

3-6-2024

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STUKALYUK, STANISLAV and KOZYR, MYKOLA (2024) "Highways for red wood ants (Hymenoptera: Formicidae): a new method to increase the size of anthills," *Turkish Journal of Zoology*. Vol. 48: No. 2, Article 4. <https://doi.org/10.55730/1300-0179.3167>
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Highways for red wood ants (Hymenoptera: Formicidae): a new method to increase the size of anthills

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Received: 03.12.2023 • Accepted/Published Online: 18.02.2024 • Final Version: 06.03.2024

Abstract: Red wood ants (RWA, *Formica rufa* group) play a key role in forest ecosystems as effective entomophages and participants in the circulation of organic matter. The aim of our study was to evaluate the efficiency of using the highway method to accelerate the growth of anthills, specifically focusing on height, diameter, volume. The study was conducted in Kyiv, Ukraine, from May to October 2023. In the experimental group, highways were constructed on ant trails, totalling nine *Formica polyctena* Forster, 1850 anthills and eight *Formica rufa* Linnaeus, 1761 anthills. These highways consisted of a continuous line of logs ranging from 10 to 15 cm in diameter. The control group consisted of 11 *F. polyctena* anthills and eight *F. rufa* anthills, with all trails running along the forest floor surface. Height and diameter measurements were conducted monthly, and anthill volumes were calculated during data processing. Analysis of anthill linear parameters revealed a significant acceleration of growth in the experimental group. The average anthill diameter, height, and volume for both ant species in the experimental group (12 cm height, 24 cm diameter for *F. rufa* and 29 cm diameter, 9 cm height for *F. polyctena* per season) exceeded those of the control group, where either no increase or a decrease in anthill size was observed ($p \leq 0.01-0.0001$). The increase in anthill volume within the experimental group, compared to the control group, from May 2023 to September 2023 was twice as large for both species ($p \leq 0.02-0.005$). These findings confirm the efficiency of the highway method in stimulating growth of red wood ant anthills. Accelerated anthill growth can help maintain ant populations in forest ecosystems, which is important for maintaining biodiversity and stability within these ecosystems.

Key words: Red wood ants, growth, trails, highways, *Formica rufa*, *Formica polyctena*

1. Introduction

Ants are social insects that live in nests that contain both imago and brood (Hölldobler and Wilson, 1990). These nests are typically perennial structures that can remain in the same location for decades. The location of an ant nest is usually associated with several factors, including proximity to a resource source, such as a food tree, and favourable microclimatic conditions (Zakharov, 1991). Ant species such as red wood ants (RWA, *Formica rufa* group) build aboveground mound-shaped nests (Radchenko, 2016; Seifert, 2018). Upon reaching a certain size (0.8–1.1 m in diameter), these nests acquire active thermoregulation ability (Rosengren et al., 1987; Zakharov, 1991; Stukalyuk, 2020). Such nest mounds are therefore more resistant to environmental factors than nests in the soil. Stable microclimatic conditions over a long period of time allow for existence of entire RWA nest complexes with dozens or even hundreds of nest mounds (Zakharov, 1991, 2015;

Stukalyuk et al., 2021). If conditions become unfavourable, the ant colony may move to a new location or merge with another colony. RWA can migrate up to 350 m (Zakharov, 1991, 2015).

The shape of the nest mound can indicate the state of RWA colony. For example, declining nest mounds become overgrown with herbaceous vegetation and lose their spherical shape due to uneven construction. Different stages of nest mound life can also be associated with its different shapes: young, actively growing nest mounds are usually cone-shaped, stabilised in growth, and have a hemispherical shape, while dying nest mounds are asymmetrical (Zakharov, 1991, 2015). Biotope conditions also influence the shape of nest mounds: in shaded biotopes (such as spruce forests), they are conical; in light biotopes (such as forest edges) they are flat (Zakharov, 1991; Stukalyuk et al., 2021). This statement also applies to the size of nest mounds. For example, optimal conditions

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for larger *Formica rufa* nest mounds are associated with productive or young stands and low canopy closure (Serttaş et al., 2020; Sorvari, 2022; Yilmaz et al., 2023). Conversely, in the mountainous regions of Switzerland, RWA distribution is not correlated with the forest patch size, distance to the edge, and floristic diversity; however, there is a relationship with forest structure and abundance of coniferous trees (Vandegehuchte et al., 2017). The presence of coniferous species in the forest as a favourable factor for RWA habitat is emphasised in a number of other works (Robinson et al., 2008; Sondej et al., 2018; Fitzpatrick et al., 2020; Frizzi et al., 2022; Stukalyuk et al., 2023). In RWA, the largest nest mounds are found in mixed forests (Kilpeläinen, 2008; Stukalyuk, 2022). Additionally, the size of nest mounds follows Bergmann's rule: they become larger on average as latitude increases (Juhász et al., 2020a).

The nesting material itself can also influence the shape of nest mounds: conical mounds are built from short spruce needles, whereas mounds made from longer pine needles are usually flatter (Zakharov, 1991). The flat shape is also characteristic of nest mounds in beech-dominated forests (Frizzi et al., 2022). Consequently, the shape of nest mound depends on a combination of factors. If the living conditions change, the nest mound can change its shape: it increases in height with shading and can become flatter with increasing light (Zakharov, 2015).

In favourable conditions, nest mounds grow faster. Therefore, within the optimal zone, a nest mound reaches a size sufficient for active thermoregulation in the 3d to 4th year of the colony life, while in suboptimal biotope areas, this stage may require 5 to 6 years (Zakharov, 2015). RWA nest mounds, especially large ones (diameter of 1 m or greater), can change in size during the season, depending on their condition. Notably, the size of large nest mounds can undergo significant changes; they can move through several size classes, decreasing or increasing in size (Zakharov 1991, 2015; Dyachenko, 2017). There are methods that can be used to stabilise the condition of a nest mound. These include the highway method: placing logs along forage trails, allowing ants to deliver food to the nest mound quickly (Stukalyuk et al., 2023). Considering that hundreds of workers can pass along a forage trail per minute (Stukalyuk et al., 2022a), their movement along highways can be significantly accelerated compared to trails along the forest floor surface: up to 62% (Stukalyuk et al., 2023). This increased traffic intensity may help the nest mound to grow or stabilise its size. In this paper, an experimental study was conducted to verify the efficiency of the highway method on nest mound growth rates. Maintaining the size or creating conditions for the growth of RWA colonies is of important practical value, given the role these ants play in forest ecosystems, where they

act as collectors of organic matter (Lenoir, 2001; Risch et al., 2005; Ohashi et al., 2007; Domisch et al., 2008; Kilpeläinen, 2008; Tsikas et al., 2021). Additionally, RWA are efficient biological agents in the pest plague control (Wellenstein, 1973).

Monitoring and conservation of RWA populations in Europe has become increasingly important in recent years (Balzani et al., 2022), and the highway approach may provide an opportunity to improve the overall condition of these species.

The findings of this study can be used for the development of methods aimed at maintaining and stimulating the growth of RWA nest mounds, which are important for maintaining biodiversity and strengthening ecosystems. Additionally, the estimation of the efficiency of the highway method will provide valuable information on the feasibility of using human intervention to create favourable conditions for ant colonies.

The aim of the study is to estimate the efficiency of applying the highway method to measure the linear dimensions (height, diameter, volume) of nest mounds in two RWA species (*Formica rufa*, *Formica polyctena*). Research objectives are as follows: a) Implement the highway method by placing logs along the ant forage trails and measure linear parameters in the experimental and control groups of nest mounds. b) Compare the dynamics of changes in the nest mound size and shape between the experimental and control groups during different periods of the study (May to October 2023).

2. Materials and methods

2.1. Study area

The study was conducted from May to October 2023 in Kyiv, Ukraine (Figure 1). Nest mounds were selected for the measurements within the territories of three nest complexes, two of which belonged to *F. polyctena* (one near the village of Kotsiubynske, in the Bilychi Forest, and one in Holosiyivo Forest), while one belonged to *F. rufa* (Figure 1, Holosiyivo Forest).

The *F. polyctena* complexes comprised a total of 17 and 10 anthills, respectively, while the *F. rufa* complex comprised 73 anthills. The *F. polyctena* nest complexes were located within a territory of mixed forest dominated by oak (*Quercus robur*), maple (*Acer platanoides*), and pine (*Pinus sylvestris*) in the main tree layer. Conversely, the *F. rufa* nest complex was located within the territory of larch (*Larix decidua*) plantations in a deciduous forest with the same deciduous tree species. All anthills belonging to the same complex were located in the same forest conditions. The Bilychi Forest spans an area of 4000 ha, while the Holosiyivo Forest covers 769 ha. Climatic conditions in Kyiv for the year 2023 are presented in Table 1.

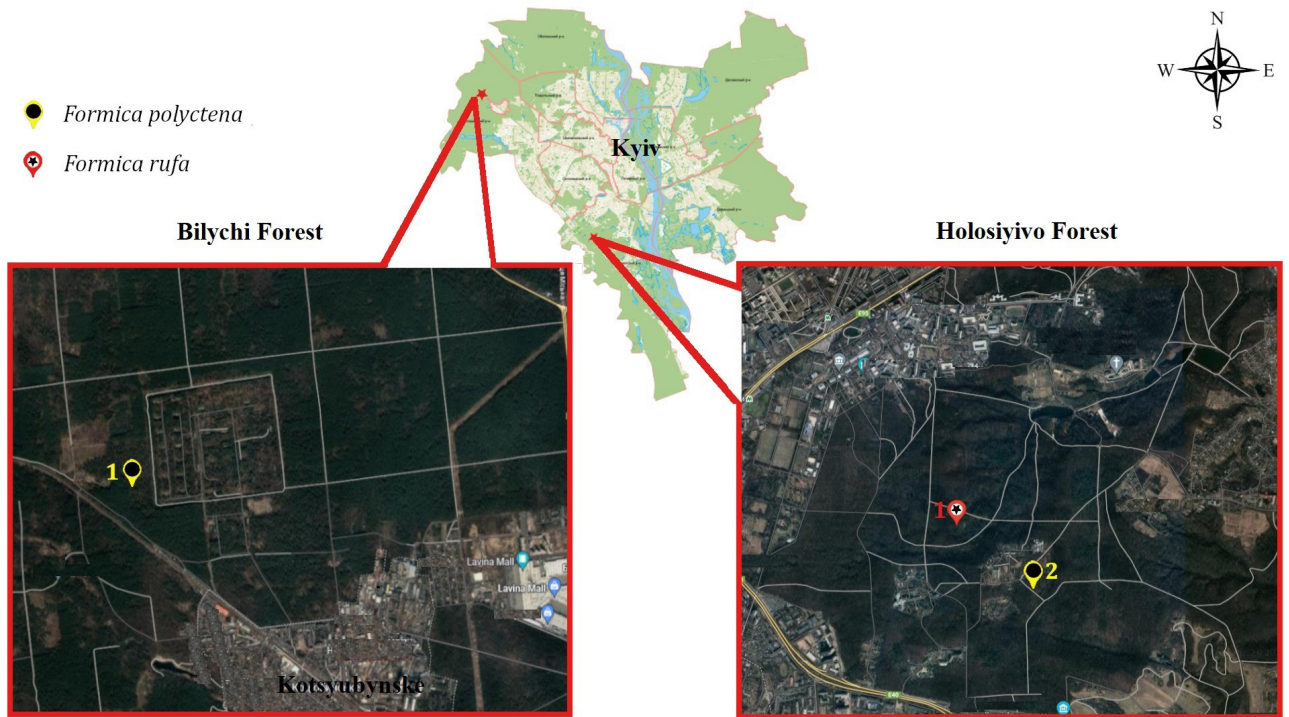


Figure 1. Location of the studied RWA nest mounds. On the left is the Bilychi Forest (*Formica polyctena*), on the right the Holosiyivo Forest (*Formica polyctena*, *F. rufa*).

Table 1. Normal climatic conditions in the study area (Kyiv)*.

Month	Average temperature, °C	Precipitation per month, mm
May 2023	20.1 during the day, 12.1 at night	72
June 2023	24.9 during the day, 16.5 at night	70
July 2023	26.7 during the day, 18.0 at night	64
August 2023	26.8 during the day, 16.8 at night	31
September 2023	20.5 during the day, 13.2 at night	33
October 2023	1.7 during the day, 7.8 at night	33

*Data retrieved from the website: <https://tur-pogoda.com.ua/ukraine/kyiv>

While air temperatures were rising until August 2023, the amount of precipitation gradually decreased from May, resulting in increasingly dry air until October 2023.

2.2. Sampling

For the study, we selected nest mounds of the same size class (Table 2) that were not adjacent to each other, in order to exclude crosseffect (Supplementary Table 1). In addition to being similar in size, the anthills had the same number of forage trails, indicating similar infrastructure. We specifically selected anthills located on the periphery of nest complexes. This is due to the fact that anthills in the centre of a nest complex may deteriorate under pressure from anthills outside, as their territory does not expand. The minimum distance between nest mounds was 10 m.

2.3. Research methods

Mapping:

After selecting a nest mound for research, a comprehensive mapping of its territory, including forage trails and foraging trees with aphid colonies, along with their linear dimensions, was carried out. The mapping was performed on graph paper at a scale of 1 m to 1 cm, using the methodologies outlined by Zakharov (2015) and Dlussky (1967).

Laying highways and forming experimental and control groups:

Half of all selected nest mounds were chosen as experimental, and the remainder served as control. The territories of control nest mounds remained unchanged

Table 2. Number of *Formica rufa* and *F. polyctena* nest mounds surveyed at each site.

Location	Species	Experimental	Control
Kotsiubynske	<i>Formica polyctena</i>	4	5
Holosiyivo Forest (observatory)	<i>Formica polyctena</i>	5	6
Holosiyivo Forest (larch planting)	<i>Formica rufa</i>	8	8
<i>Formica polyctena</i> , number of measurements for all months		48 (D) + 48 (h)	48 (D) + 48 (h)
<i>Formica rufa</i> , number of measurements for all months		66 (D) + 66 (h)	54 (D) + 54 (h)
<i>Formica polyctena</i> , the number of trails		3.0 ± 0.6	4.0 ± 0.8
<i>Formica rufa</i> , the number of trails		2.6 ± 0.3	2.2 ± 0.3
<i>Formica polyctena</i> , average diameter		110.4 ± 5.7	120.6 ± 5.9
<i>Formica polyctena</i> , average height		33.0 ± 2.6	30.8 ± 3.1
<i>Formica rufa</i> , average diameter		113.7 ± 9.4	119.7 ± 4.0
<i>Formica rufa</i> , average height		35.0 ± 4.5	31.2 ± 2.3

throughout the observation season. Highways were laid along the entire length of all trails in the experimental group (Figure 2).

Logs with diameters ranging from 10 to 15 cm were selected as highways. The highways were placed directly on the ants' trails. One week after the placement, in May 2023, a control examination of the experimental nest mounds was carried out to verify that the ants had moved to the highways offered to them. In instances where the ants did not completely migrate to the highways, their arrangement was modified until the ants migrated along the entire length of the highways. The highways consisted of several logs laid end to end along each trail.

Nest mound measurements:

For each nest mound, its height and diameter were measured following the method outlined by Arnoldi (1979), with a measurement error not exceeding 1 cm. Measurements of nest mounds were conducted monthly, specifically on the 15th day of each month. The diameter was determined by measuring the width of the nest at its widest and narrowest points. To achieve consistency, pegs were driven into these measuring points to ensure accurate measurements in the same place in subsequent months. The average diameter for each nest mound was then calculated from the two diameter values obtained. Similarly, the height of the nest mound was measured using the same approach, except that the ruler was placed on top of the peg so that it was parallel to the ground surface. The accuracy of the height parameter obtained was validated using a construction level meter.

In the calculations, we employed both the linear parameters of the nest mounds (height and average diameter, measured in cm) and computed ones (nest mound volume, measured in m³). The volume was calculated using the cone formula:

$$S \times H / 3 \text{ (Formula 1),}$$

where H is the height of the nest mound and S is the base area of the nest mound.

2.4. Statistical analysis

The calculations were performed using Past software (v.4.13). The arithmetic mean and the standard error of the mean were calculated for each parameter (diameter, height, volume). The significance of differences in the nest mound size between months (May and September) was determined using the Kruskal-Wallis test. The reliability of changes in volume and linear dimensions of nest mounds between the experimental and control groups throughout the observation season was determined using posthoc Dunn's test (p-value, z-value). This was achieved by subtracting the linear dimensions and volumes of the nest mounds for each preceding month from those of the subsequent month. Negative values indicate a decrease in nest mound size, while positive values indicate an increase. Consequently, a series was obtained for each group of nest mounds in both ant species, where dynamics of changes were recorded from June to October 2023. To compare the linear sizes of the nest mounds and their volumes, we analysed data from May and September 2023. We selected May as it corresponds to the start of the observation period, while September was chosen as the end of the season when ants are still quite active and can carry out construction activities. October is characterised by a significant decrease in ant activity as they prepare for hibernation.

3. Results

Comparison of *F. rufa*, *F. polyctena* nest mound sizes at the beginning (May 2023) and in the end (September 2023) of the study period:

The differences in the nest mound sizes between the experimental and control groups, in terms of diameter and height, were found to be significant (Supplementary Table 1, Table 3). If in May 2023 the nest mounds of both groups were smaller, by September 2023 the size of the nest mounds in the experimental group had increased significantly compared to those of the control group.



Figure 2. Highways built on the forage trails of RWA. A: Highways constructed from the nest mound. B: Movement of RWA workers along the highways.

Table 3. Kruskal-Wallis test results for diameter and height of anthills of *F. rufa*, *F. polyctena* in the experimental and control groups in May and September 2023.

Species	H	DF	p-value
<i>Formica rufa</i> , diameter, May and September 2023	8.032	14	0.045
<i>Formica rufa</i> , height, May and September 2023	10.71	14	0.012
<i>F. polyctena</i> , diameter, May and September 2023	16.17	18	0.001
<i>F. polyctena</i> , height, May and September 2023	16.01	18	0.001

Dynamics of changes in the size of nest mounds of *F. rufa*, *F. polyctena* (diameter and height) from the experimental and control groups for the period from May to October 2023:

The historical data for the nest mound size in both groups of *F. rufa*, *F. polyctena* are presented in Figures 3A and 3B, respectively.

If at the beginning of the study (May 2023) the nest mounds of both groups were approximately the same in height and diameter, by August 2023, the nest mounds of *F. rufa* from the experimental group exceeded those of the control group in diameter (Figure 3A). The height of the control nest mounds remained virtually unchanged throughout the study period, while the experimental nest mounds began to grow in height as early as June 2023. Furthermore, their height remained consistent until October 2023 (Figure 3A). For *F. polyctena*, the diameter of the nest mounds in the experimental group started to increase in June 2023, and the height continued to rise from June to September 2023 (Figure 3B). Conversely, the diameter of nest mounds in the control group decreased from September 2023, even when compared to their parameters in May 2023 (Figure

3B). Examination of the changes in the linear dimensions of the nest mounds during the observation period reveals significant differences between them (Table 4).

The nest mounds of the experimental group for *F. rufa* and *F. polyctena* exhibited an increase in both diameter and height, whereas those of the control group showed a slight decrease in both parameters (Table 4). The differences in sizes of the *F. polyctena* nest mounds in the experimental group at the end of the season (in October) are less observable.

Comparison of changes in the volume of nest mounds of *F. rufa*, *F. polyctena* of the control and experimental groups in May and September 2023:

A pairwise comparison of nest mound sizes indicated that, by September 2023, the nests in the experimental group had exhibited an increase in volume compared to those of the control group (Table 5).

This was true for both the linear dimensions of *F. rufa* and *F. polyctena* nest mounds (Figures 4A–4D) as well as their volume.

In both RWA species, nest mound volumes in the experimental group increased approximately two times by

Table 4. Changes in size parameters of nest mounds *F. rufa*, *F. polycтена* (diameter and height) from the experimental and control groups for May–October 2023.

Species, parameter, and group	Increase (+) or decrease (-) in size per season, cm	Z	p-value
<i>F. rufa</i> , D, control	-8.8 ± 4.1	3.153	<0.001
<i>F. rufa</i> , D, experimental	24.6 ± 5.3		
<i>F. rufa</i> , h, control	-2.1 ± 1.7	3.103	<0.001
<i>F. rufa</i> , h, experimental	12.5 ± 2.6		
<i>F. polycтена</i> , D, control	-9.9 ± 3.2	3.761	<0.0001
<i>F. polycтена</i> , D, experimental	29.6 ± 4.7		
<i>F. polycтена</i> , h, control	-0.4 ± 2.0	2.476	<0.01
<i>F. polycтена</i> , h, experimental	9.4 ± 2.9		

Table 5. Changes in the volume of nest mounds of *F. rufa*, *F. polycтена* in the control and experimental groups in May and September 2023.

Species, parameter, and group	Decrease (-) in size per season of activity, m3	Kruskal-Wallis test between 2 months	Z	p-value
<i>F. rufa</i> , V, control	0.1175 ± 0.009 (May)	H = 0.044, p = 0.833	2.838 (September control vs. September experimental)*	0.02
	0.1153 ± 0.016 (September)			
<i>F. rufa</i> , V, experimental	0.1362 ± 0.038 (May)	H = 4.864, p = 0.027		
	0.2481 ± 0.035 (September)			
<i>F. polycтена</i> , V, control	0.1197 ± 0.0179 (May)	H = 0.157, p = 0.691	3.302 (September control vs. September experimental)*	0.005
	0.1127 ± 0.0089 (September)			
<i>F. polycтена</i> , V, experimental	0.1141 ± 0.0172 (May)	H = 12.11, p = 0.0004		
	0.2325 ± 0.0158 (September)			

*May control vs. May experimental is not significant (Z = 0.19 for *F. rufa*; Z = 0.26 for *F. polycтена*).

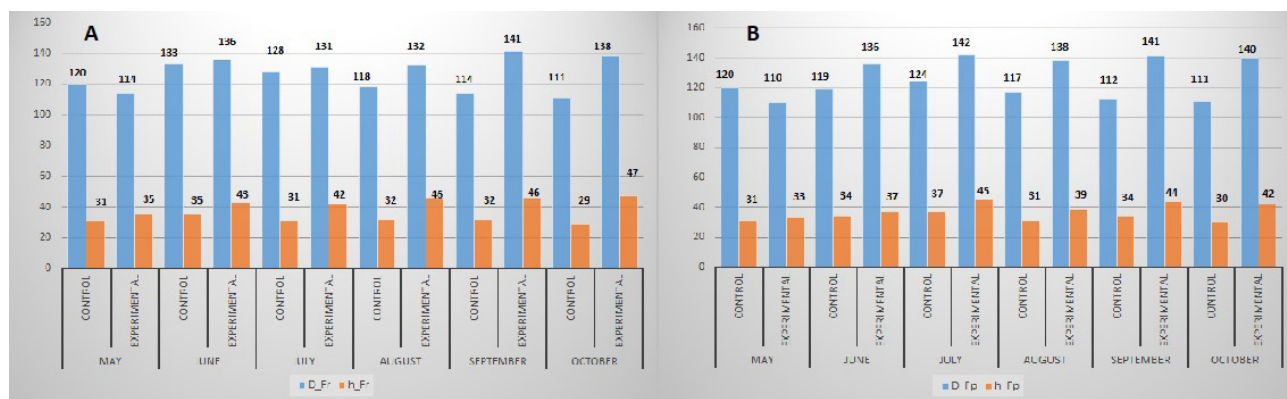


Figure 3. Changes in linear indicators of height and diameter of the nest mounds in the control and experimental groups of *F. rufa* (A) and *F. polycтена* (B) during the 2023 season.

September 2023 (Table 5). In September 2023, nest mound volumes in the control group remained approximately the same as they were in May 2023.

For the control *F. polycтена* nest mounds, the height to diameter ratio averaged 0.26 in May 2023, increased to 0.28–0.30 from June to September, and remained at 0.28 in October. In the experimental group, these indicators changed more sharply: by 0.30 in May, 0.27 in June, 0.31 in

July, 0.28 in August, 0.31 in September, and 0.30 in October. Consequently, the nest mounds in the experimental group displayed higher ratios compared to those in the control group. For *F. rufa*, these indicators for control were 0.26 in May and June, 0.24 in July, 0.22 in August, 0.29 in September, and 0.26 in October.

For the experimental group, the ratio was 0.30 in May, 0.32 in June and July, 0.30 in August, 0.32 in September,

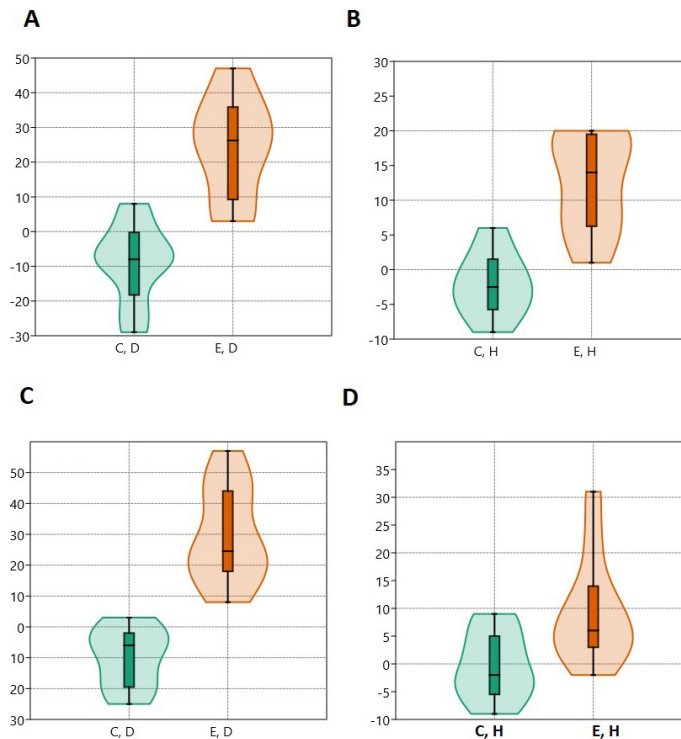


Figure 4. Seasonal increase or decrease in linear dimensions of *F. rufa* (A, B) and *F. polycтена* (C, D) nest mounds for May–September 2023. A, C – diameter (D), B, D – height (h). Vertical – parameters (in cm), horizontal – groups of nest mounds (C – control, E – experiment).

and 0.34 in October. The nest mounds in the experimental group showed a consistent increase in the height to diameter ratio, indicating construction activity of ants and the active growth of nest mounds.

4. Discussion

The seasonal nest-building activity of RWA involves the rearing of a generation of alates. In spring, some workers are occupied with caring for the larvae initially, followed by the alates. Following the nuptial flight, which usually occurs in late April and May (Stukalyuk et al., 2021), these workers are released from the alate care and switch to foraging and nest building (Zakharov, 1991). Consequently, we observed the growth of the nest mounds in early summer. In early autumn, the colony prepares for hibernation by actively expanding its underground part, which is reflected in the changes in nest mound parameters observed in September. It should be noted that these changes are more pronounced in the experimental group of nest mounds and may correspond to those found in RWA optimal habitats. RWA nest complexes, or supercolonies, can reach great sizes. For instance, in *Formica aquilonia* Yarrow, 1955, with a complex comprising 176 nest mounds and a total forage area of 17.6 ha, the estimated

number of workers was 80 million (Zakharov, 1978). The nest complexes studied by us were smaller: an actively growing *F. rufa* complex had half as many nest mounds, while *F. polycтена* had either 10 times fewer or more. The less pronounced growth of *F. polycтена* nest mounds in the experimental group may have been due to the fact that they were in the stage of stable existence, without the formation of a large number of layerings (daughter anthills). The use of highways enabled the stabilisation of *F. polycтена* nest mound conditions, leading to a slight increase in both linear indicators and volume compared to the control group. Within a nest complex's central part, stratification either does not occur or occurs only when old nest mounds die, as the food supply remains limited (Zakharov, 1991).

Furthermore, the central part of such a complex can be repopulated in the event of degradation of the nest mounds located there. This feature informed our decision to study the peripheral part of nest complexes, where external nest mounds have the opportunity to develop and expand. In different years, nest mounds may experience varying rates of increase or decrease in parameters. In favourable years for *Formica lugubris* Zetterstedt, 1838, the increase in diameter can reach 10–20 cm, although on average it does

not exceed 2–6 cm. The rate of decrease in unfavourable years can be 8–10 cm (Zakharov, 1991). For *F. rufa* and *F. polyctena*, these parameters can range from 5–30 cm for increase to 10–30 cm for decrease (Dyachenko, 2017). According to our data, the average height of *F. rufa* and *F. polyctena* nest mounds as part of the complex can change by 1–6 cm in different years in both directions, and the diameter 5–15 cm (Stukalyuk et al., 2023). Overall, this aligns with the data we obtained for the experimental group of *F. rufa* and *F. polyctena* nest mounds. It is possible that the highway method is primarily effective for peripheral nest mounds, while for those located in the central part of the nest complex, it stabilises their condition due to limited food resources. In critical cases, when several nest mounds merge into a single large one as a population concentration strategy (Zakharov, 1991), the diameter of the nest can increase by 50 cm per year, while its height may grow by 15–20 cm (Stukalyuk et al., 2023). It is noteworthy that under unfavourable conditions, such as shading and varying light conditions, RWA can vertically move and colonise empty cavities within the crowns of old oak trees (Stukalyuk, 2017).

Illumination plays a key role in the selection of a nest mound site by RWA, as these species have specific requirements for its parameters (Stukalyuk et al., 2022b; Stukalyuk and Maák, 2023). An important condition for maintaining the linear size of nest mounds is the presence of conifers in the forest composition, as they are smaller and therefore more vulnerable in deciduous forests (Vandegehuchte et al., 2017; Juhász et al., 2020b; Stukalyuk et al., 2023).

As part of a nest complex (supercolony), the diameter of nest mounds can increase by up to 70% of the original size over a 4-year observation period in *F. aquilonia* (Zakharov, 1991) and by up to 30% in *F. polyctena* (Gösswald et al., 1968). Comparing the average diameter of nest mounds across the entire nest complex reveals less variability, with increases ranging from 1 to 8 cm and decreases from 6 to 10 cm in the case of *F. aquilonia* (Zakharov, 1991). According to other data, the increase in nest mounds artificially resettled and protected from the influence of wild boars and woodpeckers was 125% of the initial parameters over a 4-year observation period, compared to 10% in unprotected nest mounds (Wellenstein, 1965). Moreover, forest type influences the development of *Formica polyctena* nest mounds, which develop more rapidly in mixed forests comprised of spruce, pine, oak, and birch, compared to coniferous forests primarily consisting of spruce (Wellenstein, 1973).

The growth of nest mounds is closely related to their survival. For RWA, which inhabit nest mounds up to 60 cm in diameter, it is crucial to reach a threshold of 80–100 cm within 1–2 years. This threshold corresponds to

the size of a colony with autonomous thermoregulation (Zakharov, 1991; Stukalyuk et al., 2020). This is particularly critical for nest mounds in urban forests (Vepsäläinen and Wuorenrinne, 1978; Stukalyuk et al., 2022b, 2023). We studied adult nest mounds with a dome diameter of 1 m or more, i.e. capable of autonomous thermoregulation. Such anthills exhibit higher survival rates compared to small nests; they may decrease in size but do not become extinct (Dyachenko, 2017). Climatic conditions during ants' active season may also play an important role. As the temperature decreased from August and into October 2023, the amount of precipitation remained at a consistently low level from May to July 2023 (Table 1). Such dry weather could have contributed to the fact that nest mounds from the control group of both species stopped growing, their diameter and height even slightly decreased as compared to the earlier period when precipitation levels were higher (Figures 3A and 3B). Conversely, the nest mounds in the experimental group maintained their stable indicators of linear dimensions, which they reached in the May to July period of 2023. Humidity and temperature indicators inside *F. polyctena* nest mounds are inversely related (Véle and Holuša, 2008), i.e. at a constant low humidity, they heat up more. In turn, RWA have a certain optimum of illumination parameters (indirectly related to temperature) where they prefer to settle (Stukalyuk and Maák, 2023).

It can be assumed that at high temperatures, the nest mounds in the control group may diminish somewhat in size due to the loss of moisture from the nesting material, causing it to dry out. Conversely, in the experimental group of nest mounds, it appears that there remains significant construction activity, with constant movement of nesting material within the nest mound, as well as its supply from the forage area, ensuring the maintenance of their linear parameters. The height to diameter ratio of a nest mound can indicate its viability; with a threshold value of 0.25, nest mounds are capable of active growth and development (Dyachenko, 2017). In our experimental group, this ratio for both species is higher, indicating their greater viability.

A logical continuation of our research would be a similar experiment with small nest mounds, ranging from 0.4 to 0.6 m in diameter, which can have mortality rate of 60%–80% in the first year (Zakharov, 1991), although in optimal habitat conditions only 30% of anthills die (Dyachenko, 2017). The implementation of the highway method may not only accelerate the growth of such nest mounds but also increase their survival rates. Additionally, it is also interesting to compare the growth rates between small nest mounds with a highway system and large nest mounds without one.

It is interesting to note that RWA nest complexes exhibit greater resistant to external negative factors, such

as climatic and anthropogenic influences (Zakharov, 1991; Stukalyuk et al., 2023). Therefore, one might anticipate higher efficacy of the highway method in this case, compared to single anthills.

In the previous studies, the linear parameters of RWA nest mounds were annually measured and compared between years (Zakharov, 1978, 1991, 2015; Dyachenko, 2017; Stukalyuk et al., 2022, 2023). These parameters change most substantially at the beginning of summer and in September, and the size of nest mounds can fluctuate significantly (within the annual norm), especially during the driest months, which typically occur in the middle and end of summer. We associate the increase in linear parameters and volume of nest mounds with the fact that food is delivered faster in the group of experimental nests, and also the speed of workers' movement on highways is higher (Stukalyuk et al., 2023a). *F. rufa* workers can transfer 0.03 mL of liquid food per turn, while *F. polyctena* can transfer 0.02 mL (Dyachenko, 2017). In sunny weather, *F. rufa* foragers returning to the nest with prey (protein food) can account for up to 2% of the total number, while for *F. polyctena*, this is 1.1% (Dyachenko, 2017). Considering that the speed of workers' movement along highways is 50%–62% higher than on the forest floor for both species, we can state that a larger amount of food is moved per unit time on the highway (Stukalyuk et al., 2023a). During outbreaks of mass pest reproduction, the supply of protein food to the nest mound increases, particularly in polygynous RWA species whose colonies are larger than monogynous ones (Wellenstein, 1973). Thus, highways may have a greater capacity than trails that run along the surface of the forest floor. Larger anthills are able to produce a greater number of alates and are therefore guarantors of the conservation of RWA populations (Sorvari and Hakkarainen, 2005).

The provision of highways to growing nest mounds is expected to accelerate their growth and production of alates, which may further contribute to RWA conservation. Additionally, large nest mounds, which visit a greater number of foraging trees in the spring, establish a greater number of daughter anthills in summer compared to small anthills (Wellenstein, 1973). This means that large growing ant colonies also produce a larger number of daughter colonies, which unite to form a nest complex, known as a supercolony (Zakharov, 1991, 2015). Another crucial condition for stable growth is the maintenance of forest growth conditions, as any changes such as felling can lead to a decrease in linear dimensions or depopulation (Sorvari et al., 2014).

It should be noted that the growth of red wood ant populations, even when artificially induced, may not always have positive consequences for forest ecosystems. For example, red wood ants promote the intensive reproduction of aphid colonies on the trees they visit

(Skinner and Whittaker, 1981). Additionally, the diet of red wood ants can include many entomophages, which can account for up to 15%–20% of all collected insects (Adlung, 1966). Finally, red wood ants are known to defend only those trees from phytophagous trees that contain food sources for the ants, such as aphid colonies (Maňák et al., 2015). In the feeding area of red wood ants, the abundance of some other insect groups is reduced, including lepidopteran larvae (Skinner and Whittaker, 1981) and ground beetles (Hawes et al., 2002; Reznikova and Dorosheva, 2004; Thunes et al., 2018). It is also known that lichen and epiphyte species richness can be negatively associated with red wood ant nest mound density (Thunes et al., 2018). Red wood ants can indirectly slow down the radial growth of 30–60-year-old adult spruce trees by visiting aphid colonies, although this effect is insignificant at the forest ecosystem level (Kilpeläinen et al., 2009). These data are supported by another study showing that trees more than 200 m away from nest mounds grow faster than trees growing in close proximity (Frouz et al., 2008). Therefore, measures to increase red wood ant populations need to be approached with caution.

5. Recommendations

Highways can be quite durable, lasting at least two seasons, as our observations have shown. This durability may be related to the integrity of the logs and branches from which they are made and the absence of decomposition processes that result from fungal infection. For maximum efficiency, highways should cover all major infrastructure in the forage area, at least the largest trails. Expanding the forage area of the RWA can be facilitated by releasing some workers from trails that have become highways. These workers can then expand into external territories, which can also be developed by laying trails leading to unoccupied forage trees. This can be accomplished by using logs that have already been used by the ants, as they contain pheromones that can guide ants to new trees. Subsequently, new trails are built on the old sections. Highways need to be checked regularly (at least once a month) for integrity and repaired if necessary. The possibility of such an artificial construction of the forage area should be investigated in the future. We found a significantly greater increase in the height or diameter of nest mounds with highways; therefore, this method can be recommended for widespread use by foresters. The display of highways may also be of research and practical interest. If a part of the highway is built at an angle from the trail surface to a certain height above the trunk of the forage tree, ants can more easily reach such trees compared to having to overcome the vertical surface of the trunk.

6. Conclusion

A comprehensive study of changes in *F. rufa* and *F. polyctena* nest mounds, caused by the introduction of new infrastructure in the form of highways, allows us to draw a number of important conclusions that go beyond simply stating the success of this change.

Firstly, the increase in the size of the nest mounds after the changes were made indicates not only functional efficiency of the proposed highways but also ants' ability to adapt ecologically. This phenomenon can be interpreted as the ants' response to environmental changes and their ability to successfully adapt to new conditions.

Secondly, it is worth paying attention to the potential impact of the introduced changes on the ant population. Assessing ant abundance, reproductive rates, and survival rates can show how these changes affect the health and structure of the population. A third important observation is that differences in the responses of different ant species to new infrastructure highlight their unique roles in the ecosystem. Studying these differences may help to better understand the growth potential of nest mounds of different red wood ant species when highways are used.

In addition, analysing the long-term effects of such changes will improve our understanding of the stability of impacts, as well as may provide valuable insights into how anthills maintain their size in subsequent seasons.

Overall, these results highlight the importance of infrastructure for nest mound formation and open up prospects for further research into ant-environment interactions in urban environments.

The results of the study confirm that the introduction of highways was successful in increasing the size of the nest mounds of both RWA species. This suggests that making changes to the structure of the forage area (by replacing all trails on forest floor with highways) turned efficient in increasing the size of nest mounds.

The increase in nest mound sizes indicates that *F. rufa* and *F. polyctena* are highly ecologically adapted to changing conditions. This ability of the ants was demonstrated by their response to new infrastructure, thus highlighting their adaptive potential.

The observed differences in the responses of *F. rufa* and *F. polyctena* indicate unique characteristics of each ant species. This finding could have important ecosystem implications and highlights the diversity of the roles played by ants in urban environments.

The study also provides a basis for long-term monitoring of changes in ant colonies. It is important to continue monitoring and assessing the sustainability of the increased nest mound sizes in subsequent seasons. In this case, it is worth paying attention to seasonal changes in the linear dimensions of anthills as an adaptation to changing environmental conditions.

Successful changes in nest mound parameters (height, diameter, volume) not only highlight the importance of infrastructure solutions for improving RWA living conditions, but also potentially have a positive impact on the ecosystem as a whole.

The results of the study open up new opportunities for a better understanding of ants' interactions with environmental change and can serve as a starting point for further research in urban ecology.

Acknowledgements

The authors would like to thank the anonymous reviewer whose comments and suggestions significantly improved the quality of the article. The research leading to this publication received funding from "The support of the priority research areas development of Ukraine, KPKVK 6541230" (for S. Stukalyuk).

Conflict of Interest

The authors declare that they have no conflict of interest.

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Supplementary material

Supplementary Table 1. Primary data on the diameter and height of red wood ant nest mounds in all months of the study.

Month	Control <i>F. Rufa</i>		Experimental <i>F. rufa</i>		Month	Control <i>F. polycтена</i>		Month	Experimental <i>F. polycтена</i>	
	Diameter cm	Height cm	Diameter cm	Height cm		Diameter cm	Height cm		Diameter cm	Height cm
May	110	30	82	34	May	85	40	May	95	34
	112	30	91	25		120	20		90	30
	105	40	91.5	30		120	20		94.5	32
	112.5	22	104.5	25		110	32		95	15
	122.5	40	110	28		150	30		95	40
	130	30	150	32		135	49		115	22
	130	28	149	63		117	26		115	40
	136	30	132	43		127	29		125	38
June	115	36	105	42	June	122	32	June	145	32
	129	36	120	50		65	30		138	46
	132.5	43	125	41		75	22		107	34
	135	29	135	30		125	30		115	41
	135	38	138	32		120	40		125	32
	138.5	35	153	42		153	35		128.5	35
	140	32	152	62		140	50		135	18
	139	33	159	49		125	32		150	46
July	118	33	110	39	July	137	33	July	157	25
	107	33	111	46		130	37		120	42
	125	36	114	42		74	33		132	40
	133	26	128	27		96	31		155	39
	138	31	133	28		132	34		148	50
	140	31	149	37		127	39		130	39
	138	30	155	67		148	41		117	40
	130	27	153	55		143	55		119	37
August	93.5	24	102.5	35	August	131	38	August	128	42
	95	27	116	40		132	31		143	40
	102.5	25	108	40		135	35		155	45
	117	24	129	33		80	37		166	44
	135	30	137	31		92	34		141	48
	135.5	27	142	38		128.5	32		140	47
	140	28	165	57		124	30		161	50
	125	28	161	50		135	33		155	54
September	91.5	34	130	38	September	130	34	September	138	46
	87	31	129	47		118	26		120	36
	94	33	128	38		120	25		125	31
	110	28	134	45		127	28		120	35
	126	41	141	38		73	40		135	44
	141	32	156	40		102	36		151	40
	135	36	156	73		122.5	34		165	41
	129	26	155	51		116	33		139	41
September	89	27	129	35	September	122.5	38	September	134	43
	83	28	128	45		115	38		158	44
	95	31	124	41		116	29		146	37
	104.5	24	131	43		123	30		132	40
	118.5	35	136	45		120	29		122	46
	138	30	153	52		72	31		136	35
	131	34	155	70		95	27		122	39
	128	24	151	49		123	29		145	48

Supplementary Table (Continued).

October					October	110	28	September	150	42
						129	33		160.5	47
						117	47		143	45
						112	28		138	46
						121	26		154	47
						118	25		151	45
								130	45	
								119	44	
								133.5	33	
								119	37	
								142	46	
								152	42	
								159	44	
								141	43	
								138	44	
								153	46	
								156	44	
								128	44	