus* include up to several hundred nests and count several hundred thousand workers. The ratio of mono- and polycalic colonies in different localities may characterize the level of invasion of this species (Table 2).

The presence of only monocalic colonies in Novy Svet may indicate either the initial stage of invasion or conditions unfavorable for colony growth. At the same time, great numbers of polycalic colonies in Yevpatoria and Sudak correspond to a high level of invasion and may be related both to favorable conditions and to an earlier occupation of these territories.

Table 2. The number of *Lasius neglectus* colonies of different categories in different localities in Crimea (percentage in parentheses)

Locality	Monocalic with one tree in foraging territory	Monocalic with several trees in foraging territory	Polycalic
Novy Svet	7 (100.0)	–	–
Karadag biological research station	6 (86.0)	–	1 (14.0)
Kurortnoe	6 (60.0)	–	4 (40.0)
Yevpatoria	10 (42.0)	3 (13.0)	11 (45.0)
Sudak	25 (40.0)	13 (20.0)	25 (40.0)
Total	54 (49.0)	16 (14.0)	41 (37.0)

Table 3. Distribution of *Lasius neglectus* colonies by the number of nests and the number of controlled trees in the studied localities

Number of nests in colony	Number of colonies (percentage in parentheses)	Number of trees controlled by one colony		
		mean	min	max
1	70 (63.1)	1.4 ± 0.1	1	7
2	18 (16.2)	2.7 ± 0.2	1	5
3	7 (6.3)	4.4 ± 0.5	2	6
4	6 (5.5)	4.8 ± 0.5	4	7
5	2 (1.8)	7.5 ± 0.5	7	8
6	5 (4.5)	7.8 ± 1.7	4	14
7	1 (0.9)	9	–	–
9	1 (0.9)	10	–	–
20	1 (0.9)	23	–	–

The number of nests in *L. neglectus* colonies probably increases in several steps (Table 3). At the beginning of invasion, two thirds of the colonies are monocalic and the mean number of controlled trees only slightly exceeds that of nests. Then, as the colony grows, several neighboring trees are included in its controlled area, which may eventually result in building of new nests and formation of polycalic colonies and federations.

Colonies with 2–6 nests formed the prevalent group (34.3%) among polycalic ones, whereas polycalic colonies with 7–20 nests, i.e., potential federations, comprised less than 3%. The size of foraging territories and the number of controlled trees increased sharply in colonies with five or more nests.

Monocalic colonies controlled half as many trees as colonies with two nests ($p < 0.05$); the first abrupt change in the number of controlled trees took place in transition from monocaly to polycaly. Polycalic colonies with 3 nests controlled 1.5 times as many trees as

those with 2 nests ($p < 0.05$), and their foraging territories were larger. At the same time, the difference in the mean number of controlled trees between colonies with 3 and 4 nests was non-significant, so that such colonies could be classified in one category. Polycalic colonies with 5 and 6 nests were also classified by us in a separate category; their foraging territories included 1.5 times as many trees as those of colonies with 3 and 4 nests ($p < 0.05$). Thus, transition to colonies with 5 or 6 nests was also marked with a considerable change in the mean number of trees within the foraging territory. For colonies with 7 and more nests statistical calculations were not performed due to insufficient data (only one colony in each category); yet, such nests preserved the tendency for increasing the number of controlled trees 1.5–2-fold as compared with colonies with 3 or 4 nests.

Significant Pearson's correlations ($p < 0.05$) were found between the following parameters: the number of nests in a colony and the number of visited trees

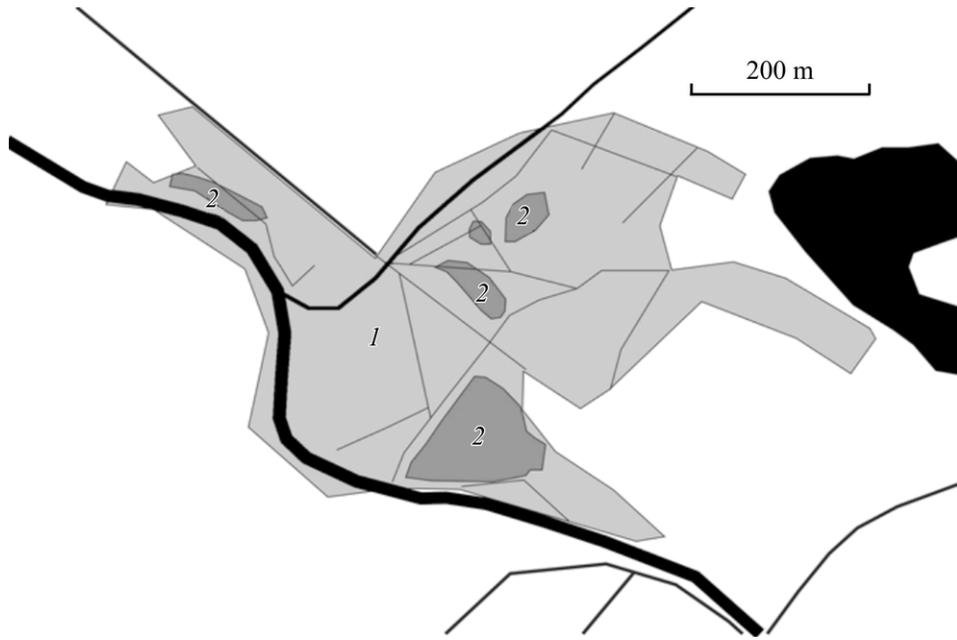


Fig. 3. Boundaries of the primary federation of *Lasius neglectus* in Gagarinsky Park (Simferopol) in 1999 (1) and 2013 (2).

(0.91); monocaly, polycaly, and the number of nests (0.59); monocaly, polycaly, and the number of controlled trees (0.58). Thus, transition of *L. neglectus* from monocaly to polycaly resulted in increasing the numbers of controlled trees and, correspondingly, expanding of the foraging territory.

The levels of social organization of colonies in *L. neglectus*. There are several levels of social organization characteristic of *L. neglectus* in the territory of Crimea. The initial and the most frequently observed level is monocaly. In transition to polycaly the colony size increases and a foraging nest is constructed (simple polycaly, PLC₁); colonies with 2 nests (central and foraging ones) and 2 trees found by us probably correspond to this stage. In transition to polycaly with brood nests (PLC₂) the feeding territory expands to include from 4 to 9 controlled trees.

In our opinion, the next level of the social organization of colonies, namely that of federation, may occur in a colony whose foraging territory includes not less than 20 trees. Of all the colonies found by us in Crimea, only two corresponded to the federation level: the model colony in Sudak and a colony in Simferopol. In transition to each next level of social organization (monocaly, PLC₁, PLC₂, federation) the number of nests and controlled trees increases by 1.5–2 times.

We have not recorded exchanges of workers or brood between colonies (which would be characteris-

tic of the secondary federation) even in large polycalic colonies with PLC₂ or in the potential primary federation of *L. neglectus* in Simferopol. The primary federation status of these “supercolonies” of *L. neglectus* is also supported by the literary data (Tartally, 2006).

The primary federation of *L. neglectus* in Simferopol. In 1998 and 1999, we found the largest polycalic colony of *L. neglectus* in Gagarinsky Park in Simferopol (Fig. 3). It existed within an area of at least 40 ha and quite corresponded to the characteristics of a primary federation. The nests were mainly located along asphalt pavements and were connected with surface trails. The ants visited practically all the trees in the park and formed forage trails on their trunks, along which foragers were actively moving. In 2013, only 3 or 4 scattered colonies unconnected with each other and located at long distances were observed there instead of the federation. These colonies were located in the central part of the former federation, and reduction of the federation territory (Fig. 3) started from the periphery. We did not find any evident factors which could lead to the disappearance of the federation; during these years there was neither reconstruction nor development in the park territory. Yet, according to our observations, approximately one fifth of the coniferous trees which had been visited by the ants had dried up by 2013, and this could have reduced the potential trophic resources.

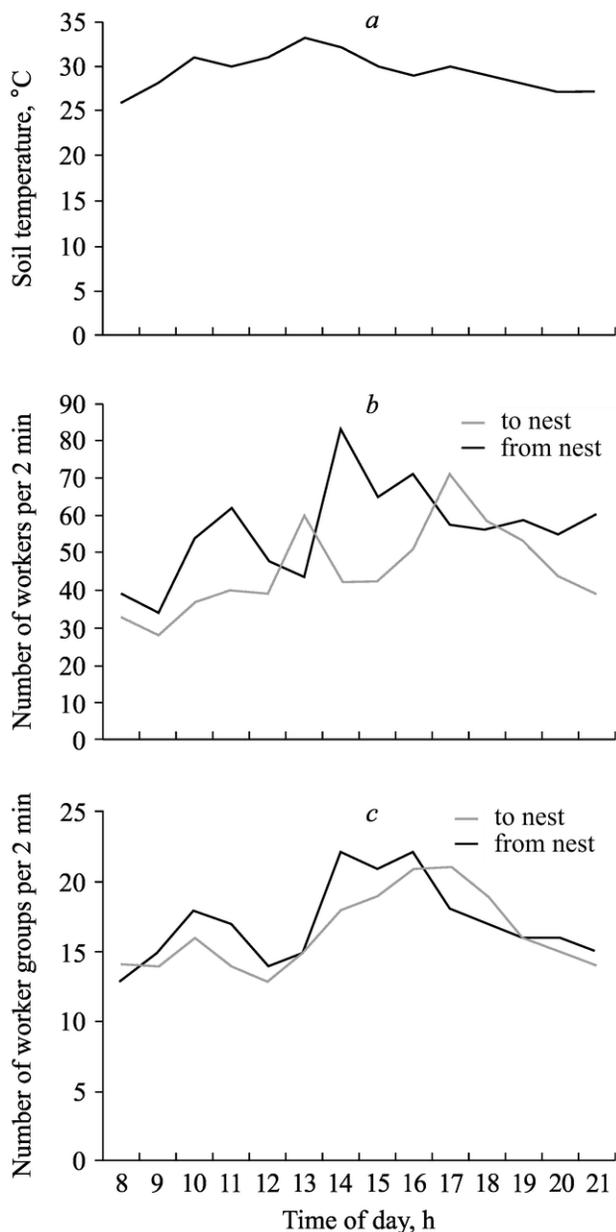


Fig. 4. Diurnal activity of *Lasius neglectus* on 3 forage trails of a model polycyclic colony: (a) soil temperature; (b) mean activity of workers; (c) mean activity of groups of workers.

Reduction in *L. neglectus* populations was also recorded in some European countries (Tartally et al., 2016).

Diurnal activity of *Lasius neglectus*. According to our observations, workers of *L. neglectus* were also active at night, but we did not make any quantitative assessments during that period. Similar to the parameters of diurnal activity of other Crimean ant species, in which night activity ceases at soil temperatures

lower than +14°C, this may be so in *L. neglectus* as well (Stukalyuk and Radchenko, 2010; Stukalyuk, 2013; Stukalyuk and Ivanov, 2013).

Lasius neglectus is characterized by alternating activity cycles, i.e., changes in the direction of the streams of workers moving towards and away from the nest (Figs. 4b, 4c). We found no significant correlation between the soil temperature (Fig. 4a) and intensity of the movement of workers or groups of workers. The most probable reason for this is the small range of temperature fluctuations in the daylight time in shaded places typically inhabited by *L. neglectus*, which allowed the workers to remain highly active in the daytime. Correlation was found only between the total number of workers and the time of day (0.61). In all probability, gradual warming-up of the ground surface in the morning and its cooling at night caused increase and decrease in the workers' activity in the foraging territory. No significant differences in the intensity of the two opposite streams of workers during the day were observed for 2 out of 3 forage trails (Wilcoxon *T* test, $p < 0.05$). Thus, the number of workers moving away from and towards the nest was approximately the same during the day. The difference recorded for the third trail may have been determined by the overlapping streams of workers from two unaccounted-for neighboring nests. There was one such nest at each of the two other trails.

Analysis of the mean number of workers moving in both directions for all the three trails revealed distinct alternation of cycles. The stream of workers moving away from the nest prevailed from 8 to 12 a.m., from 2 to 4 p.m., and after 8 p.m. Mass return to the nest was recorded at 1 and 5 p.m. (Fig. 4b). Thus, longer, 3–4-hour cycles corresponded to streams of workers moving away from the nest, and shorter, 1-hour cycles, to those moving towards the nest. The difference is determined by the fact that foragers moving from the nest actually have different destinations since they have to disperse over the tree crown to visit different aphid colonies.

Workers of *L. neglectus* moved along forage trails not singly but in groups. These groups also revealed distinct alternation of longer and shorter cycles but on the whole the gradient of their movement changed faster; therefore the cycles were short in most cases.

Spearman's correlations were observed between the following parameters: 0.94 and 0.95 between the general level of activity and the direction of one of the streams (towards the nest or away from it), and also

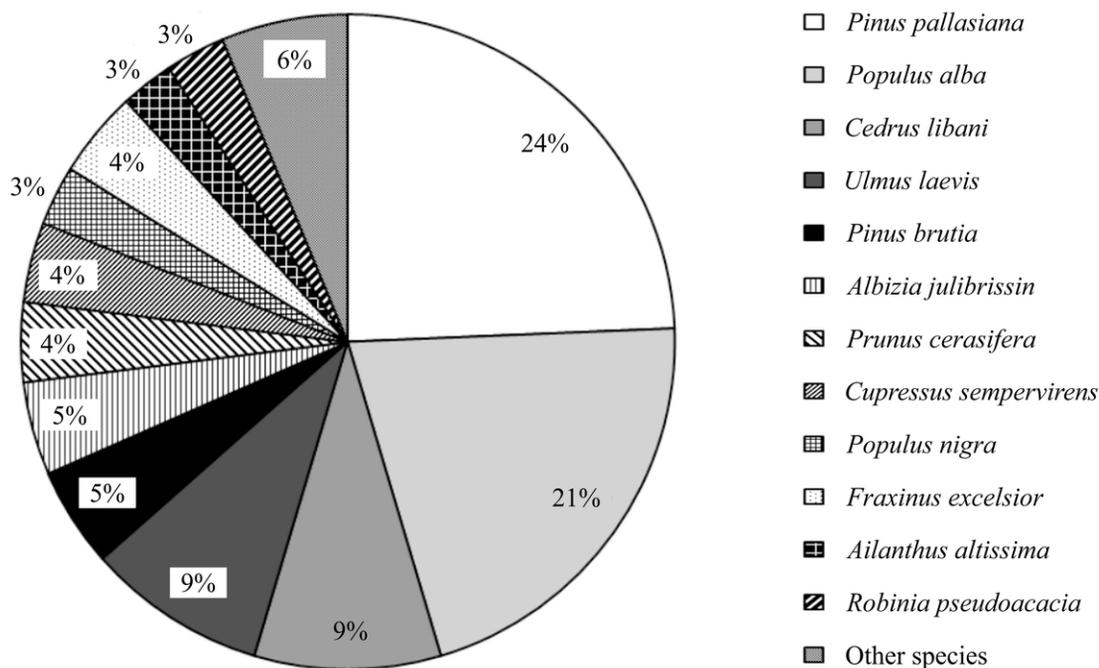


Fig. 5. Fractions of different species of trees visited by *Lasius neglectus* foragers in Crimea: percentage of all the trees on which forage trails were found.

0.78, between the streams of workers moving in the opposite directions. Thus, when general activity on the trails intensified, an increase in the activity of one stream caused an increase in the other (Fig. 4c). Nevertheless, groups moving away from the nest were prevalent; it was only in the evening, at 5–6 p.m. that their activity was lower than that of groups returning to the nest. This difference may be related to mobilization of worker groups occurring regularly at a certain time of day, whereas return to the nest depended only on the filling of the forager’s crop with honeydew. On the whole, the stream of workers returning to the nest was more uniform than the opposite one and contained fewer groups.

There were also positive correlations between the number of workers and the number of groups on the trails: 0.84 ($p < 0.05$) for workers and groups moving from the nest, and 0.64 for workers and groups moving towards the nest. Only one correlation was revealed for the oppositely directed streams: a correlation of 0.57 between all the workers moving from the nest and groups of workers returning to the nest. Therefore, the stream of workers moving from the nest was more structured and connections between workers and their groups were closer, probably as the result of mobilization of workers to the foraging territory.

The activity of both workers and their groups on the forage trails revealed alternation of longer and shorter cycles of the differently directed streams: away from and towards the nest. One cycle (from one gradient change to the next) was 1–2 h long and corresponded to mass emergence of workers and their groups from the nest or to their return. The longer cycle probably resulted from overlapping of several shorter cycles, whereas the differently directed streams could become leveled when some workers returned to the nest and others left the nest at the same time.

Tree species visited by *L. neglectus*. In the territory of Crimea, we recorded foragers of *L. neglectus* on 26 species of trees and shrubs, of which 12 were most actively visited (Fig. 5).

Most trees visited by *L. neglectus* were introduced species typically growing in parks; over one third of them were conifers. It is significant that most of the introduced trees were either never visited by the native ant species or only single individuals occurred on them. The trees most often visited by *L. neglectus* were the black pine *Pinus pallasiana*, the white poplar *Populus alba*, the cedar of Lebanon *Cedrus libani*, the Russian elm *Ulmus laevis*, the Turkish pine *Pinus brutia*, and the Persian silk tree *Albizia julibrissin*.

Table 4. Age related parameters of plant species visited by *Lasius neglectus* in Crimea

Tree species	Number of examined trees	Mean trunk diameter, m	Age group, years
<i>Pinus pallasiana</i>	74	0.262 ± 0.009	61–80
<i>Populus alba</i>	64	0.412 ± 0.014	81–100
<i>Cedrus libani</i>	28	0.342 ± 0.017	141–160
<i>Ulmus laevis</i>	27	0.349 ± 0.032	61–80
<i>Pinus brutia</i>	15	0.352 ± 0.023	81–100
<i>Albizia julibrissin</i>	14	0.166 ± 0.020	21–30
<i>Prunus cerasifera</i>	12	0.132 ± 0.015	11–20
<i>Cupressus sempervirens</i>	12	0.263 ± 0.023	61–80
<i>Populus nigra</i>	9	0.478 ± 0.033	41–60
<i>Fraxinus excelsior</i>	13	0.241 ± 0.027	61–80
<i>Ailanthus altissima</i>	8	0.255 ± 0.015	41–60
<i>Robinia pseudoacacia</i>	9	0.129 ± 0.015	31–40

Table 5. Co-occurrence of *Lasius neglectus* and native ant species in Crimea

Category of colony	Mean number of native species per 1 tree	Mean number of jointly visited trees
Monocalic	1.2 ± 0.1	1.3 ± 0.1
Polycalic	1.3 ± 0.1	1.9 ± 0.5

Mature and old trees aged over 40 years were most actively visited (Table 4).

Three of the above tree species were visited only or mainly by workers from monocalic colonies: *A. julibrissin* (100%), *Prunus cerasifera* (67%), and *Pinus nigra* (56%). The Persian silk tree was common in alleys stretching along the coast while other species were represented by single trees separated by spacious asphalted areas unapproachable to ants. Formation of polycalic colonies of *L. neglectus* would be difficult or impossible under such conditions.

The white poplar, the Russian elm, and the black pine, i.e., the most common tree species in Crimea, were most often visited by the native ant species together with *L. neglectus*.

Relations between *Lasius neglectus* and other ant species. There were 10 ant species co-occurring with *L. neglectus* on tree trunks: *Camponotus fallax* (Nylander, 1856), *C. aethiops* (Latreille, 1798), *C. truncatus* (Spinola, 1808), *C. piceus* (Leach, 1825), *C. lateralis* (Olivier, 1792), *Dolichoderus quadripunctatus* (Linnaeus, 1771), *Formica cunicularia* Latreille, 1798, *F. glauca* Ruzsky, 1896, *Plagiolepis taurica* Santschi, 1920, and *Crematogaster schmidtii* Mayr, 1853. On the soil surface they were joined by *Tetramorium cae-*

spitum (Linnaeus, 1758) and *Tapinoma erraticum* (Latreille, 1798).

Five of these species, namely *Camponotus fallax*, *C. truncatus*, *C. lateralis*, *D. quadripunctatus*, and *Crematogaster schmidtii*, are dendrobionts, i.e., they may have nests or forage trails on trees visited by *L. neglectus*. The remaining species are herpetobionts; they less frequently visit plants of the tree layer and consequently compete less with *L. neglectus* for carbohydrate resource. *Crematogaster schmidtii* is an obligate dominant in multispecies ant assemblages (Stukalyuk and Radchenko, 2010). The species most often recorded together with *L. neglectus* were *Camponotus truncatus* (31% of cases), *F. cunicularia* (27%), and also *Crematogaster schmidtii* and *Camponotus piceus* (10% each). Of these, only *Crematogaster schmidtii* has sufficiently large colonies and makes forage trails on trees; its workers occurred on the same tree with *L. neglectus* only in those cases when colonies of both species were small. Ants of the other species usually move singly over the trunks and can more easily enter the foraging territory of *L. neglectus*.

On average, native ant species were recorded on 12.8% of the total number of the trees visited by *L. neglectus*. The number of co-occurring species was

the same on trees controlled by monocalic (1.2 ± 0.1) and polycalic colonies of *L. neglectus* (1.3 ± 0.1 species, $p < 0.05$; see Table 5).

DISCUSSION

Is *Lasius neglectus* a native or an invasive species in Crimea?

The native origin of *L. neglectus* may be indicated by high percentage of monocalic colonies (63% of the total number of examined colonies, from 40 to 100% of the colonies in different Crimean localities), and also by the finding of this species outside residential areas.

However, a number of circumstances point to the invasive status of *L. neglectus* in Crimea. First, the species was recorded only in human settlements, with the only exception of the Kanakskaya Balka ravine. However, the latter locality is close to Privetnoe and Rybachie villages; in and near the ravine there are several health resorts and private houses and many “exotic” trees and shrubs, therefore its territory cannot be considered a completely natural landscape. Second, intensive study of the Crimean ant fauna both in the natural ecosystems and in settlements was started as early as in the first third of the XX century by V.A. Karavaev, since the 1970s it was conducted by E.N. Malii, and since the 1980s and up to the present time it has been carried out by the authors. We have examined hundreds of specimens of the genus *Lasius* from Crimea kept at the Institute of Zoology of the National Academy of Sciences of Ukraine, the Zoological Museum of Moscow State University, the Zoological Institute of the Russian Academy of Sciences (St. Petersburg), and other institutions, and found out that the first records of *L. neglectus* in Crimea were made in the late 1970s. Third, workers of this species mainly forage on introduced trees on which the native ant species are extremely rare or absent.

In our opinion, the available data indicate that *L. neglectus* is most probably not a native species in Crimea but an introduced invasive species.

Lasius neglectus is sufficiently widespread in Crimea. It could have been initially introduced into large urban areas of Simferopol, Yevpatoria, Sudak, and Yalta together with planting stock, since a large polycalic colony was found in the territory of Nikitsky botanical garden. From such places *L. neglectus* could have subsequently dispersed into smaller residential

areas where at present its polycalic colonies are either scanty or unrecorded.

It is interesting to note a considerable reduction of the area inhabited by this ant species in Gagarinsky Park in Simferopol: in 1999 the federation of *L. neglectus* occupied 40 ha but in 2013 it did not already exist as a single whole. A similar picture of stagnation and disappearance of populations of this species was also recently recorded in other European countries (Tartally et al., 2016).

The exact time of invasion of *L. neglectus* into Crimea is rather difficult to determine, but it probably happened in the early 1970s, similar to West European countries.

Since the level of ant aggression is primarily related to the dynamic density of workers in the territory, which in turn depends on the colony size (Zakharov, 2015), foragers from large polycalic colonies of *L. neglectus* are more aggressive and competitive during contacts with native ant species which have a lower level of social organization. Polycalic colonies of *L. neglectus* become the main consumer of carbohydrate food (honeydew of aphids) in a given biocenosis and thus reduce accessibility of this resource to other ant species, finally replacing them and impoverishing the ant fauna. For instance, 10 ant species were found within the territory of *L. neglectus* federation in Budapest, and 17 species in control plots (Nagy et al., 2009). At the same time, as shown by the example of the monocalic colony of *L. neglectus* in Kiev (Stukalyuk, 2017), complete replacement of native ant species does not happen at the initial stage of invasion.

Polycalic colonies of *L. neglectus* in Crimea occupy up to 3 ha, and their foraging territories include not more than 20 trees. This is considerably less than in the Mediterranean and Central Europe where federations of this species may occupy up to 3600 ha (Czechowska and Czechowski, 2003; Espadaler et al., 2007). A high percentage of monocalic colonies was recorded in many localities of Crimea.

As distinct from many countries of Central and South Europe, in Crimea *L. neglectus* does not exert a considerable influence on the native ant fauna. The resources (honeydew of aphids) of the jointly visited trees seem to be sufficient for all the ant species, although *L. neglectus* may play the dominant role in their consumption. In case of monocalic colonies, the small colony size may prevent *L. neglectus* from controlling the presence of other ant species on trees.

Foragers from polycalic colonies of *L. neglectus* usually form 1 or 2 trails on the trunk and are rarely seen outside them. By contrast, ants of native species, with the exception of *Crematogaster schmidtii*, move singly over the trunks without forming forage trails, whereas the foraging territories of large colonies of *C. schmidtii* and *L. neglectus* do not overlap.

CONCLUSIONS

1. *Lasius neglectus* was found in 16 localities of the Crimean Peninsula: 6 localities in 1978–1981 and 10 in 1998–1999 and 2013.

2. Two thirds of the 111 colonies of *L. neglectus* studied in Crimea were monocalic, the rest were polycalic (most of them PLC₁ and PLC₂, and there were also 2 federations). The high percentage of monocalic colonies distinguishes the Crimean population of *L. neglectus* from populations from other territories. Transition from monocaly to polycaly (to PLC₁, then to PLC₂, and then to federation) in Crimean *L. neglectus* is accompanied by a 1.5–2-fold increase in the number of nests and controlled trees.

3. Diurnal activity of workers and groups of workers of *L. neglectus* on forage trails is characterized by alternation of longer and shorter cycles of differently directed foraging streams.

4. Foragers of *L. neglectus* in Crimea visit 26 species of trees, over one third of which are conifers. The most attractive trees are *Pinus pallasiana*, *Populus alba*, *Cedrus libani*, and *Ulmus laevis*. The introduced tree species are practically never visited by native ants, which reduces their competition with *L. neglectus*.

5. Twelve native ant species were recorded together with *L. neglectus* (2 species on the soil surface and 10 on trees). The number of co-occurring native species did not differ between the trees controlled by monocalic and polycalic colonies of *L. neglectus*. On the whole, it can be assumed that *L. neglectus* does not replace the native ant species in Crimea.

6. We suppose that *L. neglectus* is an invasive species in Crimea; its invasion probably started in the early 1970s.

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