

Research article

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Active thermoregulation in *Lasius fuliginosus* nests in spring (Hymenoptera: Formicidae)

Stanislav STUKALYUK^{1,*}, Yury RADCHENKO², Vira BALABUKH³

¹Institute for Evolutionary Ecology, NAS of Ukraine, Department of Ecological Monitoring, Lebedeva st., 37, Kyiv, 03143 Ukraine – asmooney@gmail.com;
ORCID: <http://orcid.org/0000-0002-9775-0750>

²Ukrainian State University of Science and Technologies, Department of Ecology, Heat Engineering and Labor Protection, Lazaryana St., 2, Dnipro 49010 Ukraine – ORCID: <http://orcid.org/0000-0002-5055-6707>

³Ukrainian Hydrometeorological Institute, SES of Ukraine, NAS of Ukraine, Department of Applied Meteorology and Climatology, Nauky prosp., 37, Kyiv, 03028, Ukraine – ORCID: <https://orcid.org/0000-0003-3223-7531>

*Corresponding author

Abstract

The aim of the study was to investigate characteristics of temperature conditions in *Lasius fuliginosus* nests in spring to possibly prove the spring warmup hypothesis. In spring (05.03 to 31.05.2024), 3 loggers, allowing measurements of temperature conditions were mounted on the outer walls of 3 *L. fuliginosus* nests in a deciduous forest near Kyiv (Ukraine). The temperature measurements were taken at 15-minute intervals. Simultaneously, the atmospheric air temperature was measured during the same period (at 3-hour intervals). Nests 1 and 2 were typical for this species: both in empty cores of oak trees (1 m diameter), while Nest 3 was auxiliary and located under a 0.05 m layer of oak bark. The physical data (air and nest wall temperatures) were used to construct a mathematical model of the thermal processes occurring in the core of a carton nest. The modelling showed that the anthills' ability to maintain nest temperature in spring depends on their size and location inside the tree trunks exposed to environmental influence. The temperature inside a nest follows the average daily air temperature with a slight delay due to thermal inertia of the tree. The nest in tree #1 proved to be the most stable: even during cold spells as low as -5°C, the temperature in the core remained +25°C thanks to metabolic heat. Nest #2 also maintains the required temperature (+25°C) during temperature falls to +5°C. However, nest #3 does not provide conditions for offspring development during sudden cold snaps: the heat emitted is insufficient to compensate for losses at air temperatures below +20°C. This nest is not designed for active thermoregulation. It has been shown that *L. fuliginosus* are able to actively warm up their nest in spring, and the warmup rates (up to 25–26°C) are similar to the temperature conditions in the red forest ants' anthills (*Formica rufa* group).

Key words: active thermoregulation, *Lasius fuliginosus*, carton nests, mathematical model.

Introduction

Lasius fuliginosus (Latreille, 1798) are the only representatives of the subgenus *Dendrolasius*, genus *Lasius* in Europe (Radchenko 2016). This species has a wide range: from Europe to Western Siberia, including Transcaucasia, the Caucasus, northern Kazakhstan and as far east as Altai. In Ukraine, they live wherever there is woody vegetation, most often in the southern forest zone and in the forest steppe (Radchenko 2016). Less often they can be found in city and forest parks (Stukalyuk et al. 2022a). This ant species is one of those dominant in forests (Dobrzańska 1966; Markó et al. 2013; Ślipinski et al. 2014; Stukalyuk 2017), they prefer shady and humid areas, and is oligothermic in relation to warmth conditions (Seifert 2018). Most often, they are found in floodplain, deciduous and mixed forests;

less often in coniferous (pine) forests (Czechowski et al. 2002; Radchenko 2016). They can form large colonies, from hundreds of thousands to 2.5 million workers (Dobrzańska 1966; Czechowski et al. 2002; Zakharov 2015; Radchenko 2016; Seifert 2018; Stukalyuk et al. 2022). Most colonies are monogynous (Elst & Gadau 2018), although some reports suggest that they may be oligogynous or polygynous (Czechowski et al. 2002). Establishment of a new colony is associated with parasitic lifestyle, with the host species belonging to the subgenus *Chthonolasius* (Czechowski et al. 2002). In some cases, when several queens occur in a colony of the host species, mixed colonies with workers of the two species can exist for some time (3 to 7 years). *L. fuliginosus* is an active trophobiont species (Depa et al. 2022) and aphids can constitute a significant part of the protein diet (Dobrzańska 1966; Zakharov 2015).

Their foraging area is protected from other dominant species; they build permanent trails to foraging trees with aphid colonies (Dobrzańska 1966; Czechowski et al. 2002; Stukalyuk et al. 2022b). Foragers can be mobilised from trails and tunnels to food sources (Dobrzańska 1966; Quinet & Pasteels 1996; Quinet et al. 1997; Bonser et al. 1998), especially protein (Stukalyuk & Akhmedov 2022). In addition to the main nest, there are usually several additional nests (active in summer) containing workers and brood (Dobrzańska 1966; Zakharov 2015). *L. fuliginosus* build nests most often at the base of trees, in cavities inside trunks, less often inside stumps and logs, and can settle inside abandoned beehives or man-made buildings. Cases where their nests are found in the ground or under stones are rare (Seifert 2018). These ants' nests are made of carton, and form galleries and chambers. In general, *L. fuliginosus* carton nest is of sponge-like structure (Khuong et al. 2011). The nest can be partly underground and located in the roots of an inhabited tree, where the ants winter over (Zakharov 2015). Some data suggests that their foraging strategy can explain the characteristics of the nest structure to a greater extent than the evolutionary history of the ant species (O'Fallon et al. 2023). It follows that *L. fuliginosus* colonisation in the butt-log portions may be due to easy access to aphid colonies on the same tree as the nest and on nearby trees.

Nest warmup is necessary to maintain normal physiological and functional state of an ant colony (including *L. fuliginosus*). Normally, nest warmup (which determines the rate of brood development, especially in spring) is passive in most ant species, but a number of ant species can settle under stones, the warmup thereof accelerates brood development (Stukalyuk & Radchenko 2022). Ants with large colonies (including *L. fuliginosus*) living in temperate climates usually possess the active thermoregulation ability (Kravchenko 1973; Brandt 1980; Bachem & Lamprecht 1983; Frouz 2000; Stukalyuk et al. 2020) This enables earlier start of brood development, even when the ambient temperature is too low. In red wood ants (*Formica rufa* species group), the nest can warm up by 12–17°C in 12 hours (Dlussky 1975, 1980). This data was later confirmed by other researchers (Gorny et al. 2015; Stukalyuk et al. 2020). For *L. fuliginosus*, such data was presented in a single paper (Kravchenko 1973). It is worth noting that this paper is not available to a wide range of Western scientists, as it is in Russian. In this paper, temperature measurements were carried out in summer (June and July) and measurement frequency was limited (once every 1 or 2 hours). Besides, the study used material from only one nest. Lack of information on possible spring warmup of *L. fuliginosus* nests and limited available information on the temperature conditions in this ant species' nests (Kravchenko 1973) determined relevance of this research. Our paper presents, for the first time, analysis of data from 3 months of continuous monitoring of temperature conditions in three nests of *L. fuliginosus* during spring.

The aim of this research was to investigate characteristics of temperature conditions in *L. fuliginosus* nests in spring. Objectives of this research included: 1) analyse air temperatures in spring 2024; 2) analyse data from loggers mounted on the walls of the studied nests; 3) construct a mathematical model simulating thermal processes in nests located inside trees; 4) make comparative analysis of differences in temperature conditions in the nests depending on their location inside the trunk and proximity to the trunk surface. The hypothesis of this research is that *L. fuliginosus* are capable of active thermoregulation in spring. This enables this ant species to develop brood (the first generation, winged females and males) more quickly. Scientific questions of this search are:

- I. Does temperature conditions inside nests differ between locations?
- II. How long does it take ants to warm up the nest to the optimal temperature of 25–26°C?
- III. How quickly do the nests cool down depending on location and how often do the ants have to warm them up within one month?
- IV. Do *L. fuliginosus* have active thermoregulation in spring?

Materials and Methods

Nest characteristics

The research was conducted in spring 2024, from 3 March to 31 May. Three *Lasius fuliginosus* nests were selected, located at a distance of 30–50 m from each other in the deciduous forest of Feofaniya (Kyiv, Ukraine, coordinates 50.336722127183066, 30.492077003083903). The forest is located on the south-western outskirts of Kyiv and has an area of more than 100 hectares. The dominant tree species are oak (*Quercus robur* L.), maple (*Acer platanoides* L.) and hornbeam (*Carpinus betulus* L.). Oak forms the main layer, with hornbeam and maple underneath. This habitat is typical of *L. fuliginosus* and was the reason for its selection.

Below are the characteristics of the nests studied.

Nest 1. Oak tree, 1.0 m in diameter. The exit is at ground level, in the depth of a hole of 0.05 m diameter. The nest is in the core of a trunk up to the height of 0.4 m; approximate volume of the nest is about 10 l. The sensor is installed in the wall of the lower part of the nest, through the entrance at the base of the oak trunk (Fig. 1A). The height of the nest is 0.4 m, its diameter is ca. 0.5 m (occupies the pith). The nest appears to be almost cylindrical in shape.

Nest 2. Oak tree, 0.7 m in diameter. There is a notch in the lower part of the trunk, 0.5 m high and 0.1 m wide at the bottom and 0.05 m at the top. The nest is in the wood layer and the trunk pith, at the height between 0.3 m (the exit is directly into the notch) and nearly 1 m (Fig. 1B).



Fig. 1 – Photos of the three *Lasius fuliginosus* nests, March 2024. A, Nest 1, B, Nest 2, C, Nest 3. The arrows indicate points of the mounted sensors.

The sensor is in the wood layer (nest material) at the height of 0.3 m, 0.2 m deep into the nest. The nest is cylindrical, 0.7 m high. The cylinder is 0.5 m in diameter (from the depth of 0.1 m to the trunk core).

Nest 3. Oak tree, 1.2 m in diameter. There is a depression in the lower part (no bark layer), 0.4 m high, 0.6 m wide and 0.8 m deep. The nest is under the bark, the bark is 0.05 m thick, located from the height of 0.4 m to the height of 1.5 m, approximate radius of the nest is 0.6 m (Fig. 1C). There are carton passages under the bark, but they do not go deep into the trunk. There are no exits from above, only into the depression (its upper part). The sensor is in the passages under the bark at the height of 0.5 m. The nest is in the shape of a thin layer along the trunk, half its circumference. The nest is 0.9 m high (from 0.4 m to 1.5 m).

Thus, three models can be considered based on the obtained nest characteristics. Model 1 (Nest 1) is a classic nest, in the trunk core, resting on a layer of soil. Model 2 (Nest 2) is also a classic nest, in the trunk core, but raised above ground. Model 3 (Nest 3) is a nest above the ground, but under a 5 cm layer of bark, in the shape of a flat layer. All nests have only one exit.

Also, to have an understanding of the structure of oak layers, we examined a nearby oak stump. Its diameter is 1.0 m. The ring layer of wood is 0.15-0.4 m thick. There is a notch in the middle, 0.6 m high including the stump, 0.6 m wide and 0.85 m long. There is no bark layer, but this is within 0.05 m. It should also be taken into account that about a third of the trunk core volume is not occupied by wood but by softer pith, where voids develop primarily and ants settle often. In wood, they usually occupy passages made by wood engravers.

Research methods

Measurements of nests and temperature conditions in their walls

To measure the air temperature inside the nests, we used the TZ-TempU02 logger, firmware version 5.12. (TZone, Taiwan). This sensor can continuously measure air temperature every 15 minutes for 3 months, with an error of 0.1 C. A total of 8369 measurements were taken for each of the three nests. Measurements were taken during 87 days and 4 hours. Measurements were taken from 5 March to 31 May 2024. Each of the sensors was inserted as deeply as possible into the nest. However, for each of the nests, the sensor was immersed in the wall of the nest itself, rather than in the centre of the nest. This was necessary to avoid causing irreparable damage to the anthill in early spring, when night frosts can kill it completely. The data from the loggers therefore reflects the temperature conditions at the surface of the carton nest in the hollow of the tree trunk (oak). All nests were active on 5 March 2024, as the weather was warm and sunny and the ants were gathering at the entrance of the nests, i.e. hibernation was over. The nest parameters (location in the trunk) were determined using a thin steel wire (probe). We measured external parameters: the width of the notch in the trunk, the entrance to the nest. The wire was then carefully inserted into the nest entrance to determine how far it went into the trunk. Where it was possible, presence of cavities in the trunk could be determined by tapping. The flexible steel wire easily passed through the carton structures created by the ants, but did not cause significant damage to the nest due to its small diameter.

On 31 May 2024, all the sensors were removed from their nests and brought to laboratory conditions where, after being connected to a PC, PDF files with their data were

generated. The data was then converted into the Microsoft Excel format required for further statistical calculations. In addition to calculating average monthly temperatures, the average air temperature in the nests during the day and at night was calculated separately for each month. Day was defined as the time when the sun was above the horizon, and night as the time after sunset and before sunrise. For accurate data on sunrise and sunset at the Kyiv latitude, data was taken from <https://ru.365.wiki/world/ukraine/kyiv/sun/calendar/may/>. In parallel, air temperature data was obtained from the Kyiv meteorological station, the Boris Sreznevsky Central Geophysical Observatory of the State Emergency Service of Ukraine, in the Demiyivska metro station area (Kyiv, Ukraine). Here, data was measured at 3-hour intervals. This data was needed for comparison with the air temperature data obtained in the nests.

Mathematical modelling

As it is impossible to measure the temperature distribution in the central part of *Lasius fuliginosus* nests, mathematical modelling of heat exchange in the tree-environment system was carried out.

The part of the trunk with the nest in it was approximated by a multilayer cylinder with a radius corresponding to dimensions of the carton nest, the wood layer and the bark layer. Daily ambient temperatures were obtained from the local weather station. The temperature field was determined by sequential calculations from the initial state with a uniform temperature distribution along the radius.

Radiative-convective heat exchange with the environment was assumed to occur at the tree surface with a total heat transfer coefficient $\alpha_{\text{total}} = 20 \text{ W}/(\text{m}^2 \cdot \text{K})$ (Rumyantsev 2006). The thermophysical properties were taken from the papers (Gorny et al. 2015; Kazantsev 1975; Tsyvin 1973): thermal conductivity of the nest $\lambda_{\text{gn}} = 0.42 \text{ W}/(\text{m} \cdot \text{K})$, wood $\lambda_{\text{wood}} = 0.2 \text{ W}/(\text{m} \cdot \text{K})$, bark $\lambda_{\text{bark}} = 0.087 \text{ W}/(\text{m} \cdot \text{K})$; heat capacity $C_{\text{nest}} = 2763 \text{ J}/(\text{kg} \cdot \text{K})$, $C_{\text{wood}} = 2390 \text{ J}/(\text{kg} \cdot \text{K})$, $C_{\text{bark}} = 2728 \text{ J}/(\text{kg} \cdot \text{K})$; density $\rho_{\text{nest}} = 200 \text{ kg}/\text{m}^3$, $\rho_{\text{wood}} = 819 \text{ kg}/\text{m}^3$, $\rho_{\text{bark}} = 478 \text{ kg}/\text{m}^3$.

At a certain point in time, corresponding to the beginning of the spring warmup, an internal heat source inside the carton nest came into play.

In Gorny et al. (2015), its power is assumed to be 100 W, without specifying any particular value needed for substitution into the heat conductivity equation in our mathematical model. Indirect calculations allowed us to determine that in Gorny et al. (2015) it goes off a source with a power of ca. $P = 190 \text{ W}/\text{m}^3$. At the same time, in Stukalyuk et al. (2020), the source power is reported to be 1.25 W/kg, which gives a value of 250 W/m³ for a nest density of 200 kg/m³. Finally, for our case of carton nests, we assumed $P = 190 \text{ W}/\text{m}^3$.

An explicit finite difference approximation scheme for the heat conductivity differential equation was used to solve the problem. The system of equations was written using the analysis node heat balance method (Brovkin 2014).

Statistical analysis

The obtained data massive was analysed using Past Software Statistics (version 4.17). For air temperature parameters, the mean (for month, and time of day: day and night), error of the mean, standard deviation and median, minimum and maximum values were computed. Reliability of the differences in temperature values between months and between day and night was verified using the Chi-square criterion, indicating the p-values. Paired comparisons of parameters between nests were made using the Dunn post-hoc test (p-values with Bonferroni correction and z-values).

Results

Comparison of average monthly nest temperatures and ambient air temperatures

A comparison of the temperatures measured in *Lasius fuliginosus* nests with the average air temperature data from the weather station revealed the following trends:

The average air temperature in March was 4.9°C, which is close to the average temperature in Nest 1 (4.2°C) and Nest 2 (4.0°C), but significantly lower than the average temperature in Nest 3 (5.7°C). The difference between the temperature in Nest 3 and the air temperature was 0.8°C.

The mean air temperature in April was 12.62°C. The temperature in Nest 1 (11.8°C) and Nest 2 (12.2°C) was slightly below this value, while the temperature in Nest 3 (12.5°C) was close to the average air temperature.

The mean air temperature in May was 16.21°C. In Nest 1 the temperature was significantly lower than this value (11.8°C), in Nest 2 it was close to the average air temperature (14.8°C), in Nest 3 the temperature was slightly lower than the average air temperature (14.6°C), but still higher than in Nest 1. The results obtained cannot be explained only by the influence of the ants' vital processes on the temperature in the nests. It is possible that these differences are also related to the fact that the sensors interacted differently with the nests and the air, despite being in approximately the same conditions.

Analysis of temperature logger data for the three *Lasius fuliginosus* nests in spring 2024

The average temperature in Nest 3 in March exceeded the temperature in Nest 1 by 1.5°C and in Nest 2 by 1.7°C (Table 1, Figs 2A, B). These differences were confirmed by statistical analysis, where the difference between Nest 3 and the others was the most pronounced (Table 2). This is probably due to the fact that this nest was exposed to sunlight for longer than the others. The lower autonomy in temperature conditions of this nest was subsequently confirmed by our calculations.

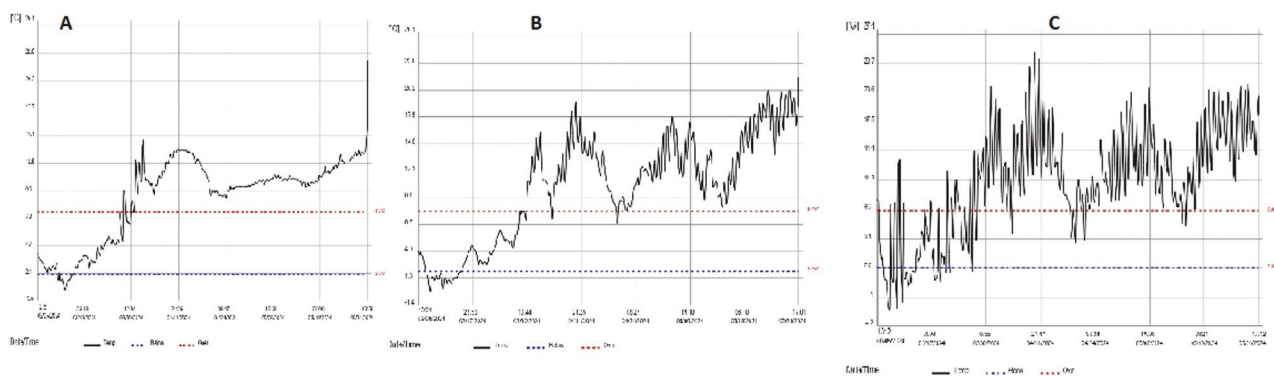


Fig. 2 – Temperature change in the three *Lasius fuliginosus* nests from March to May 2024. A, Nest 1, B, Nest 2, C, Nest 3.

In April, Nest 3 also had the highest temperatures, but the difference from the other nests was less pronounced compared with March (Fig. 2C). The average temperature in Nest 3 was 1.1°C higher than in Nest 1 and 0.3°C higher than in Nest 2 (Table 1). Statistical analysis showed significant differences, especially between Nest 3 and Nest 1 (Table 2).

In May, the temperature in Nest 2 was higher than in the other nests. The difference between Nest 2 and Nest 1 was 3.1°C and 0.2°C with Nest 3 (Table 1). These differences were particularly pronounced, as confirmed by the high *z*-statistic values for Nest 2 compared with the others (Table 2).

When looking at **day and night temperatures**, the differences were also significant. In March, the daytime temperature in Nest 1 was 0.4°C higher than the nighttime temperature, while in Nest 3 the difference reached

3.6°C (Table 3). In April and May, the differences between day and night temperatures persisted, especially in Nest 3, where the day temperature was 3.9°C higher than the night temperature in April and 3.8°C higher in May. The largest differences were observed in May in Nest 2, where the day temperature was 12.6°C higher than the night temperature. These differences were significant (Table 4). Thus, the data shows that during the spring the temperature in the nests varied according to the time of day (higher during the day) and month (highest in May), with the greatest variation in day and night temperatures in Nest 3 (because it was measured directly under the bark and not in the trunk core as in the other two nests). The day and night temperature data also confirms the fact that the trees were exposed to sun during the day and that the temperature was naturally higher in the areas where the loggers were placed.

Table 1 – Average monthly temperatures from sensors in three *Lasius fuliginosus* nests in spring 2024.

Nest number and month	N	Min	Max	Mean	Std. error	Stand. Dev	Median
Nest 1 March	2541	0.5	13.9	4.196	0.045	2.286	3.6
Nest 2 March	2540	-0.4	14.1	3.989	0.056	2.829	3.6
Nest 3 March	2540	-3.2	22.3	5.672	0.095	4.823	4.6
Nest 1 April	2880	9.2	16.4	11.541	0.028	1.536	11.1
Nest 2 April	2880	6.5	19.9	12.242	0.048	2.578	12.1
Nest 3 April	1920	4.2	26.4	12.534	0.100	4.404	11.7
Nest 1 May	2948	10.2	25.1	11.751	0.022	1.216	11.3
Nest 2 May	2949	8.1	25.1	14.800	0.058	3.190	15
Nest 3 May	2181	5.7	26.1	14.605	0.085	3.971	14.5
H (chi2) March	114.1						
P	1.64E-25						
H (chi2) April	112.4						
P	3.81E-25						
H (chi2) May	1517						
P	0						

Table 2 – Results of statistical analysis (z-statistic) for differences in mean temperature in the three studied *Lasius fuliginosus* nests in spring 2024.

Nest number and month	Nest 1 March	Nest 2 March	Nest 3 March
Nest 1 March		4.638	6.017
Nest 2 March	4.638		10.65
Nest 3 March	6.017	10.65	
	Nest 1 April	Nest 2 April	Nest 3 April
Nest 1 April		10.21	7.122
Nest 2 April	10.21		2.012
Nest 3 April	7.122	2.012	
	Nest 1 May	Nest 2 May	Nest 3 May
Nest 1 May		36.19	29.46
Nest 2 May	36.19		3.92
Nest 3 May	29.46	3.92	

Mathematical model results

Using the developed mathematical model of heat exchange and taking into account the experimental data obtained from loggers mounted in the three nests, a study of the thermal state of the nests during the spring warmup period was carried out.

Firstly, in order to assess physical accuracy of the results obtained using the model, computations were carried out for the case where the nest is abandoned by the ants. It was found that the temperature in the centre and on the surface of the nest changes similarly to the change in ambient temperature, with a slight time lag due to the thermal inertia of the materials. The temperature on the outer surface of the bark is either slightly higher or slightly lower than the air temperature, due to the warmup of the tree during the day and the cooling at night. This fact does not contradict the nature of the heat exchange processes in the tree-environment system.

The results of modelling the daily temperature variations in oak nest No. 2 from 2 to 22 April are shown in Fig. 3.

In Gorny et al. (2015), red wood ants' nests covered with an outer dome of small twigs, leaf petioles and similar materials were studied. Warmup rates of 0.75 to 1.7°C/hour were recorded. In our case, the rate of temperature rise for nests in tree trunks is different from that for nests on the ground. This is mainly due to the thermophysical properties of the materials, conditions of heat exchange with the environment, and location and geometric shape of the nest.

In order to determine **ant colonies' active thermoregulation ability**, temperature distribution along the radius of the trunk containing the nest was determined during the warmup process from the initial state at a constant average daily air temperature of +10°C, which is typical of early spring weather conditions.

For tree #1 it was found that the warmup rate of the nest centre gradually decreases and is: 0.79°C/hour in the first 12 hours, 0.33°C/hour in the next 12 hours and 0.22°C/hour in the last 12 hours before the transition to the warmed state. The temperature distribution over the cross section of tree #1 at individual times is shown in Fig. 4A.

We then modelled **cooling of this warmed nest** in the environment at an air temperature of +20 °C, assuming that in this case the family stops actively emitting heat. The nest cooled down, but more slowly than it had warmed up. The cooling rate was: 0.62 °C/hour in the first 12 hours, 0.17 °C/hour in the next 12 hours and 0.04 °C/hour before the temperature started to rise due to heat influx from the environment. How the temperature was changing in the cross section of tree #1 in the absence of heat emission inside the nest is shown in Fig. 4B.

When modelling the nest in tree #2, the same air temperature was set (+10 °C). According to the modelling results for nest #2, the warmup rate of the nest centre was: 0.80 °C/hour in the first 12 hours, 0.34 °C/hour in the next 12 hours and 0.22 °C/hour in the last 12 hours before the transition to the warmed state. The temperature distribution over the cross section of tree #2 at individual times is shown in Fig. 5A.

Next, similar to the modelling of thermal processes in tree #1, we considered the cooling of the warmed nest at an average daily air temperature of +20 °C. The cooling rate was: 0.55°C/hour for the first 12 hours; 0.02°C/hour for the next 12 hours. Thereafter, as in the first case, the temperature began to rise at a rate of 0.02°C/hour due to heat input from the environment. The change in temperature across the cross section of tree #2 in the absence of heat emission is shown in Figure 5B.

The nest in tree #3 is fundamentally different in structure from the first two: it is located directly under the bark layer and is therefore more susceptible to the influence of the external environment. The radial thickness of the nest is only 50 mm, so the metabolic heat released in such a

volume is insufficient for intensive warmup and compensation of heat loss to the environment.

Taking this into account, an average daily air temperature of $+20^{\circ}\text{C}$ was set when modelling the nest in tree #3.

Even with such favourable conditions, the rate of warmup of the nest in tree #3 was extremely low. According to the simulation results it was: $0.18^{\circ}\text{C}/\text{hour}$ in the first 12 hours and $0.06^{\circ}\text{C}/\text{hour}$ in the next 12 hours. Later it decreased more and more and at the end of 3 days it was negligible $0.02^{\circ}\text{C}/\text{hour}$. At the same time, the maximum temperature in the nest was below the required $+25^{\circ}\text{C}$. The temperature distribution over the cross section of tree #3 at certain times is shown in Fig. 6A.

It is worth noting that in this case not all of the released heat goes to the environment. Some of the heat is directed towards the centre of the trunk where the temperature is lower.

As a result, this heat accumulates in the central part of the trunk and stabilises the nest temperature in the future.

When the ants stop releasing metabolic heat, the temperature in the volume of the tree equalises. The cooling rate of the nest was: $0.17^{\circ}\text{C}/\text{hour}$ for the first 12 hours, $0.05^{\circ}\text{C}/\text{hour}$ for the next 12 hours, and then $0.03^{\circ}\text{C}/\text{hour}$ and less. The change in temperature across the cross section of tree #3 in the absence of heat emission inside the nest is shown in Fig. 6B.

In conclusion, we can see that in the nest of oak #1, located in the trunk core, the temperature can exceed the air temperature by 30°C . This means that even with an air temperature of -5°C , the temperature of $+25^{\circ}\text{C}$ can be maintained in the nest for some time!

For the nest in oak #2, which is also located in the trunk core, but in a tree with a smaller diameter, the temperature in the centre of the nest cannot exceed the air temperature by more than 20°C (see Figs 5A, B).

The nest in oak #3, which is a thin layer under the bark, is the least prone to active thermoregulation. The temperature in the nest space cannot exceed the air temperature by more than 4°C (Fig. 6B).

The modelling also showed that the frequency of commencement of the metabolic heat release process to maintain the required temperature in the nest depends on the nest location in the tree and is determined by the value of daily variation in air temperature. It was found that for the nest in tree #1, the temperature in the nest falls from 26°C to 18°C within just one day if the release of metabolic heat ceases due to rise of the air temperature to 20°C . This is due to the fact that the average daily air temperature up to that point was $+10^{\circ}\text{C}$ and the tree massif was not sufficiently warmed across its thickness. As a result, the temperature in the nest drops rapidly as it is compensated for by the volume of the tree trunk. This forces the family to restart the warmup mechanism.

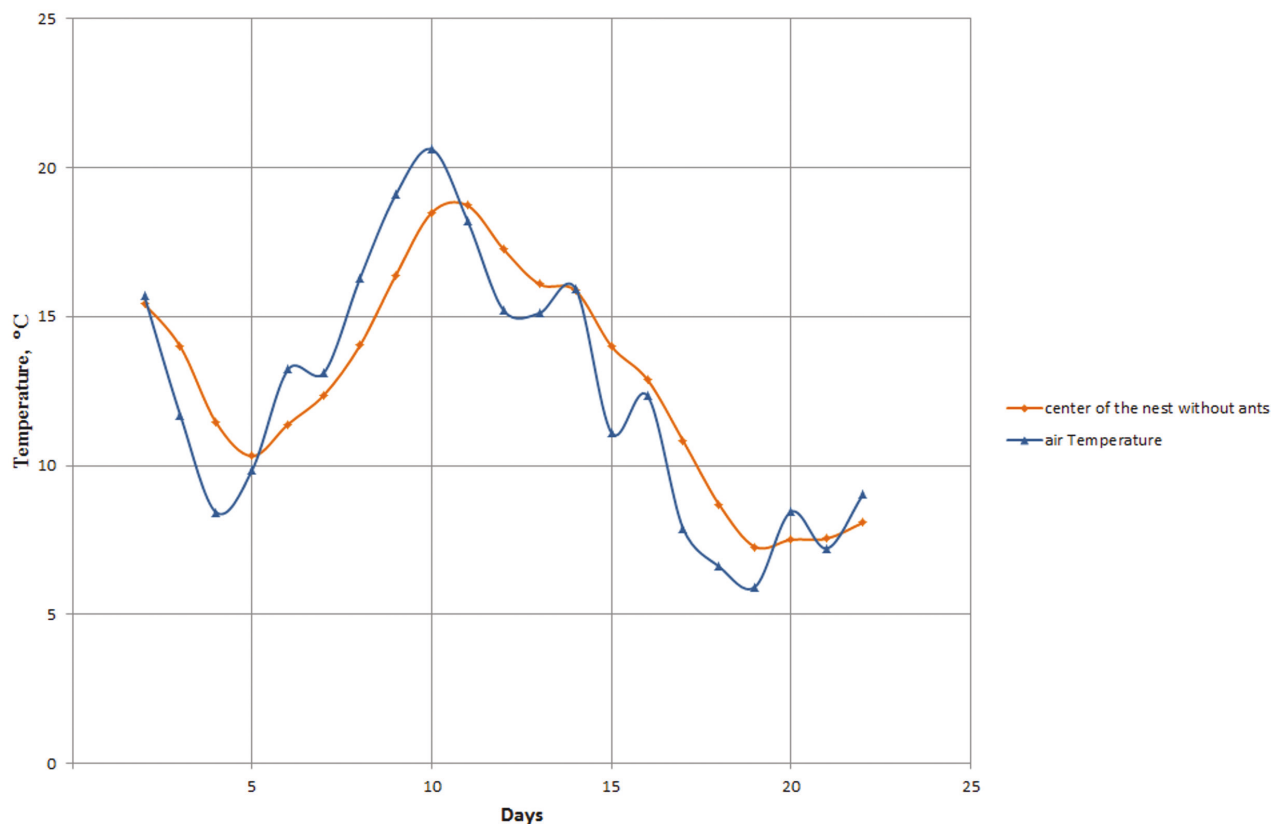


Fig. 3 – Temperature change for tree #2 (April 2024).

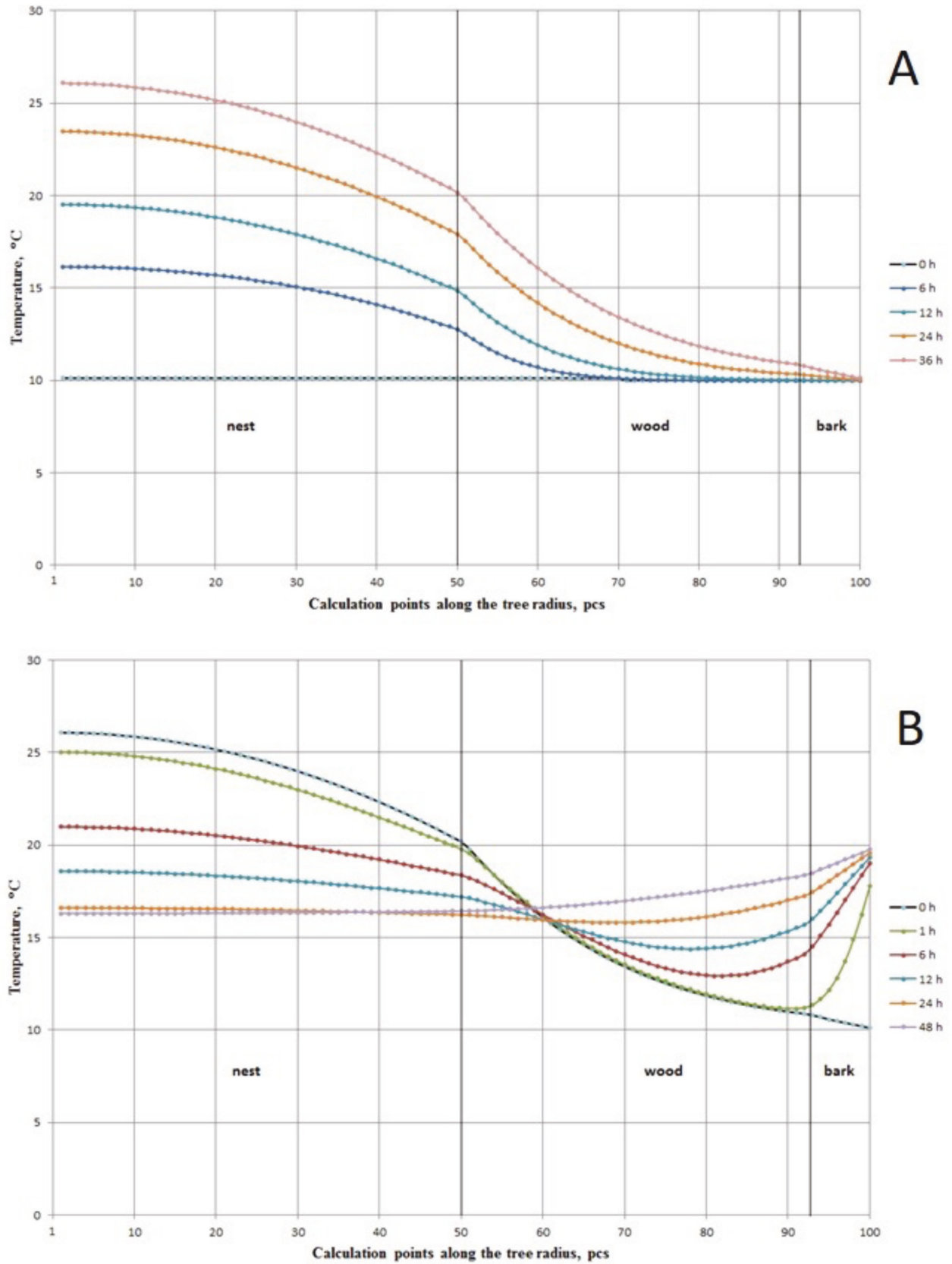


Fig. 4 – Temperature diagrams for the nest in Tree 1. A, warmup, B, cooling.

If the warmup mechanism is not triggered (the family is no longer able to emit heat), the egg-laying process will not start and the colony will die or start developing later (see Discussion).

Unlike the nest in tree #1, the nest in tree #2 is quite stable under similar conditions because the smaller size of the trunk means that it is heated more evenly across its thickness. As a result, after cooling down to 19°C by the end of the first day, it will be practically in thermal equilibrium with the environment. In this case, it may no longer be necessary to activate the warmup mechanism.

As the modelling shows, the temperature of the nest in tree #3 is mainly influenced by the ambient temperature and not by the release of metabolic heat. This heat is not sufficient to compensate for heat loss when the average daily air temperature exceeds the limits required for egg-laying. In this respect, the family is almost entirely dependent on, and unable to withstand, sudden changes in the ambient temperature regime.

Discussion

Differences in air, wall and centre of nest temperature

To estimate the temperature differences for the central parts of each nest in March, April and May, taking into account the need to warm up to 25–26°C, it is necessary to consider both the air temperature and the conditions for thermoregulation within the nest. It is important to note that ants are likely to activate warming-up only when the temperature inside the nest falls below the desired level and the nest requires additional thermal metabolic energy.

In all three *Lasius fuliginosus* nests in March, the temperature in the centre is significantly lower than the target level (25–26°C, i.e. the optimal temperature for brood development (Zakharov 2015)). This means that in order to maintain the desired temperature (around 25–26°C), ants must actively release metabolic heat to compensate for the significant cooling. In particular, nests 1 and 2, with a tem-

Table 3 – Average day and night temperatures in three *Lasius fuliginosus* nests in spring 2024.

Nest number and month	N	Min	Max	Mean	Std. Error	Stand. Dev	Median
Nest 1 March day	1296	0.6	13.9	4.411	0.070	2.525	3.6
Nest 1 March night	1245	0.5	11.9	3.971	0.056	1.985	3.5
Nest 1 April day	1680	9.2	16.4	11.61	0.038	1.585	11.1
Nest 1 April night	1200	9.2	14	11.446	0.042	1.460	10.9
Nest 1 May day	1912	10.2	25.1	11.751	0.030	1.350	11.2
Nest 1 May night	1036	10.6	13.8	11.751	0.028	0.920	11.4
Nest 2 March day	1293	-0.2	14.1	4.080	0.080	2.891	3.6
Nest 2 March night	1247	-0.4	13.5	3.894	0.078	2.761	3.7
Nest 2 April day	1680	6.6	19.9	12.566	0.066	2.740	12.5
Nest 2 April night	1200	6.5	17.6	11.788	0.065	2.256	11.7
Nest 2 May day	1912	8.2	25.1	15.306	0.073	3.206	15.7
Nest 2 May night	1037	8.1	19.8	13.866	0.091	2.941	13.8
Nest 3 March day	1295	-3.1	22.3	7.457	0.136	4.895	6.7
Nest 3 March night	1245	-3.2	16.8	3.815	0.112	3.972	3
Nest 3 April day	1100	5.2	26.4	14.204	0.140	4.660	13.7
Nest 3 April night	820	4.2	16.9	10.294	0.095	2.745	10.6
Nest 3 May day	1439	6.8	26.1	15.885	0.102	3.873	16.4
Nest 3 May night	742	5.7	17.8	12.123	0.103	2.817	12.5
H (chi2) March	5080						
P	0						
H (chi2) April	5379						
P	0						
H (chi2) May	3502						
P	0						

Table 4 – Results of statistical analysis (z-statistic) for differences in mean day and night temperatures in three studied *Lasius fuliginosus* nests in spring 2024.

Nest number and month	Nest 1 March day	Nest 1 March night	Nest 1 April day	Nest 1 April night	Nest 1 May day	Nest 1 May night
Nest 1 March day		2.139	42.46	37.3	47.58	43.08
Nest 1 March night	2.139		44.25	39.03	49.34	44.71
Nest 1 April day	42.46	44.25		2.001	4.256	5.711
Nest 1 April night	37.3	39.03	2.001		5.918	7.103
Nest 1 May day	47.58	49.34	4.256	5.918		2.159
Nest 1 May night	43.08	44.71	5.711	7.103	2.159	
	Nest 2 March day	Nest 2 March night	Nest 2 April day	Nest 2 April night	Nest 2 May day	Nest 2 May night
Nest 2 March day		0.9503	38.6	31.24	55.96	41.33
Nest 2 March night	0.9503		39.21	31.9	56.39	41.9
Nest 2 April day	38.6	39.21		4.648	17.55	7.476
Nest 2 April night	31.24	31.9	4.648		20.71	11.11
Nest 2 May day	55.96	56.39	17.55	20.71		7.563
Nest 2 May night	41.33	41.9	7.476	11.11	7.563	
	Nest 3 March day	Nest 3 March night	Nest 3 April day	Nest 3 April night	Nest 3 May day	Nest 3 May night
Nest 3 March day		13.96	27.66	10.25	37.74	17.93
Nest 3 March night	13.96		40.79	22.49	51.66	29.75
Nest 3 April day	27.66	40.79		14.67	7.779	6.495
Nest 3 April night	10.25	22.49	14.67		22.59	7.265
Nest 3 May day	37.74	51.66	7.779	22.59		13.72
Nest 3 May night	17.93	29.75	6.495	7.265	13.72	

perature of 4°C, require significant warming-up to reach 25–26°C.

In April the air temperature increases significantly, but for all nests the temperature in the centre is still below the target. In nests 1 and 2, warmup is required to reach the necessary temperature (a difference of 13–14°C). In Nest 3, ants can raise the temperature by no more than 4°C, according to our calculations, and it will depend more on the environmental conditions.

In May the air temperature is much higher, and in nests 2 and 3 the temperature in the centre of the nest (14.8°C and 14.6°C respectively) is still below the target of 25–26°C, which requires warming-up by 10–11°C. Nest 1 with a temperature of 11.8°C needs warming-up by 14–15°C to reach the desired temperature.

Nest centre temperature difference with warming-up

In March, the difference between the nest centre temperature and the target temperature will be greatest for all three nests, especially for nests 1 and 2 (up to 22°C difference), requiring intensive warming.

In April the difference is smaller, but still around 13–14°C for nests 1 and 2, indicating the need for significant warmup.

In May, the difference remains for all nests (again, Nest 3 is most dependent on environmental conditions, especially air temperature), Nest 1 needs to be warmed up by 14–15°C and Nest 2 by 10–11°C.

Nests 1 and 2 will need to be warmed up almost throughout the period, with the greatest difference in March and April, when warmup is most intense. Nest 3, which is closer to the outer layer of the tree, will require the most warmup and will not be active in terms of heat production by the ants until the average daily temperature is around +20°C. This is necessary to maintain an effective temperature of 25–26°C in this nest.

*Features of active thermoregulation in *Lasius fuliginosus* nests in spring*

Zakharov (2015) points out that red wood ants can maintain the temperature necessary for brood development (up to 28°C) in any part of the nest dome where it is possible

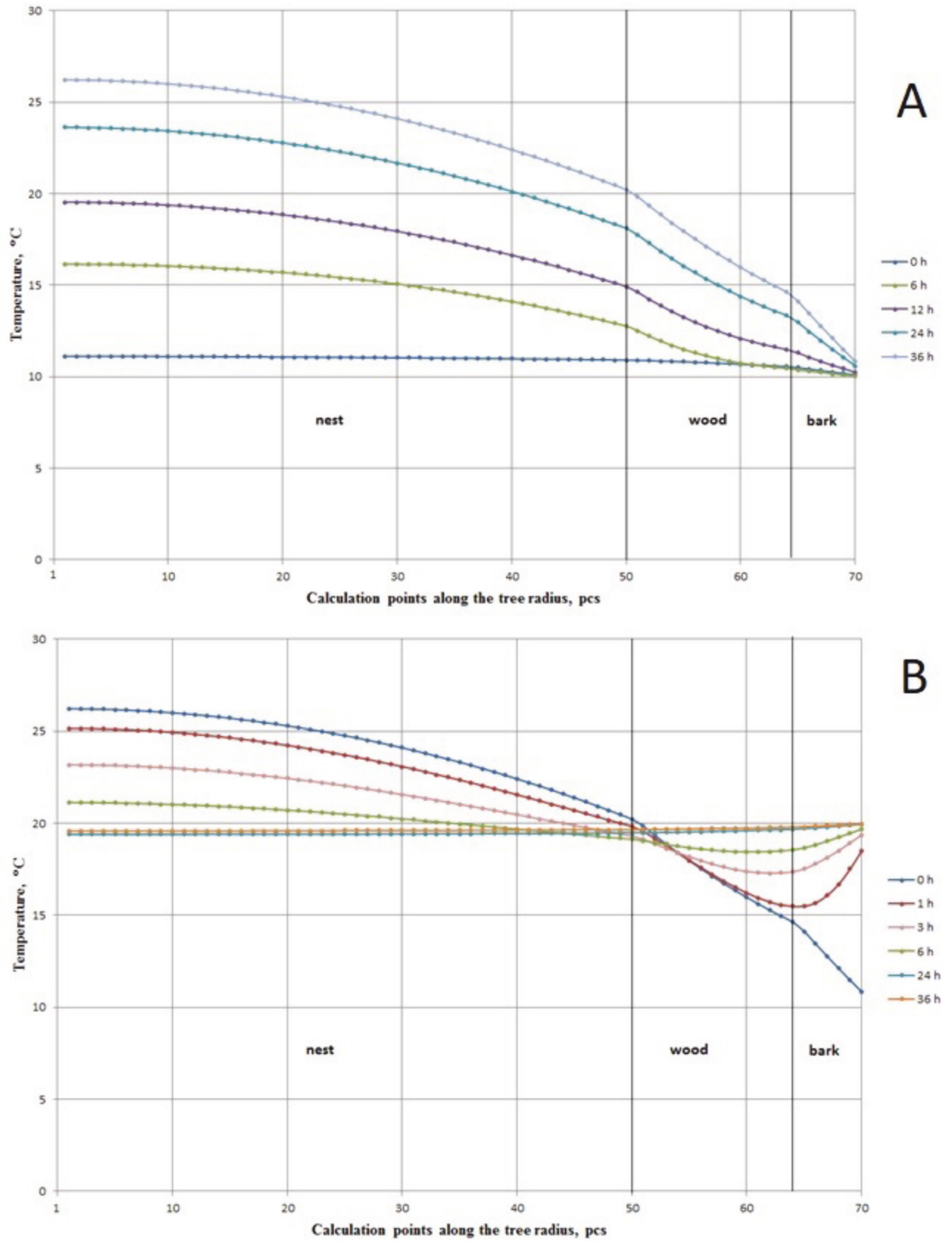


Fig. 5 – Temperature diagrams for the nest in tree #2. A, warmup, B, cooling.

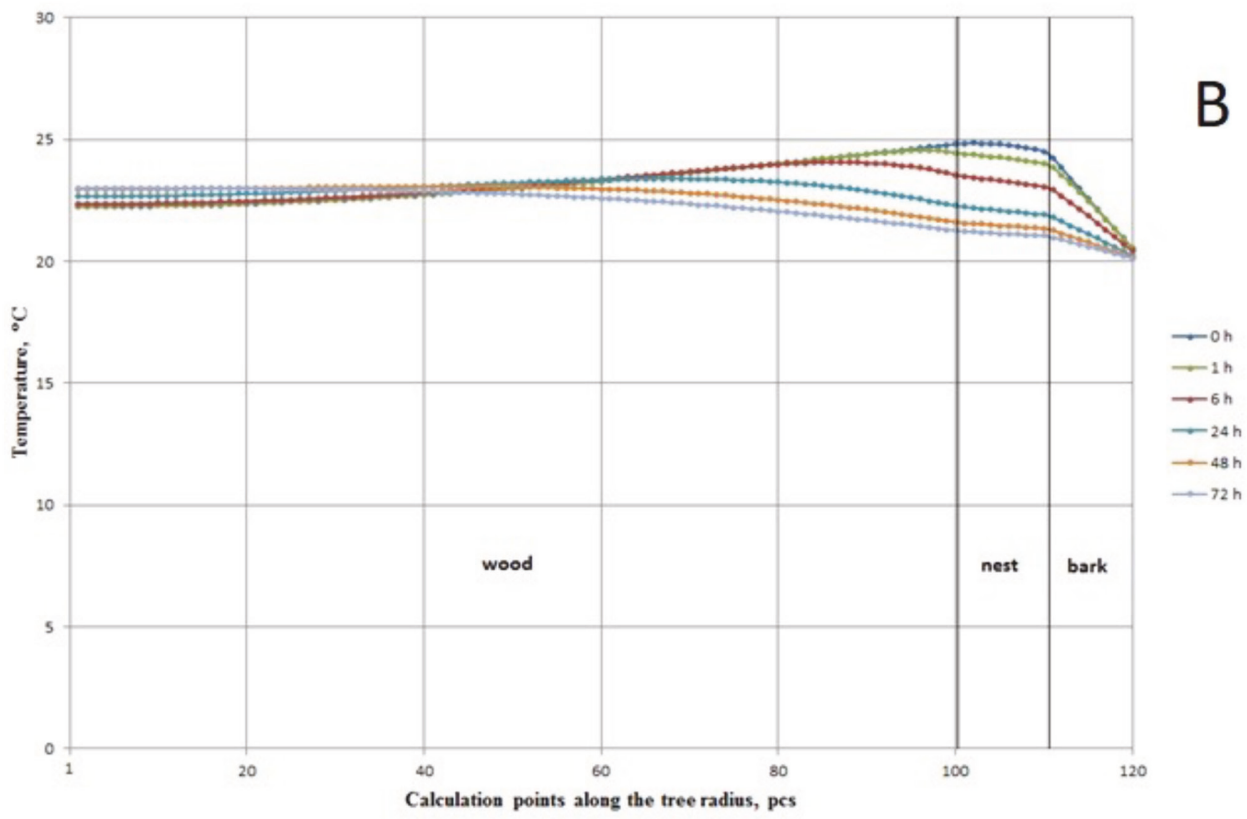
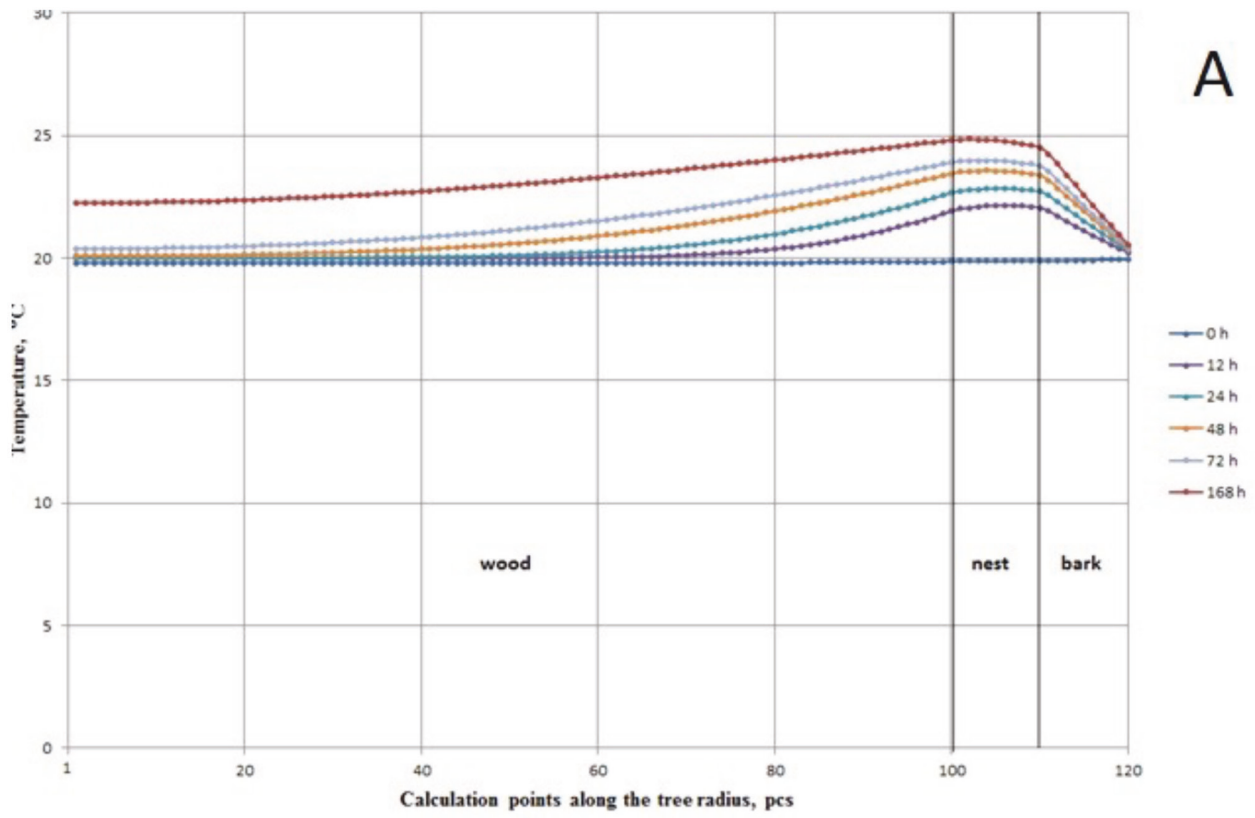


Fig. 6 – Temperature diagrams for the nest in tree #3. A, warmup, B, cooling.

or easier to do so. This is usually the central zone of the anthill (nest cone). In case of over-warmup, this zone may move to the underground part of the nest or to the northern part of the dome (Zakharov & Zakharov 2014). The authors of that research point out that installing a logger at one point in the nest may give incorrect results. We accept this comment and note it as one of the limitations of our research. At the same time, unlike red wood ant anthills, *L. fuliginosus* nests are located in a closed space inside a tree trunk, and temperature conditions is more stable here. Therefore, logger measurements, enhanced by a mathematical model, can provide data close to reality (for the central part of the nest).

Based on the experimental and modelled data, it can be concluded that *L. fuliginosus* colonies exhibit the spring warmup. Otherwise, it is impossible to explain the accelerated development of the brood in this ant species, when winged females and males appear at the beginning of summer and participate in the nuptial flight throughout the summer until the beginning of September (Stukalyuk et al. 2022c). In addition, at least 3 generations of workers can develop during the summer, and in red wood ants, according to some data, at least 4 generations during the same season (Zakharov 2015).

According to literature, *L. fuliginosus* begins its activity in April in more northern regions (Russia Midlands: Zakharov 2015) in relation to Ukraine. Oviposition, according to this author, lasts April into July, hibernation takes place with larvae of 2–3 instars, worker imagoes appear May into August. Consequently, the spring period is key for *L. fuliginosus* in terms of rearing brood of all castes (females, males, workers) and the presence of spring warmup already from March is a mandatory condition. We explain the earlier emergence of *L. fuliginosus* in the climatic conditions of Ukraine compared with the Midlands by the observed emergence dates of this species (5 March). As a consequence, the warmup should start in March and not in April. Warmup support is only needed during low ambient temperatures and during brood development, and ants stop warming-up when one of these conditions changes. This has been observed for red wood ants in autumn (Kadochova & Frouz 2014), although the only paper on *L. fuliginosus* found higher temperatures inside the nest compared with the air temperature in summer (by 0.5–5.0°C, according to (Kravchenko 1973)).

During hibernation in the underground part of the nest, *L. fuliginosus* still has a temperature sufficient for survival (-1.5°C at a depth of 0.5–0.6 m, with a snow depth of 0.5 m in the vicinity of Novosibirsk, Russia), while the lower lethal temperature for workers is within -12°C (Zhigul'skaya & Chesnokova 2020). This data may suggest how Nest 3 in our research could have survived the winter period as well as early spring (March).

Carton glued with aphid honeydew (Maschwitz & Holdobler 1970; Czechowski et al. 2002) warms up quickly

in the confined space of the trunk. In addition to ants, fungi living in this substrate may also contribute to the nest warmup (Elliott 1914). The species composition of fungi in the carton material is constant and can be maintained by ants for at least several years (Brinker et al. 2019). As for the bacterial communities, in carton nests they are mostly represented by genera common to soil and dead wood (Kaczmarczyk-Ziemia et al. 2020).

A number of authors note the active role of the so-called heat carriers in red wood ants in warming the nest (Zahn 1958; Heimann 1963), although this is impossible for *L. fuliginosus*, as workers of this species do not come to the surface *en masse* to warm up, according to our observations. Dimensions of the carton nest of *L. fuliginosus* measured by Kravchenko (1973) are comparable to those we found: 60×30 cm. This means that the model we used and the measurements made (for nests 1 and 2) are comparable to those made by other authors and are valid. Kravchenko (1973) gives temperature values close to those used by us (25°C), in the central zone of the nest in the presence of ants (23.0 ± 1.5°C). The population of the nest studied by this author also corresponded to the average *L. fuliginosus* colony size (300 thousand) established by us earlier for this species in Kyiv and Oblast, Ukraine (Stukalyuk et al. 2022a).

The nest studied by Kravchenko (1973) was different as it was located between two openings in the oak trunk, whereas the nests we studied had only one exit. Such differences could indicate different thermal processes: there would be draught of atmospheric air between the two openings, which would cool the nest a little; whereas in our case, due to the presence of a single opening, such a draught would not be observed, and the thermal conditions would be more stable. Therefore, depending on the location of the *L. fuliginosus* nest in the tree trunk (above ground, with an underground part, under the bark or in the pith) and the number of openings (one or more), the thermal processes for different nests may differ significantly. This was also demonstrated in our research. Kravchenko (1973) suggests in his paper that the decrease in temperature in the nest is related to ventilation (moreover, ants can enlarge nest entrances themselves), while the increase in temperature is caused by the heat released by ants and their brood. Further evidence that the increase in temperature inside the nest is associated with ants is the fact that after removal (killing) of the colony population, the temperature inside the nest did not differ from the reference (cavities with wood dust) (Kravchenko 1973). Similar data was obtained for the termite *Nasutitermes acajutlae*, whose warmup of carton nests was observed only in nests containing brood and adults. The nest material (carton) has insulating properties that allow termites to maintain high humidity, which is necessary for successful development of the brood (Fuller & Postava-Davignon 2014). In contrast, in other termite species that build solid nests of compressed clay rather than carton, the system of central

and lateral passages is designed for ventilation and temperature reduction within the nest (Jost 2021).

Considering the comparable colony sizes of red wood ants and *L. fuliginosus* [(hundreds of thousands on average, see Stukalyuk et al. (2022c)], we can assume similar mechanisms of active thermoregulation in spring, ensuring a similar number of generations of workers and gender zoids during the season.

Conclusions

The modelling showed that all three colonies are able to maintain nest temperatures in spring to varying degrees. In comparison with classic anthills, nests in tree trunks are more susceptible to the influence of the external environment. At the same time, their capabilities are determined by the nest size and position in the tree mass.

During the spring warmup, despite the metabolic heat released, temperatures in the nests fluctuate similarly to average daily air temperatures with a slight time lag. This delay is due to the thermal inertia of the tree trunk containing the nest.

The nest in tree #1 proved to be the most stable. Even short-term frosts as low as -5°C do not harm the colony, as metabolic heat keeps the temperature in the nest centre at least $+25^{\circ}\text{C}$.

The nest in tree #2 is also capable of active thermoregulation, but to a lesser extent. The nest temperature of $+25^{\circ}\text{C}$ required for development is maintained during a cold spell of at least $+5^{\circ}\text{C}$. The nest in tree #3 is not able to provide the necessary conditions for hatching in spring in case of unfavourable temperature changes (e.g. a sudden sharp cold spell of one or two days). The amount of metabolic heat released is not sufficient to compensate for the heat loss from the nest, even when the air temperature drops sharply below $+20^{\circ}\text{C}$. It should be noted that this nest is auxiliary (brood) and its architecture does not imply full activation of active thermoregulation. Based on this, it can be assumed that active thermoregulation in the auxiliary nests of *L. fuliginosus* is absent or within $4\text{--}5^{\circ}\text{C}$, similar to small red wood ants' nests (up to 0.7 m in diameter).

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Competing Interests

The authors declare that they have no relevant financial or non-financial interests to disclose.

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