

Species composition of plants and trophically related aphids in the territory of the *Lasius niger* (Hymenoptera: Formicidae) nest complex

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Abstract

Ants can form large nest complexes with thousands of nests, such as *Lasius niger* for the suburbanized areas of Ukraine. *L. niger* inhabits meadows, abandoned fields, pastures, and young plantations of coniferous trees. The question of what constitutes the basis of the carbohydrate diet of *L. niger* ants in such large nest complexes remains unclear. In 2017-2018, 38 plant species were identified in the territory of the *L. niger* nest complex (Kyiv region, Ukraine). 4 species of plants (*Cirsium arvense*, *C. setosum*, *Onopordium acanthium*, *Oenothera rubricaulis*) were visited by *L. niger* foragers in 70–95% of cases. On these species of plants, colonies of aphids acted as sources of carbohydrate for ants. A total of 43 species of aphids were found, of which 32 were localized on the aerial parts of plants, the remaining species - on the roots and root neck of the plants. *L. niger* monopolize 98% of carbohydrate baits in the territory of the nest complex. A large number of myrmecophilous aphid species promotes effective trophobiosis of *L. niger* in the territory of the nest complex. This favors the stability of the supply of the carbohydrate resource to the ant colonies inhabiting the nest complex. The existence of the *L. niger* nest complex is possible in herbaceous plant communities when this ant species is capable of mutualistic relationships with a large number of myrmecophilous aphid species.

Keywords: *Lasius niger*, nest complex, aphids, attractive plants, trophobiosis.

Received: 1 August 2022; Revised: 30 December 2022; Online: 31 December 2022

Introduction

Ants are able to form large settlements (nest complexes), which, under favourable conditions, include hundreds and thousands of nests. Such nest complexes can exist both in the form of independent colonies and in the form of a single supercolony. The latter is most often associated with invasive ant species. Nests in supercolonies are interconnected by a system of trails, workers from different nests do not show aggression towards each other or its level is minimal (Giraud *et al.*, 2002; Espadaler *et al.*, 2007; Stukalyuk and Netsvetov, 2018). The low aggressiveness between workers from different parts of the nest complex is especially pronounced in invasive ant species, some of which are unicolonial. These species include the Argentine ant (*Linepithema humile*), two large nest complexes of which have been recorded in Southern Europe (Giraud *et al.*, 2002). Somewhat smaller colonies are formed by the invasive garden ant *Lasius neglectus*,

which is also widespread in Europe (Espadaler *et al.*, 2007).

In addition to invasive ant species, large settlements are also found in native species. A nest complex with hundreds of nests interconnected by trails through which the population and brood are exchanged is a common phenomenon for red wood ants *Formica rufa*, *F. polyctena*, *F. aquilonia* (Zakharov, 2015). In Japan, the ant species *Lasius sakagami* is capable of forming supercolonies (Yamauchi *et al.*, 1981). For the full existence of such supercolonies, it is necessary to have favourable conditions, such as a sufficient number of nesting sites and the availability of food resources. In urban areas, nesting sites for ants are limited (Pecarevic *et al.*, 2010; Slipinski *et al.*, 2012; Radchenko *et al.*, 2019; Stukalyuk *et al.*, 2020), here it is difficult to find a suitable place for settlement for ant species that build above-ground nests or live in dry wood.

Supercolonies, which include millions and tens of millions of workers, need a constant supply of food resources. Many species of ants capable of forming supercolonies or large polycalic colonies are trophobionts, i.e., the main part of their diet is honeydew secreted by aphids. These species include both invasive ants (*Lasius neglectus*, *Crematogaster subdentata*) (Stukalyuk and Netsvetov, 2018; Espadaler *et al.*, 2007) and native species of ants (*Lasius fuliginosus*, *Formica rufa*, *F. polyctena*) (Zakharov, 2015). *Crematogaster subdentata* an invasive ant, both in the primary and in the invasive range, are able not only to collect aphids, but also store dried aphids as a source of protein food (Stukalyuk and Netsvetov, 2018).

The aphid colonies are protected by ants from their natural enemies – wasps, ladybugs, etc. As a rule, woody plants are a perennial source of resources on which aphids live and feed (Zakharov, 2015; Stukalyuk *et al.*, 2020). Therefore, the territories of supercolonies, as a rule, include trees, together with the aphid colonies living on them, in the composition of the common forage area. The study of relationships between plants, aphids and ants in the territory of supercolonies or nest complexes seems to be extremely important, since it sheds light on the possibility of their existence in specific urban and suburban conditions.

On the territory of urban landscapes, ants have a high abundance, comparable with natural biocenoses, mainly in parks and forest areas. These data were obtained from Kyiv, Warsaw, Helsinki, Moscow, Sofia and other European cities (Antonova and Penev, 2006; Vepsäläinen *et al.*, 2008; Lapeva-Gjonova *et al.*, 2010; Slipinski *et al.*, 2012; Putyatina *et al.*, 2018; Radchenko *et al.*, 2019; Stukalyuk *et al.*, 2020). In most of these cities, one of the most numerous ant species is *Lasius niger*, which was found in almost all surveyed biotopes – squares, parks, lawns, tree alleys along busy streets and highways.

In open spaces (abandoned agricultural fields, pastures) *L. niger* is able to form huge settlements, or nest complexes. Such settlements are composed of individual colonies, or polycalic colonies, but are not true supercolonies. Two nest complexes (A and B) that we discovered earlier in the Kyiv region (Ukraine), located on areas of 11.8 ha and 13.3 ha, included more than 14 thousand and 15

thousand nests, respectively. In terms of the number of nests, these complexes are the largest of those described in Europe for native ant species. On the territory of both nest complexes, tree and shrub vegetation occupies small areas, less than 3% of the area of the nest complex. Therefore, a natural question is what constitutes the basis of the nutrition of ants living in the territory of the nest complex, where grass vegetation is the main one. In this article, we tried to establish the species composition of aphids, analyze the attendance by ants on different plant species growing on the territory of one of the nest complexes (complex B), and also establish a relationship between the presence of invasive plant species and their attractiveness to ants.

Materials and Methods

Research region

The site under the study was located between the city of Vyshneve and the Sofiivska Borshchahivka village, Kyiv-Svyatoshinsky district, Kyiv region (coordinates of the central part of the nest complex B 50°23'25.7"N 30°20'11.4"E) on an abandoned arable field, which is at the stage of restoration succession. According to our calculations based on successional changes in vegetation and archival data, the field was no longer cultivated since 7-10 years. It has a flat relief with small elevations and lowlands with very dry clay soil.

Habitat characteristics

Ruderal and semi-ruderal communities of thermophilic and drought-adapted plant species, often form dense thickets. The biotope often includes invasive plant species, which may be dominant or subdominant. This habitat is considered as the initial stage of succession under constant anthropogenic load. This type of habitat is common in settlements, along roads, construction sites, wastelands, pastures, along rivers.

Plant communities

To conduct research, we have chosen the following algorithm: a) study of the species composition of plants growing on the territory of the nest complex, taking into account their projective cover; b) study of the species composition of aphids on terrestrial (stems, leaves) and underground (roots) parts of plants; c) study of the density of *L. niger*

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workers on plots and on carbohydrate baits; d) studying the number of *L. niger* workers visiting plants of different species and comparing the attractiveness of different plant species to ants, taking into account the presence of aphids.

All studies were carried out on the territory of one nest complex (complex B). During the research in June 2017, 14 geobotanical sites were observed in places with different density of anthills. Of these, 5 sites were observed in the central zone of the nest complex (the density of nest mounds is more than 16 per 100 m²), 5 - on the periphery of the nest complex (the density of nest mounds is 6-10 per 100 m²), 4 - on the outskirts of the territory of the nest complex, where the density of nest mounds is minimal (up to 5 nests per 100 m²). Each geobotanical site covered an area of 100 m² and was completed using standard geobotanical techniques. Further processing and analysis of descriptions was carried out using the LibreOffice5.0 software package. The names of plant species are given according to Mosyakin and Fedoronchuk (1999). To determine plant species, the Dobrochaeva *et al.* (1999) was used.

Accounting for attractive plants

On the territory of nest complex B in June 2017, 2820 plants of 15 species were examined for attendance by ants. Cereals were not taken into account. Each plant was examined for 2 min and the number of ants on it was recorded. A total of 1139 ants of the same species, *L. niger*, were found. 3 dominant invasive plant species were observed: *Phalacrolooma annuum* (L.) Dumort. (990 plants), *Lepidotheca suaveolens* (Pursh) Nutt. (210), *Ambrosia artemisiifolia* L. (150). 12 species of plants were classified as native. There were: *Cirsium setosum* (Willd.) Besser (30 plants), *Cirsium arvense* (L.) Scop. (150), *Euphorbia virgata* Waldst. et Kit. (300), *Raphanus raphanistrum* L. (270), *Potentilla argentea* L. (300), *Artemisia absinthium* L. (270), *Tripleurospermum inodorum* (L.) Sch. Bip. (60), *Verbascum thapsus* (90). Such records are necessary to compare the attractiveness of plants of different species for aphids and ants in the territory of the nest complex.

Aphids

The collection of aphids was carried out in 2017–2018 according to the methods adopted in aphidology. The collected aphids were fixed in 70% ethanol in laboratory test tubes. Aphids were selected from aboveground and underground parts of monocots and dicots herbaceous plants growing on the territory occupied by the *L. niger* nest complex. Aphid preparations were prepared according to the generally accepted method based on Faure-Berlise liquid. A total of 186 aphid samples were collected, 267 preparations were made. Aphid species were determined according to Blackman and Eastop, 2006.

Ants

The choice of sites with different density of nests was carried out in advance, in April 2017. At this time, the herbage is still low and anthills are clearly visible (Fig. 1).



Figure 1. The *Lasius niger* nest complex B.

To assess density of ants in the forage area of nest complex B, 150 plots 50 × 50 cm were examined in June 2017. The inspection time for each plot was 2 minutes. The number of ants inside each plot was taken into account. Subsequently, 150 carbohydrate baits were laid out here. The distance between the baits was 2 m. After 30 minutes, the number of ants attracted to the baits was recorded. Considering that *L. niger* is a trophobiont species, the presence of a carbohydrate resource is important for it. Therefore, we have chosen exclusively carbohydrate baits. Also, the attendance of carbohydrate baits only by *L. niger* foragers will make it possible to establish to what extent they monopolize the resource on the territory of the nest complex. Plots and baits were placed in groups of 50 in zones with different density of nest mounds - in zone 3 (up to 5 nests per 100 m², the outskirts of the nest complex), in zone 2 (6–10 nest mounds per 100 m², the peripheral part of the nest complex), in zone 1 (more than 16

nest mounds per 100 m², the central part of the nest complex).

The search for nests of other ant species was also carried out on the territory of the nest complex B. For this, open areas (roads, paths), stones in open spaces, and fallen tree trunks (in an area with forest vegetation) were examined. In addition, 30 *L. niger* nests were excavated in June 2018 to identify nests of other ant species, as well as kleptobiont ants such as *Solenopsis fugax*.

Statistical analysis

For all statistical data processing, Past 4.03 was used. Differences between the means are displayed on graphs in boxplot mode: plot type – violin and box. This type of plot displays the spread of the data, the standard error of the mean, and the sample size. This type of plot is used to analyze large samples (more than 20 variables). Changes in the number of workers visiting the plots and baits in different zones of the nest complex were evaluated using the Mann-Whitney test. One-way ANOVA was used to compare the attractiveness of different plants to ants because this test is suitable for samples with more than two plant species.

Results and Discussion

General characteristics of plant communities: In general, the vegetation cover on the territory of nest complex is not dense, and its projective cover ranges from 40 to 65%. Herbage one-or two-layered. Its height is in the range of 20-30 cm and very rarely reaches 50-70 cm. Vegetation cover has a complex character. In addition to grass communities, there were small areas of tree and shrub vegetation, with a total area of up to 3 ha.

Vegetation cover: Among phytocenoses, the most common were *Elytrigia repens* (L.) Nevski (dominant) and *Phalacroloma annuum* (L.) Dumort (subdominant)(Table 1).

Much less common were communities dominated by *Dactylis glomerata* L. and *Calamagrostis epigeios* (L.) Roth. From our point of view, communities with *Dactylis glomerata* could have been over sown to use them as hayfields. Based on the results of the analysis of our materials, it can be argued that the vegetation of the study area has the most common combinations of phytocenoses: *Elytrigia repens purum*, *Elytrigia repens* +

Phalacroloma annuum, *Dactylis glomerata* + *Achillea millefolium* + *Phalacroloma annuum*, *Calamagrostis epigeios* + *Elytrigia repens*, *Calamagrostis epigeios* + *Phalacroloma annuum*, *Phalacroloma annuum purum*. The number of plant species in the geobotanical plots varies from 5 to 17. The average is 9 species (Table 1). In total, we noted 38 species in the study area. The most common are *Phalacroloma annuum*, *Raphanus raphanistrum* L., *Elytrigia repens*. Plant species *Convolvulus arvensis* L., *Potentilla argentea* L., *Cirsium arvense* (L.) Scop., *Rorippa austriaca* (Crantz) Besser, *Melandrium album* (Mill.) Garcke, *Artemisia absinthium* L., *Potentilla neglecta* Baumg, *Carduus acanthoides* L. were slightly less common. Species *Dactylis glomerata*, *Calamagrostis epigeios*, *Oenothera rubricaulis* Klebahn, *Cirsium setosum*, *Tripleurospermum inodorum* are even rarer, but with a large projective cover. Other plant species are singly marked: *Asclepias syriaca*, *Acer negundo* L., *Achillea millefolium* L., *Agrostis capillaris* L., *Ambrosia artemisiifolia* L., *Arctium lappa* L., *Artemisia vulgaris* L., *Bromus hordeaceus* L., *Euphorbia cyparissias* L., *Euphorbia* sp., *Euphorbia virgata* Waldst. & Kit., *Galium verum* L., *Pilosella officinarum* F. Schultz & Sch. Bip., *Hypericum perforatum* L., *Lythrum salicaria* L., *Medicago lupulina* L., *Populus tremula* L., *Rumex acetosa* L., *Rumex acetosella* L., *Silene nutans* L., *Verbascum thapsus* L., *Vicia angustifolia* Reichard, *Vicia cracca* L., *Onopordum acanthium* L.

The most common plant species on the surface of nest mounds were *Elytrigia repens*, *Rorippa austriaca*, *Convolvulus arvensis*, *Raphanus raphanistrum*, *Potentilla argentea*, *Melandrium album*, *Dactylis glomerata*, *Phalacroloma annuum*, *Achillea millefolium*, *Calamagrostis epigeios*.

Plant species *Elytrigia repens* (geobotanical plots 1-3, 5-7, 10, 13) dominates in the central areas of the nest complex, while the peripheral areas, as well as the borders of the nest complex, were occupied by the invasive species *Phalacroloma annuum* (geobotanical plots 4, 14).

Activity of ants: The density of *L. niger* workers on the plots is maximum in the central part of the nest complex. On the periphery of complex, density of ants, on an average, is already 4 times less than in the centre ($p \leq 0.05$), and on the borders of the nest

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complex, it is 195 times less than in the central part ($p \leq 0.001$).

On an average, 1.7-8.3 times more ants come to baits than recorded on the same plots ($p \leq 0.05$). For *L. niger*, the Pearson correlation between the number of ants on the plots and on baits is slightly lower (0.66, $p \leq 0.0001$) than for *Myrmica rubra* (0.85, $p \leq 0.0001$). It may indicate greater food attractiveness of baits or faster mobilization to baits for *M. rubra* under competitive conditions with *L. niger*. The change in the quantitative indicators of the number of *L. niger* workers on baits from the centre to the

periphery (3.2 times less, $p \leq 0.05$) and further to the borders (42 times less, $p \leq 0.05$) persists. Among other ant species, *M. rubra* is represented in one of the sites (near the trees). However, their number on sites, as well as on baits, is 4 and 2.6 times less than in *L. niger*, respectively. The maximum density of *L. niger* workers occurs in areas free from *Phalacrolooma annuum* (-0.58, $p \leq 0.0001$). The reasons for this are discussed below. The intensity of the foraging activity of *L. niger* varies significantly between the examined zones (Fig. 2).

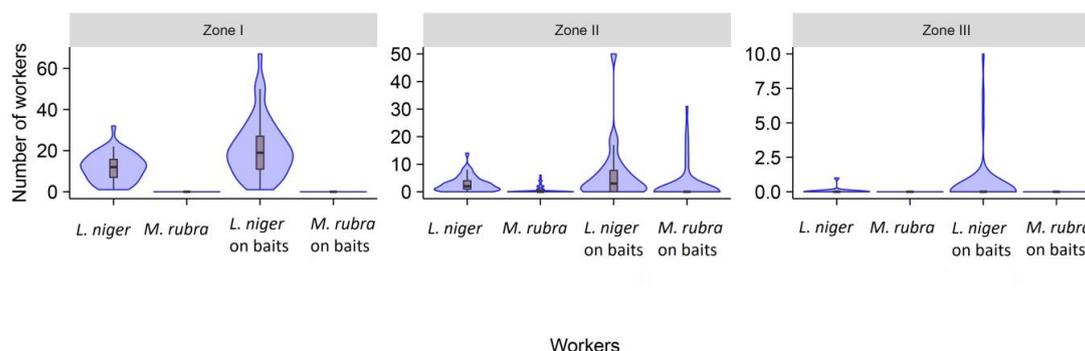


Figure 2. Average density on plots and baits of *Lasius niger* and *Myrmica rubra* foragers in different zones of nest complex B. Zone I – central part, II – periphery, III – borders of nest complex.

The highest density of worker ants per quadrat was recorded within central zone (I), followed by zones in periphery (II, Fig. 2, $p \leq 2.467E-10$) and in the borders of nest complex (III, $p \leq 3.363E-18$). The total number of ant workers maintaining the baits was significantly higher than the number of ant workers per quadrat (100 m²) in all zones ($p \leq 0.006595$ for zone I, $p \leq 4.537E-05$ for zone II, and $p \leq 1.019E-08$ for zone III).

The *L. niger* ant workers occupied the majority of baits, while only 8 baits were occupied by the *M. rubra* workers. The number of *L. niger* workers visiting the baits was also significantly higher than that of *M. rubra* workers (Fig. 2, $p \leq 1.014E-13$).

The density of *L. niger* workers per plot varies significantly within nest complex B. In the central part, the average density of workers in the forage area is 46.8 per plot / 2 min, with a maximum of 128 workers and a minimum of 8 per plot / 2 min. In the peripheral part, these values are smaller and average 12 workers / 2 min, from 4 workers to 56 individuals / 2 min.

The species composition of ants in the territory of the *L. niger* nest complex

Colonies of the kleptobiont ant *Solenopsis fugax* were recorded in the nest mounds of *L. niger* in 10% cases (in 3 mounds out of 30 excavated). One *Camponotus vagus* colony and one *Dolichoderus quadripunctatus* colony were found on the territory of the forest vegetation site. Ants *Tetramorium caespitum* (mainly on dirt roads) were recorded on the territory of the grassy communities of the nest complex, and single colonies of *Formica rufibarbis* and *F. pratensis* were also recorded near the borders of the nest complex.

Species composition of aphids on host plants within the *L. niger* nest complex

The most significant aphid species *Aphis fabae* s. l. (in this article it is considered as a complex of closely related species and/or subspecies of aphids, including *Aphis fabae* ssp. *fabae* (= *Aphis fabae* s. str.), *Aphis fabae* ssp. *cirsiiacanthoidis* (= *Aphis cirsiiacanthoidis*), *Aphis fabae* ssp. *solanella* (= *Aphis solanella*), *Aphis fabae* ssp. *mordvilkoii* (= *Aphis mordvilkoii*)). Within the

Table 1. Vegetation on the territory of the nest complex B

Vegetation syntaxa / Dominant plant species	Number of geobotanical plot													
	1	7	2	5	3	6	13	10	8	9	11	12	4	14
D.s. Cl. <i>Artemisieta vulgaris</i>														
<i>Artemisia absinthium</i>	.	1	+	+	+	1	3	.
<i>Achillea millefolium</i>	1	3
<i>Artemisia vulgaris</i>	+	+
<i>Carduus acanthoides</i>	+	+
<i>Arctium lappa</i>	+
<i>Potentilla argentea</i>	+	.	1	1	.	1	2	.	+	+
<i>Potentilla neglecta</i>	+	.	.	.	1	.	.	1	.	1	.	.	1	.
D.s. Ord. <i>Agropyretalia repentis</i> = D.s. Al. <i>Convolvulo arvensis</i> - <i>Agropyron repentis</i>														
D.s. Com. <i>Calamagrostis epigeios</i>														
<i>Calamagrostis epigeios</i>	+	4	4	.	.
D.s. Ass. <i>Agropyretum repentis</i>														
<i>Cirsium arvensis</i>	+	1	1	.	.	1	1	1	.	.
<i>Convolvulus arvensis</i>	+	.	.	.	+	1	1	1	1	1	+	.	.	.
D.s.Com. <i>Dactylis glomerata</i>														
<i>Elytrigia repens</i>	5	4	4	3	4	4	4	3	.	.	2	.	.	.
<i>Dactylis glomerata</i>	+	4	4	3
D.s. Com. <i>Phalacroloma annuum</i>														
<i>Phalacroloma annuum</i>	1	1	1	4	4	1	.	1	1	2	1	1	3	5
Other species														
<i>Melandrium album</i>	+	+	1	.	.	+	+	.	.	+
<i>Raphanus raphanistrum</i>	1	1	1	1	1	+	+	+	+	+	.	+	+	.
<i>Rorippa ausriaca</i>	1	1	+	.	.	+	+	+	.	.	.	1	.	.
<i>Acer negundo</i>	+	+	.	+	.	.	.
<i>Agrostis capillaris</i>	1	.	.	.
<i>Asclepias syriaca</i>	+
<i>Bromus hordeaceus</i>	+
<i>Rumex acetosa</i>	1	+	.
<i>Vicia cracca</i>	+
<i>Euphorbia virgata</i>	.	.	.	+	.	.	1
<i>Ambrosia artemisiifolia</i>	+	.	.
<i>Euphorbia cyparissias</i>	.	+	+	1
<i>Euphorbia sp.</i>	+
<i>Galium verum</i>	.	.	+
<i>Pilosella officinarum</i>	+	.	+
<i>Hypericum perforatum</i>	+
<i>Lythrum salicaria</i>	+	+	.	.	+
<i>Medicago lupulina</i>	+
<i>Oenothera rubricaulis</i>	+	.	+	+	.	.	+	.	.
<i>Onopordium acanthium</i>	+
<i>Populus tremula</i>	+
<i>Rumex acetosella</i>	+

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<i>Silene nutans</i>	+	+	.	.	.
<i>Verbascum thapsus</i>	+
<i>Vicia angustifolia</i>	.	+

Note: D.s. Ord/Com/Ass/Al/Cl = Diagnostic species Order/ Community/ Association/ Alliance/ Class

Table 2. List of aphid species on plants in the territory of *Lasius niger* nest complex B

Plant species	Aphid species + Location on the plant
<u>Monocot plants</u>	
<i>Elytrigia repens</i>	On the roots <i>Anoecia corni</i> , <i>Anoecia vagans</i> ; <i>Forda formicaria</i> , <i>Geocica utricularia</i> ; <i>Tetraneura ulmi</i> . On the aboveground parts of plants, <i>Metopolophium dirhodum</i> , <i>Rhopalosiphum padi</i> ; <i>Schizaphis graminum</i> ; <i>Sipha elegans</i> , <i>Sipha maydis</i> ; <i>Sitobion avenae</i> .
<i>Dactylis glomerata</i>	On the roots <i>Anoecia corni</i> , <i>Baizongia pistaciae</i> ; <i>Forda formicaria</i> , <i>Tetraneura ulmi</i> , <i>Rhopalosiphum oxyacanthae</i> On the aboveground parts of plants <i>Atheroides serrulatus</i> ; <i>Metopolophium dirhodum</i> ; <i>Rhopalosiphum padi</i> ; <i>Schizaphis graminum</i> ; <i>Sipha maydis</i> ; <i>Sitobion avenae</i>
<i>Calamagrostis epigeios</i>	On the roots <i>Anoecia corni</i> , <i>Tetraneura ulmi</i> On the aboveground parts of plants <i>Laingia psammae</i> ; <i>Metopolophium dirhodum</i> ; <i>Rhopalosiphum padi</i> ; <i>Schizaphis graminum</i> ; <i>Sipha maydis</i> ; <i>Sitobion avenae</i>
<i>Agrostis capillaris</i>	On the roots <i>Anoecia corni</i> , <i>Baizongia pistaciae</i> ; <i>Forda formicaria</i> ; <i>Tetraneura ulmi</i> On the aboveground parts of plants <i>Rhopalosiphum padi</i> ; <i>Schizaphis agrostis</i> ; <i>Sipha glyceriae</i> ; <i>Sitobion avenae</i>
<i>Bromus hordeaceus</i>	On the roots <i>Anoecia corni</i> On the aboveground parts of plants <i>Metopolophium dirhodum</i> ; <i>Rhopalosiphum padi</i> ; <i>Sitobion avenae</i>
<u>Dicot plants</u>	
<i>Achillea millefolium</i>	On the roots <i>Trama troglodytes</i> On the aboveground parts of plants <i>Aphis fabae</i> s. str., <i>Brachycaudus cardui</i> , <i>Metopeurum fuscoviride</i>
<i>Arctium lappa</i>	On the roots <i>Smynthuroides betae</i> On the aboveground parts of plants <i>Aphis fabae</i> ssp. <i>mordvilkoii</i> (= <i>Aphis mordvilkoii</i>), <i>Brachycaudus cardui</i> , <i>Brachycaudus helichrysi</i>
<i>Artemisia vulgaris</i>	On the roots <i>Smynthuroides betae</i> On the aboveground parts of plants <i>Aphis fabae</i> s. str., <i>Brachycaudus cardui</i> , <i>Brachycaudus helichrysi</i>
<i>Carduus acanthoides</i>	On the roots <i>Trama troglodytes</i> On the aboveground parts of plants <i>Aphis fabae</i> ssp. <i>solanella</i> (= <i>Aphis solanella</i>), <i>Brachycaudus cardui</i> ;
<i>Cirsium arvense</i>	On the roots <i>Trama troglodytes</i> On the aboveground parts of plants <i>Aphis fabae</i> ssp. <i>cirsiiacanthoidis</i> (= <i>Aphis cirsiiacanthoidis</i>), <i>Brachycaudus cardui</i> , <i>Brachycaudus helichrysi</i> .
<i>Cirsium setosum</i>	On the aboveground parts of plants <i>Aphis fabae</i> ssp. <i>cirsiiacanthoidis</i> (= <i>Aphis cirsiiacanthoidis</i>), <i>Brachycaudus cardui</i>
<i>Euphorbia cyparissias</i> L.	On the aboveground parts of plants <i>Aphis euphorbiae</i>
<i>Euphorbia virgata</i>	On the aboveground parts of plants <i>Aphis euphorbiae</i>
<i>Phalacrolooma annuum</i>	On the aboveground parts of plants <i>Aphis fabae</i> s. str.
<i>Matricaria discoidea</i> (= <i>Lepidotheca suaveolens</i>)	On the aboveground parts of plants <i>Aphis fabae</i> s. str.

<i>Galium verum</i>	On the aboveground parts of plants <i>Aphis galiiscabri</i>
<i>Pilosella officinarum</i>	On the aboveground parts of plants <i>Aphis gossypii</i> , <i>Brachycaudus helichrysi</i>
<i>Hypericum perforatum</i>	On the aboveground parts of plants <i>Aphis chloris</i>
<i>Medicago lupulina</i>	On the aboveground parts of plants <i>Acyrtosiphon pisum</i> ; <i>Aphis craccivora</i> , <i>Aphis fabae</i> , <i>Megoura viciae</i> ;
<i>Oenothera rubricaulis</i>	On the aboveground parts of plants <i>Aphis holoenotherae</i>
<i>Onopordium acanthium</i>	On the aboveground parts of plants <i>Aphis fabae</i> s. str., <i>Brachycaudus cardui</i> <i>Brachycaudus helichrysi</i>
<i>Populus tremula</i>	On the aboveground parts of plants <i>Chaitophorus populeti</i>
<i>Rumex acetosa</i>	On the roots <i>Dysaphis radicola</i>
	On the aboveground parts of plants <i>Aphis fabae</i> ssp. <i>solanella</i> (= <i>Aphis solanella</i>)
<i>Rumex acetosella</i>	On the roots <i>Dysaphis radicola</i>
	On the aboveground parts of plants <i>Aphis rumicis</i>
<i>Silene nutans</i>	On the aboveground parts of plants <i>Brachycaudus lychnidis</i>
<i>Melandrium album</i>	On the aboveground parts of plants <i>Brachycaudus populi</i>
	On the root neck, in shelters created by ants <i>Brachycaudus lychnicola</i> .
<i>Verbascum thapsus</i>	On the aboveground parts of plants <i>Aphis verbasci</i>
<i>Vicia angustifolia</i>	On the aboveground parts of plants <i>Aphis craccivora</i> , <i>Megoura viciae</i>
<i>Vicia cracca</i>	On the roots <i>Smynturodes betae</i>
	On the aboveground parts of plants <i>Acyrtosiphon pisum</i> , <i>Aphis cracca</i> , <i>Aulacorthum solani</i> ; <i>Megoura viciae</i>

Note: For root aphids, non-full-cycle species are highlighted in bold (in the Kyiv region). The remaining species are reliably dioecious, but a paracycle on roots with incomplete development is possible.

territory of nest complex of *L. niger*, we found this species of aphids in large numbers on *Cirsium arvense*, *Cirsium setosum*, *Tripleurospermum inodorum*, *Onopordium acanthium*, *Arctium lappa*, *Carduus acanthoides*, *Asclepias syriaca*. On *L. suaveolens* and *Ph. annuum* colonies of *A. fabae* were found only on single plants. The second most important is *Brachycaudus cardui*, which massively populates Compositae (*Cirsium arvense*, *Cirsium setosum*, *Onopordium acanthium*, *Arctium lappa*, *Carduus acanthoides*). Since the above species of aphids are polyphages and oligophages, they populate many plant species within the nest complex. These species are not dominant numerically, and some of them were observed singly, but a wide range of food plants allows *Aphis fabae* s. l. and *Brachycaudus cardui* to spread throughout the nest complex.

Other species of aphids were observed on the aboveground parts of dicotyledonous plants, together with their food plants. This species of aphids were observed only locally (Table 2).

In general, within the entire nest complex, the contribution of these aphid

species individually to providing ants with carbohydrate nutrition is probably not great, but they can play a significant role in certain areas within the nest complex, as well as in combination with other species.

As already noted, the tree and shrub vegetation within the nest complex occupies a small area, but there was a growth of *Populus tremula*, massively populated by the myrmecophilous aphid species *Chaitophorus populeti* (Panzer). Thus, in forest area, this aphid species plays a significant role in providing ants with carbohydrate nutrition.

It should be noted that the rhizobiont *Trama troglodytes* von Heyden was found on the roots of *Cirsium arvense*, *Carduus acanthoides*, and *Achillea millefolium*. This species forms large colonies on the roots of plants growing on or near nest mounds of *L. niger*. Until recently thought to be fully angolocyclic, but oviparous females and males have been found in Southern England (Blackman and Eastope, 2006), suggesting that a full cycle is possible, but probably very rare. Also, on the roots of *Artemisia vulgaris* and *Arctium lappa*, small colonies of *Smynturodes betae* Westwood, a pistachio aphid, whose angolocyclic populations are

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found on the roots of many secondary hosts outside the range of pistachios, were found.

We mention the findings of *Brachycaudus lychnicola* on the root collar of *Melandrium album* and *Silene nutans*, in shelters created by ants, but these aphids are quite rare.

It is important to note that within the nest complex of *L. niger* phytocenoses dominated by grasses, which are inhabited by their own aphid complex (Table 2), while many species feed on plant roots. The probability of finding aphids on the roots of plants growing on a nest mound and next to it is quite high, and in this case their contribution to the nutrition of ants can be very significant, especially since they are less affected by weather factors and pressure from parasites and predators than species that feed on above ground parts of plants. A number of them develop in the region completely with incomplete cycle, and some have a paracycle with incomplete development on the roots of cereals, i.e. larvae overwinter directly on the roots (including directly in the nest mound).

As a rule, colonies of aphids on one plant are few and far between, but given the large number of plants, their role in the feeding of ants can be significant. In our geobotanical descriptions, *Elytrigia repens*, *Dactylis glomerata*, *Calamagrostis epigeios* are dominant, and *Agrostis capillaris*, *Bromus hordeaceus* are noted singly, but the species composition of aphids on all these plants, with few exceptions, is similar. The aerial parts of grasses are dominated by aphids *Rhopalosiphum padi*, *Schizaphis graminum* and *Sipha maydis*. The first species is dioecious (they migrate to grasses from bird cherry), the rest are monoecious. *Anoecia corni*, *Anoecia vagans*, *Tetraneura ulmi*, and *Rhopalosiphum oxyacanthae* dominated among rhizobiont species on cereals. Unfortunately, in the case of root aphids, it is more difficult to estimate their prevalence. But by judging the abundance of these species on the primary fodder plants, they should be quite common on the roots of cereals. In addition, aphids of the tribe Fordini (*Forda formicaria*, *Geoica utricularia* and *Baizongia pistaceae*) were found on the roots of cereals up to St. Petersburg and Scandinavia. These species are often found on the roots of plants growing on nest mounds. Undoubtedly, root aphids play a significant role in the nutrition of ants.

Attendance by *L. niger* ants of plants

Ants were absent on the following plant species: *R. raphanistrum*, *L. suaveolens*, *P. argentea* (Fig. 3).

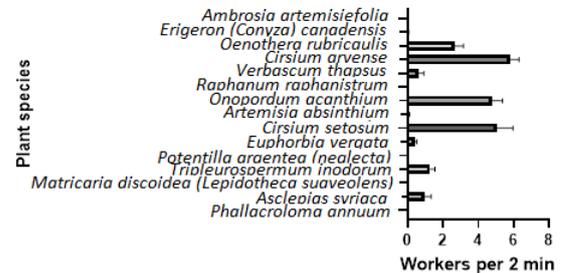


Figure 3. Average attendance by *Lasius niger* foragers of 15 species of plants in the territory of nest complex B (number of workers per 2 min per 1 plant \pm standard error of the mean).

Single ants were found on *Phalacrolooma annuum*, *E. virgata*, *A. absinthium* (from 0.006 to 0.09 individuals/1 plant/2 min). The ants most frequently visited 4 plant species (Fig. 3). They significantly differed from the other 11 plant species in terms of ant attendance ($p \leq 0.05 - 0.001$). The attractiveness of four species is explained by the high frequency of occurrence of aphid colonies: on *Onopordum acanthium* - in 95% of examined plants, on *Cirsium setosum* - in 76% of specimens, *Cirsium arvense* - 78%, on *Oenothera rubricaulis* - in 60% of plants.

Invasive dominant plants such as *P. annuum*, which are largely free of aphids, can have a negative impact on ant abundance by out-competing native species that are well colonized by aphids and frequented by ants. This is indirectly confirmed by the lower number of *L. niger* ants in the areas dominated by *P. annuum* (Fig. 2).

The influence of vegetation on the foraging of *L. niger* ants in the territory of the nest complex is primarily associated with aphids feeding on plants. According to Holec *et al.* (2006), ant foraging in summer is confined to areas with higher vegetation, for example, with the dominance of *Calamagrostis epigeios* in herbage. At the same time, the nest mounds of *L. niger*, on the contrary, are located in areas with vegetation that has a low projective grass cover. This is also confirmed by our data: the majority of nest mounds are concentrated in areas dominated by *Elytrigia repens*, i.e., in areas with herbaceous vegetation. This feature

emphasizes the similarity between *L. niger* and *L. sakagamii* - both species mainly settle in open spaces occupied by herbaceous vegetation (Yamauchi *et al.*, 1981). Other native ant species capable of forming supercolonies or large polycalic colonies, such as the red wood ants *Formica rufa*, *F. polyctena* and *F. aquilonia*, colonize forest areas and primarily visit aphid colonies located on trees (Zakharov, 2015). In this case, trees are a perennial resource that can be renewed annually. In the case of the nest complex studied by us, most herbaceous plant species belong to annuals, biennials, and much less often to perennials. Therefore, herbaceous plants visited by ants in the territory of the nest complex B can annually undergo more significant changes compared to trees as a result of fires or the expansion of areas occupied by invasive plant species unattractive to aphids and ants, such as *P. annuum*.

Lasius niger is the most abundant ant species in the study region, accounting for 5 to 45% of all ants found on woody plants in 6 types of habitats (Stukalyuk *et al.*, 2020) and from 37% to 76% of all ants visiting herbaceous plants in 6 habitat types (Stukalyuk *et al.*, 2019). *L. niger* visits 27 out of 37 herbaceous plant species (including 10 invasive species) and 22 out of 27 tree species. This wide range of visited plant species, greater than that of any other ant species, is responsible for the wide adaptive potential of *L. niger* and the potentially large number of visited aphid species that feed on these plants.

Foraging of *L. niger* ants on plants with aphid colonies can be carried out not only during the day, but also at night (Depickere *et al.*, 2004a). This increases the flow of food delivered to the nest mound. Foraging by mobilization increases with an increase in the amount of food (Depickere *et al.*, 2008), which we recorded on baits. Foraging on permanent food sources occurs within 5 min of detection and stabilizes within 40 min (Devigne and Detrain, 2002). These authors also recorded a high tolerance between ants from different nest mounds. The behaviour of *L. niger* foragers is characterized by greater mobility than in-breeding workers (Depickere *et al.*, 2004b). This causes greater interaction between foragers on the territory of the forage area, including the nest complex. Hungry individuals of *L. niger* are most often located

in the nest chamber closest to the exit, which accelerates their mobilization to the discovered food source (Mailleux *et al.*, 2011). This makes it more efficient to locate the food source. As our studies have shown, *L. niger* monopolized almost all baits on the territory of the nest complex, preventing other ant species from using them. This feature contributes not only to the successful competition of *L. niger* with other native ant species, but even with invasive ones, for example, with the Argentine ant in experiments (Cordonnier *et al.*, 2020). The successful assimilation of the food resource by *L. niger* workers within the nesting complex is also facilitated by their high density, many times higher than that of other ant species in the same area, for example, *M. rubra*. Within the boundaries of the nest complex, it was *L. niger* that made up the absolute (98%) majority of the ants that visited the baits or were found on the plots. Nevertheless, the maximum density of *L. niger* workers in the territory of the nest complex is lower than it is known for other species, for example, for *L. sakagamii* (Yamauchi *et al.*, 1981), *L. flavus* (Waloff and Blackith, 1962).

In the studied territory of the nest complex, 6 invasive plant species were identified - *Ph. annuum*, *O. rubricaulis*, *O. acanthium*, *A. artemisiifolia*, *A. syriaca*, *L. suaveolens*. On plants *Ph. annuum*, *L. suaveolens*, *A. artemisiifolia* only single colonies of *Aphis fabae* were found or aphids were absent. Hence, the low attractiveness of these plants for ants in the study area and has a negative impact on their associations. First of all, this concerns *Phalacrolooma annuum*, which is dominant in some areas of the nest complex and prevails where nest mounds are absent. Because among the invasive plant species *Ph. annuum* is a “transformer” species, i.e., capable of spreading over many territories and forming single-species communities of considerable size in place of native ones, the negative impact on ant associations of this plant increases significantly (Stukalyuk *et al.*, 2019). However, it should be noted that polyphagous myrmecophilous aphid species were recorded on these plants in many European countries, which makes them potentially attractive to ants. For example, for aphid species *Aphis fabae* (Czech Republic), *Brachycaudus helichrysi* (Balkan countries, Moldova, Czech Republic, Slovakia, Transcarpathian region of Ukraine),

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Macrosiphum euphorbiae (Czech Republic, Serbia), *Myzus persicae* (Sulzer) (Serbia), *M. ornatus* (Laing) (Italy) (Holman, 2009).

Aphids are an important source of carbohydrate food for ants. Root aphids can be a major source of carbohydrate food for ants, as shown in *L. flavus* (Odum and Pontin, 1961). A significant number of species of root aphids found by us indicates their important role in the nutrition of the *L. niger* nest complex. *L. niger* workers are known to be able to distinguish between myrmecophilous and non-myrmecophilous aphid species based on the analysis of cuticular hydrocarbons (Lang and Menzel, 2011).

Ants, in particular, *L. niger*, contribute to an increase in the size of aphid colonies, as they protect them from natural enemies (including by building special earthen pavilions directly on plants in which aphids find shelter). Some of the growing nest mounds in complex were located around sagebrush bushes. *L. niger* is more effective in protecting aphids from natural enemies directly than *Tetramorium caespitum* (Katayama and Suzuki, 2003). For *Aphis fabae*, the number of aphids per colony visited by *L. niger* was 3 to 9 times higher than in colonies where ants were absent (El-Ziady and Kennedy, 1956). Exclusion of *L. niger* from visiting colonies of apple aphids (*Dysaphis plantaginea* Passerini, and the green apple aphid, *Aphis pomi* De Geer) by using sticky barriers on trunks or by feeding ants with honey has significantly increased the pressure of natural enemies on aphid numbers (Nagy *et al.*, 2013). If honey is offered to *L. niger* ants as a honeydew substitute, this affects the increase in ant predation in relation to aphids, while alternative prey (food of protein origin) did not affect predation in any way (Offenberg, 2001). For *L. niger* ants, the number of aphids per worker is important, since an excessive number of aphids will increase the number of cases of predation by ants. At the same time, ants prey on aphids to a lesser extent, which give honeydew to workers from their own nest (Sakata, 1994). Based on the above works, *L. niger* has all the features of a trophobiont species for which aphids are the main food resource. On the other hand, the presence of *L. niger* is also very important for aphids, since ants contribute not only to conservation, but also to a significant increase in their numbers.

The life cycles of aphids on plants also have a significant impact on the attractiveness of a plant to ants. Plants visited by ants from spring to autumn are the most attractive, because they always have aphid colonies. As for the life cycles of aphids, there are dioecious and monoecious species (full cycle and non-full cycle). In the first case, aphids develop in the spring on the primary food plants, and then migrate to the secondary ones. Migration occurs from May to the end of June. Some species of aphids migrate more quickly, while others migrate over time. Monoecious species develop without migration from spring to autumn.

During the growing season, the number of aphids and the number of plants infected by them change, which leads to unequal attractiveness of plants for ants in different phenological phases and stages of the plant life cycle. Infestation by aphids is carried out: a) at the beginning of the growing season in April–May, by founding females emerging from eggs with a complete monoecious (for example, *Schizaphis graminum*) or overwintered larvae with an incomplete development cycle (in monoecious root species, possible in *Aphis holenotheae* on *Oenothera rubricaulis* plants, according to at least in some populations); b) during the period of migration of dioecious species (*Aphis fabae*, *Brachycaudus cardui*, *Rhopalosiphum padi*) from primary to secondary host plants in May–June; c) when aphids disperse throughout the season.

The physiological state of the plant is also of great importance for aphids. Plants that are in good condition are better able to provide the aphids with the nutrients they need to feed, which contributes to the development of the colony. For species such as *A. fabae* in the second generation, re-colonization is possible when aphids move to secondary shoots of the plant. Another aphid species (*Metopeurum fuscoviride*), which was protected by *L. niger* ants, migrated relatively little through the plant, putting them at risk of death if they produce less honeydew (Stadler *et al.*, 2002). Thus, the characteristics of the biology of different aphid species (life cycles, behaviour) can also be of great importance for their adaptive potential. We found aphids and *L. niger* ants on almost all examined specimens of *Cirsium arvense* plants. This indicates the

value of this plant and the other 3 most visited species for ants on the territory of the nest complex, since they are the main sources of carbohydrate food extracted from the aerial parts of plants - aphid colonies.

Conclusion

On the territory of the *Lasius niger* nest complex, 38 plant species were found, of which 4 are the most attractive for ants: *Cirsium arvense*, *C. setosum*, *Onopordum acanthium*, *Oenothera rubricaulis*. In total, 43 species of aphids were found on all plants. Of these, 32 species of aphids were found on the aboveground parts of plants, the rest were localized on the roots and root neck. A large number of myrmecophilous aphid species promotes effective trophobiosis of *L. niger* with them on the territory of the nest complex, which can increase the supply of the resource (carbohydrate excretions of aphids). Thus, the existence of colonies of *L. niger* ants as a nest complex is also possible in herbaceous plant communities, if the ant species is capable of mutualistic relationships with a large number of myrmecophilous aphid species.

Acknowledgement

The research leading to this publication has received funding from “The support of the priority research areas development of Ukraine, KPKVK 6541230” (for S. Stukalyuk).

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