

Effect of mound size on intranest thermoregulation in the red wood ants *Formicarufa* and *F. polyctena* (Hymenoptera, Formicidae)

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Abstract: Red wood ants are capable of active thermoregulation in the nest, which allows them to achieve a high number of workers and a dominant position in biocenoses. We investigated the features of the spring warm-up and the ability for active thermoregulation of the mounds of the ants *Formica polyctena* and *F. rufa* in the vicinity of Kyiv, Ukraine. We have proposed a model of thermoregulation of the mound, which takes into account the heat flow from the sun, heat exchange with air and soil, and endogenous heat generated by the ant colony. The calculation of the model for specific values showed that only *F. polyctena* mounds with a diameter of more than 0.9 m and *F. rufa* mounds with a diameter of more than 1.1 m are able to maintain a constant optimum temperature in the nest. Comparison of the calculated data with the measurement results on the studied nests showed that the diameters of the majority of mounds exceeded the critical values for both species indicating the ability of thermoregulation. The possibility of using the model to study the thermoregulation of mounds in different natural areas is discussed.

Keywords: Mound, red wood ants, heat processes, thermoregulation, *Formica rufa*, *F. polyctena*.

1. Introduction

Ants (Hymenoptera, Formicidae) are poikilotherms arthropods depending on the environmental temperature regime for their survivals (Wilson, 1971). The brood (eggs, larvae, and pupae) of ant colonies are kept and tended by nursing ants inside the nests where certain temperature and humidity conditions are provided and maintained for growth and development (Jones and Oldroyd, 2007). Most of the nests of many ant species are found either underground or in rotten wood (i.e. members of the genera *Myrmica* Latreille, *Tetramorium* Mayr, *Temnothorax* Mayr, *Camponotus* Mayr, some *Formica* Linnaeus species), but some nests are found in mounds made of soil, although less often [*Lasius niger* (Linnaeus, 1758), *Lasius flavus* Fabricius, 1781] (Dlussky, 1980).

Whatever the type of nest built, all ants need to provide optimal intranest microconditions for their survival; this is best achieved by red wood ants (*Formica rufa* group), the dominant inhabitants of temperate forests, by exhibiting a distinctive feature of autonomous heat regulation in their nests (Gösswald and Bier, 1953, 1954; Gösswald, 1955; Otto, 1962; Schmidt, 1974; Zakharov, 1991). This group

includes red wood ants (*Formica rufa* group). This type of intranest heat regulation allows red wood ant colonies in climatic conditions of Ukraine [observations of one author, SS] and the Russian Federation (data of Zakharov (2015)) produce only one generation of queens and males and 4–5 generations of workers during a season.

Heat regulation in nests of red wood ants has been the subject of a large number of previous studies (Dlussky, 1967, 1980; Martin, 1975, 1980a, 1980b, 1987; Galle, 1973; Brandt, 1980; Frouz, 1996; Kadochova et al., 2019). In one of the earliest ones, Dlussky (1967) considered solar radiation and air temperature being of great importance. Martin (1975, 1980a, 1980b) showed that there is virtually no difference in temperature between the nests built in open places and those in the forest shade, which means that the ants themselves produce and/or provide the heat needed for brood development. In general, most of the studies concerned mainly the internal factors favorable for intranest heating such as metabolic heating by the ants during springtime, the activity of microorganisms in the nests, and the temperature regime in different parts of the nest.

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It is generally believed that the main role in nest heating is played by the heat generated by insect metabolism (Dlussky, 1975, 1980). In the case of good thermal insulation, whose quality is determined by the mound size and shape, heating the nests is easily attainable since the heat generated is almost completely expended to raise the nest temperature. After raising the temperature in the nest to the desired value, the colony faces an equally important task of keeping the temperature unchanged or, at least, preventing significant cooling of the nest due to the influence of adverse environmental factors. In other words, the colony needs to provide a stationary thermal state (STS), particularly in the brood chamber.

Many studies have also been devoted to the connection between thermal conditions inside ant nests and the state of the environment (Horstmann and Schmid, 1983; Bachem and Lamprecht, 1983; Jones and Oldroyd, 2007; Kasimova et al., 2014; Gorny et al., 2015). In one study (Garaeva, 2016), a connection between mound and soil temperature was shown, and the seasonal dependence of the nest temperature on that of its environment. Similar studies were carried out for termites, yet another group of social insects (Korb, 1998a, 1998b, 2003), they demonstrated the connection between termite mounds ventilation and their thermal regime. The problem of the optimal form of a mound depending on solar insulation was also studied (Kasimova et al., 2014).

Nevertheless, the problem of the possibility of maintaining the spring warm-up state after its beginning is still poorly studied, as well as the dependence on relationship between internal microclimate and mound size. Daily fluctuations in ambient temperature, especially significant during springtime, can lead to the nest cooling. According to the evidence, the possibility of reheating the nest is limited, since the reserves of body sugars by whose metabolism heat is generated are additionally consumed (Gorny et al., 2015).

The most unfavorable conditions for the nests are during nighttime, when external factors, e.g. air temperature and insolation, can no longer contribute to maintaining the appropriate temperature in the nest. There are scarce data on the correlation between nest size and its temperature regime. According to Kadochova and Frouz (2013), mound size is positively correlated with the number of ants inhabiting the nest; an increased number of ants can themselves contribute to heat production by metabolic heat production, in addition to microbial heat production (especially in wet mounds) and maintain higher inner temperatures even in a cold environment. The small nests make use of solar radiation and nest material for nest thermoregulation. Nevertheless, no mathematical model of heat transfer processes in mounds of different sizes was used in the Kadochova and Frouz (2013) report.

In the present study, we aimed to construct a mathematical model relating to the heat transfer process in mounds of the red wood ant species *Formica rufa* Linnaeus, 1761 and *F. polyctena* Forster, 1850 after sunset.

2. Materials and methods

2.1. Mathematical modelling

A model of heat transfer processes in red wood ant mounds was constructed based on the data available from related literature (Zakharov, 1972, 2015). The mound design used for heat calculations is given in Figure 1.

The dome shape was assumed to be most similar to a hemisphere in *Formica rufa*, and a spherical segment in *Formica polyctena* and the inner cone (IC) of the nest is a cylinder. The shape of the underground part of the nest was not taken into account in calculations. The cylindrical shape of the IC in our model was chosen based on considerations of geometric similarity. According to Dlussky (1975), the IC is similar in shape to an ellipsoid of rotation. We also took into account that the shape of the mound is not decisive for calculating the amount of heat. The main focus is the mass of living ants inhabiting the nest. The heat of metabolism was calculated by the weight of the ants.

The assumptions made it possible to analytically calculate the main parameters of the system (volumes, surface areas, mass) when solving the heat problem. This implies the task of calculating the heat balance of the entire nest depending on the specific size of the mound.

Realizing the complexity of the thermoregulation processes occurring in the nest, within the framework of our mathematical model, a number of assumptions were made that are justified when considering the issue of stabilizing the temperature during the cold hours of the

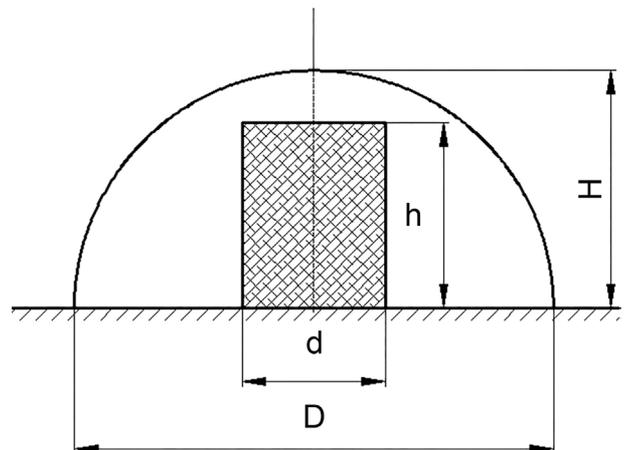


Figure 1. The size parameters used in the calculation of the model. D – diameter of mound, H – height of mound, d – diameter of the inner cone, h – height of the inner cone.

day. In the case when heat loss to the environment occurs, the heat balance equation (Equation 1) after the nest reaches the STS [in W (Watts)] is written as:

$$\pm Q_{rad} \pm Q_{conv} + Q_{met} \pm Q_{filt} \pm Q_{cond} \pm Q_s = 0, \quad (1)$$

where Q_{rad} is the radiant heat flux from the sun, including direct and diffuse radiation,

Q_{conv} is the convective heat flux into the environment from the surface of the mound,

Q_{met} is the metabolic heat of ants,

Q_{filt} is the heat transferred by air going through the mound,

Q_{cond} is the thermal conductivity through the mound and

Q_s is the heat going into the earth through the base of the mound.

Here, the + sign means the heat going into the mound, and the - sign means the heat leaving into the environment.

Daily fluctuations in the ambient temperature and in the conditions of illumination of the mound contribute to the violation of STS. However, the temperature in the nest is the more stable the more massive the dome, which serves not only as thermal insulation, but also as a thermal accumulator for the nest.

The components of the heat balance equation (Equation 1) need to be considered individually for a better understanding of the subject.

The total heat flux from the sun plays a significant role and reaches 1000 W/m² during daytime in well-lit forest areas (Yarymbash and Daus, 2014). However, after sunset, it drops sharply to the background scattered radiation level and then virtually to zero and, therefore, cannot contribute to temperature stabilization.

The heat transferred with air filtered through nest channels plays a significant role in the temperature condition of the nest. However, the inhabitants of the nest can actively regulate ventilation depending on the temperature of the nest and that of the outside air (blocking the paths along which the outside air flows). Therefore, in this case, this component may be omitted altogether, because at low ambient temperature, air exchange in the nest will be at a minimum.

The main influence on the cooling of the nest during the cold hours of the day is the heat transfer consisting of heat conduction through the mound, convection and radiation from the outer surface of the mound, and heat transfer to the deep layers of the soil.

The evaluation of thermal conductivity through mound materials is also critical for modeling. Heat transfer models in porous materials in thermophysics are based on the assumption that the heat in such materials is transmitted by thermal conductivity through the solid skeleton, and thermal conductivity and radiation through gas pores (Tayts, 1962; Brovkin, 1973). As a result, an effective thermal conductivity coefficient is calculated

which takes into account such a heat transfer mechanism. However, when it comes to rather common and ubiquitous porous structures, it makes sense to rely on experimental data obtained. For instance, the thermal conductivity (W/m K) of sawdust is 0.065–0.095, dry conifers foliage is -0.08 and of dry leaves is -0.05–0.06, which are values of approximately the same order. Thermal conductivity of the soil depends on the type (composition) and moisture and is in the range of 0.14–1.72 W/m K (Kazantsev, 1975; Kozhanov, 2008).

Natural convection and radiation from the mound surface is characterized by the total heat transfer coefficient of 5–15 W/m² K and can be calculated according to the Newton's law of cooling (Rumyantsev, 2006).

In conclusion, the heat loss of the nest (IC) into the environment will be considered as heat transfer through the coating layer in the form of a curved wall and can be expressed as in Equation 2:

$$Q_{hl_1} = Q_{cond} + Q_{conv} = \frac{t_n - t_{amb}}{\frac{\delta}{\lambda_{eff} \cdot \bar{F}} + \frac{1}{\alpha_t \cdot F_{outer}}} \quad (2)$$

Where t_n is the nest temperature (°C),

t_{amb} is outside temperature (°C),

δ is the average thickness (in m) of the coating layer of IC,

λ_{eff} is effective coefficient of thermal conductivity of the coating layer [W/m K],

\bar{F} is the mean surface area of IC and the mound (m²),

α_t is the total coefficient of the heat transfer from the mound [W/m²K] and

F_{outer} is the surface area of the dome (m²).

The heat sink into the soil (conductive heat transfer with the soil) can be estimated by the formula of stationary heat conductivity (Equation 3):

$$Q_{hl_2} = \frac{t_n - t_s}{\frac{h}{\lambda \cdot F_b}} \quad (3)$$

Where t_n is the nest temperature (°C),

t_s is soil temperature (°C); at the estimated thickness (h),

h is the estimated thickness of the soil layer under the nest (m),

λ is the thermal conductivity of the soil [W/m K] and

F_b is the surface area of the IC base (m²).

Total heat loss will amount to Equation 4:

$$Q_{hl} = Q_{hl_1} + Q_{hl_2} \quad (4)$$

This heat flux will actually reduce the temperature of the IC of the nest with the mass value of M_n at a certain rate W_c , therefore, the equality will be (Equation 5):

$$Q_{hl} = Q_c = M_n \cdot C_n \cdot w_c = M_n \cdot C_n \cdot \Delta t / \Delta \tau_c \quad (5)$$

where M is the nest mass (kg),

C_n is the specific heat capacity of the nest [J/kg K],

Δt is the change (decrease) in the temperature of the nest ($^{\circ}\text{C}$) and

$\Delta\tau_c$ is the cooling time (sec).

Q_c is the cooling flow.

Hence, knowing the mass of a nest of a given size, it is possible to calculate the decrease in temperature if heat loss in the nest is not compensated for by the heat generated by ant metabolism, or to estimate the mass of the colony needed to release the required amount of internal heat.

To assess the heat release rate of ants, we used the assumption of Dlussky (1975) that the sugar reserves accumulated in autumn in the gaster of worker ants serve as the source of thermal energy. Gorny et al. (2014) stated that a decrease in the total mass of an ant colony by 1.5%–2.5% should not affect their vital activity.

Hence, the specific amount of heat released as a result of vital functions of ants can be calculated as (Equation 6):

$$q_{met} = \frac{q_{ho} \cdot 0,015}{n \cdot 86400} \text{ W/kg}, \quad (6)$$

where q_{ho} is the heat generated by sugar oxidation (J/kg) and

n is the heating time (days).

This is not vastly different from the amount of heat produced by an adult human at rest, which is estimated at about 1.25 W/kg (Machkashi and Banhidi, 1985). Thus, the amount of heat released as a result of vital functions of ants can be calculated by the formula (Equation 7):

$$Q_{met} = q_{met} \cdot M_n \quad (7)$$

Where M_n is the mass of the nest (kg).

The mass of ant nests of various diameters was set according to the data from Dyachenko (2017).

2.2. The study site

Field studies were conducted from July to September 2016–2019 in the green zone of the Kyiv Region (points 4, 5 in Figure 2) and the city of Kyiv (all other points), Ukraine. The localization and illumination of all nests were investigated in 2016–2018, and the temperature and humidity values for selected nest complexes were studied in 2018–2019 (see below).

Nests of two red wood ants species (*F. rufa*, *F. polyctena*) were found in the following 13 localities inside the studied area (the numerical values in parenthesis correspond to the numbers of colonies): Goloseevsky forest (61 *F. rufa*, 90 *F. polyctena*); Feofania (17 *F. rufa*), Koncha-Zaspa forest (24 *F. rufa*, 7 *F. polyctena*), the forest between Khotov and Novoselki villages (22 *F. rufa*), the forest in the vicinity of Boyarka (63 *F. rufa*, 25 *F. polyctena*), the left bank of the Dnipro in Kyiv (141 *F. rufa*), Vinohradar (15 *F. rufa*, 14 *F. polyctena*), Kotsyubinske (37 *F. rufa*, 93 *F. polyctena*), Pushcha-Voditsa forest (15 *F. rufa*, 18 *F. polyctena*), Svyatoshinsky (Belichansky) forest (69 *F. rufa*, 27 *F. polyctena*), in the vicinity of Chayka village (137 *F.*

polyctena), Lysa Hora park (2 *F. rufa*), and in the vicinity of Petropavlivska Borshchagivka village (6 *F. rufa*).

We classified the forests in which the ants were found into three types: a) deciduous forests (Feofania, Lysa Hora); b) mixed forests (parts of Goloseevsky forest, in which wood ant colonies were found; the forest between Khotov and Novoselki villages; Kotsyubinskoe; partial forest in the vicinity of Boyarka; the forest in the vicinity of Chayka village); c) coniferous forests (all other points).

2.3. Measurements and methods

Measurement of the external parameters of mounds were performed in all locations using the route registration method of Dlussky (1965). According to this method, all nests located along the route in a strip of 10 m (5 m from each side of the researcher) were taken into account. In the case of finding a nesting complex rather than a single nest, the route was repeated along the nearest 10 m strip and so on until all the nests in the complex were taken into account. A total of 883 nests (472 *Formica rufa* nests and 411 *F. polyctena* nests) were found. Once determined, the following on-site measurements were performed for each nest. The GPS coordinates of the nest site were recorded using Garmin eTrex 20 (Garmin Incorporated, USA) and 3–5 workers were sampled from each single nest or nest complexes for species identifications. The species of red wood ants was identified by the author (SS) according to Radchenko (2016). The diameter of nest mounds were measured in m in 2 projections as the widest and narrowest (crosswise) in addition to their heights. The numbers of foraging trails were noted and the illumination levels of the nests were measured. In the latter case, the maximum and minimum illuminated sections of the nests (on the mound surface) and within 2 m from it were measured. During the day in the forest, the illumination is constantly changing and illuminated areas shift. Therefore, at a distance of up to 2 m from the mound, we separately measured the most illuminated area (if the mound is not illuminated by the sun rays), assuming that at another time of the day the mound was also lit.

The absolute value of the illumination [in a model is ambient light intensity (in lux)] was measured using a Solar Power Meter CEM DT-1307 in the same conditions for each nest, and the relative value (%) was calculated as the ratio of the light intensity above the nest to that in the open area. This was considered as an external factor that can contribute to the heating of the nest.

The modeling was based on the following nest shape measurements and calculations. The ratio of height to average diameter of 458 nests of *F. rufa* and 407 nests of *F. polyctena* was in the range of 0.52–0.8. Correspondingly, nests with a ratio of up to 0.26 were considered flat, nests with a ratio from 0.27 to 0.52 were considered hemispherical, and those above 0.52 were considered

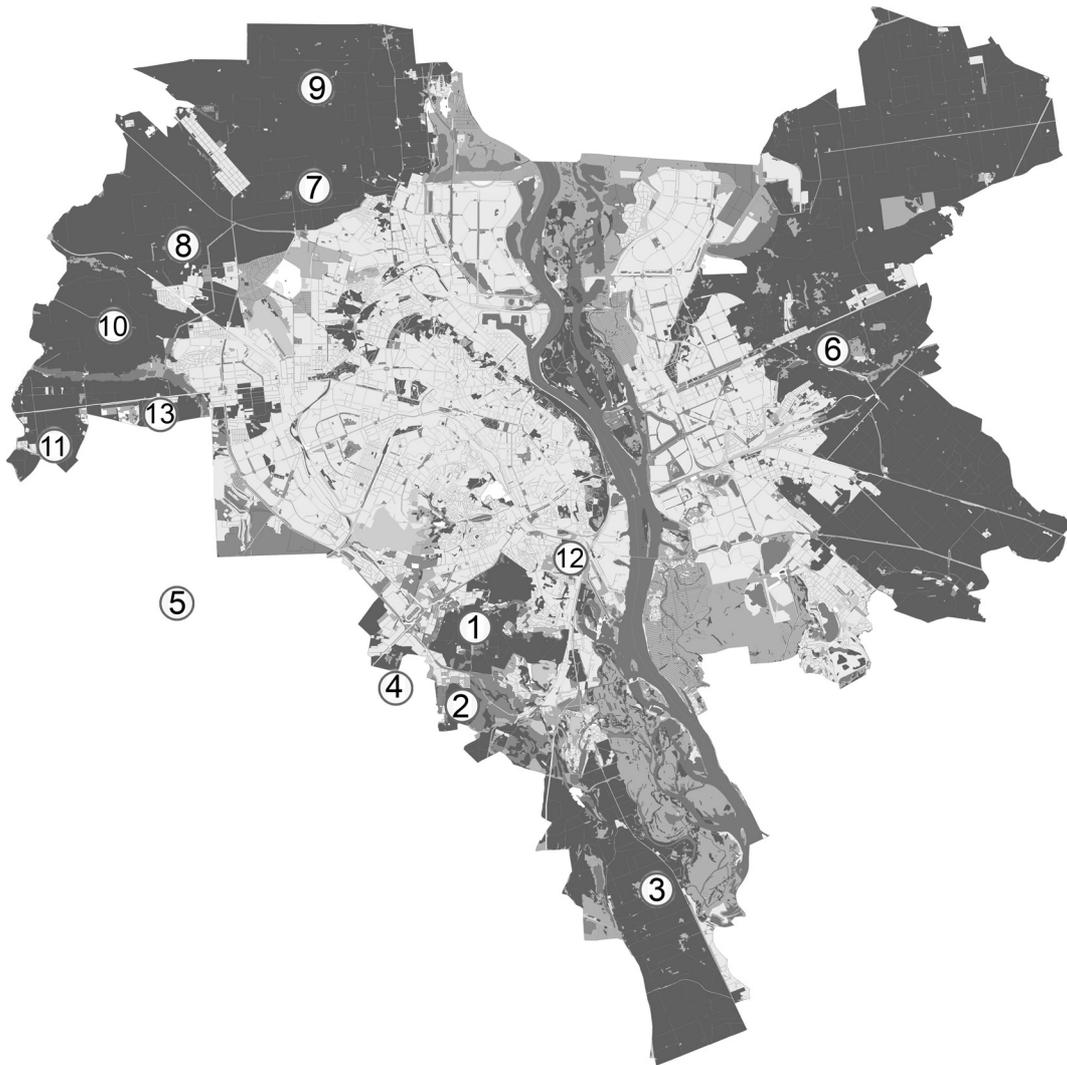


Figure 2. The location of the nests of red wood ants in the green zone of Kyiv and forests of Kyiv region (points 4 and 5), Ukraine. Gray scale: light gray–zone of high-density housing; medium gray–zone of urban and natural parks; dark gray–forest areas. 1 –Goloseevsky forest; 2 – Park/monument of landscape gardening art “Feofania”; 3 – Koncha-Zaspa forest; 4 – forest between Khotov and Novoselki villages; 5 – forest in the vicinity of Boyarka; 6 – Left Bank of Kyiv; 7 –Vinohradar district; 8 –Kotsyubinske; 9 –PushchaVoditsa forest; 10 –Svyatoshinsky (Belichansky) forest; 11 – vicinity of Chayka village of; 12 – Lysa Hora regional and landscape park; 13 – vicinity of Petropavlivska Borshchahivka village.

conical. In the model, we took specific values of this ratio: 0.5 in the case of *F. rufa*, 0.3 in the case of *F. polyctena*. These values corresponded to a hemispherical shape and fell within the range established for mounds in nature. Thus, the parameters of the height to diameter ratio used in the model do not contradict the real ones.

Temperature (°C) and humidity (%) inside the mounds were measured:

- on the surface of the mound,
- in the IC of the nest, at a depth of 10 cm in nests up to 0.5 m in diameter and at a greater depth (up to 40 cm) in larger mounds, and

- at a depth of 10 cm in the soil. Air temperature 1 m above the nest was also taken into account. Measurements in the soil and the nest were carried out using portable Sender IT 1 sensors, which simultaneously measure temperature and humidity with 0.1 accuracy.

The temperature and humidity were measured in September 2018 (at a temperature of +24 °C) and in April 2019 (1 day at +6 °C, 1 day at +19 °C), June 2019 (at +25 °C). To measure the dependence of the temperature in different parts of the nest on its size, we included 15 *F. rufa* and 6 *F. polyctena* nests in the measurements. Model nests are combined in two nest complexes (1 *F. rufa* nest complex,

15 nests; 1 *F. polyctena*, 6 nests). Therefore, these nests were considered as model temperature measurements. The seasonal temperature dynamics in nests of different sizes were measured on the same 15 *F. rufa* nests. The nest site temperature measurements of each nest (see above) at +6 °C, +19 °C in the spring, +25 °C in the summer, and +24 °C in the autumn were measured once during the day, because repeated measurements have the possibility to distort the data due to the temporary thermal change in the nest after removing the temperature sensor and the fact that return to the initial state takes a certain period of time.

We have selected nests of different size classes, with an average diameter interval of 0.5 m each. Up to 0.5 m diameter is the 1st size class, 0.51–1.0 m is 2nd class, 1.01–1.50 m is 3rd class, and 1.51–2.0 m is 4th class. Among the 21 nests of 2 complexes measured, each of the first 3 size classes comprised 5 nests, and 6 nests belonged to the 4th class. There were no nests belonging to the 4th size class (1.51 m and above) in the complex of *F. rufa* (15 nests) at hand and all nests of 4th size class were from *F. polyctena* nest complex. However, there was enough data on this class based on the 6 nests to evaluate the temperature regime of mounds of this size. Mean values of temperature and humidity were calculated for each size class of nests.

2.4. Statistical analysis

The statistical evaluation of the data was performed in Origin (v. 8.0) and in R 3.5.1 (R Core Team, 2018). The normality of the measured nest parameters was tested employing the Shapiro–Wilk test. In the case of normally distributed data, the parametric analysis methods (Pearson’s r and ttest for the significance of differences at $P < 0.05$) were used. The nonparametric Kruskal–Wallis test and the Mann–Whitney U test were used for data without normal distribution. The Kernel density estimation (KDE) was used to calculate the probability density function of studied datasets.

3. Results

The nests of *F. rufa* and *F. polyctena* were found to have the same height to diameter ratio, which determines the hemispherical shape of the mound (Table 1).

A hemispherical shape is most prevalent among nests of *F. rufa* and *F. polyctena*, with approximately the same proportions in both species.

Conical and flat nests were much less common. Variability of the mound shapes in *F. rufa* is large: the proportion of cone-shaped nests exceeds that of *F. polyctena* by 2.0 times ($P < 0.05$), and flat ones by 1.5 times ($P < 0.05$). But in both species all three shapes can be seen.

F. rufa is characterized by the predominance of small nests of size classes 1 and 2 with an average diameter of up to 1 m, while *F. polyctena* nests are larger, as revealed by the presence of more nests with a diameter of 1.5 m and above (Table 2). This suggests a different degree of thermal autonomy in these species, which is associated with different nest sizes. The larger nest size in *F. polyctena* indicates a larger colony size of this species compared to *F. rufa*.

The size of the nest can also be related to its aggregation. In both species, nests that are part of a complex exceed single mounds in terms of average height and diameter ($P < 0.05$, Table 1) by up to 25%.

The linear dimensions and the diameter of the nests of both species of ants do not depend on the illumination of the space under the foliage (Figure 3).

Nevertheless, the choice of nesting site itself correlates with illumination as most nests are located in places with about 4% of the illumination in open space, regardless of their status and type of forest (Figure 4).

This preference is more pronounced for single nests in both *F. polyctena* and *F. rufa* in coniferous and in mixed forests respectively. Apparently, such values of illumination are most favorable for the construction and functioning of the nests of both species of ants.

Table 1. The number and percentage of nests of different shapes and average diameter of mounds of red wood ants *F. rufa* and *F. polyctena*.

Species	The average h/d ratio	The number and percentages of nests of different shapes		Average diameter (d) (in m) and height (h) (in m) of single mounds and mounds from nest complexes		
		Shape	Count (%)	Category	d	H
<i>F. rufa</i>	0.423 ± 0.009	Flat	83 (18%)	Single	0.67 ± 0.21	0.27 ± 0.01
		Hemisphere	284 (62%)			
		Cone	90 (20%)	Nests from complexes	0.89 ± 0.05	0.36 ± 0.02
<i>F. polyctena</i>	0.405 ± 0.006	Flat	54 (13%)	Single	1.05 ± 0.04	0.39 ± 0.02
		Hemisphere	314 (77%)			
		Cone	39 (10%)	Nests from complexes	1.29 ± 0.16	0.46 ± 0.05

Table 2. Quantitative indicators of the average diameter of of mounds of different size classes.

Size class, m	Species	The number of nests
I (up to 0.5)	<i>F. rufa</i>	130
	<i>F. polycтена</i>	36
II (0.51–1.0)	<i>F. rufa</i>	255
	<i>F. polycтена</i>	161
III (1.01–1.5)	<i>F. rufa</i>	69
	<i>F. polycтена</i>	142
IV (1.51–2.0)	<i>F. rufa</i>	18
	<i>F. polycтена</i>	61
V (2.01–2.5)	<i>F. rufa</i>	0
	<i>F. polycтена</i>	8
VI (2.51–3.0)	<i>F. rufa</i>	0
	<i>F. polycтена</i>	2
VII (more than 3.01)	<i>F. rufa</i>	0
	<i>F. polycтена</i>	1

Illumination of nests of different shapes differs only in *F. rufa* in coniferous forests; their median distributions differ significantly (Kruskal–Wallis test, $P < 0.05$, Figure 5).

A pairwise comparison of illumination of nests with different shapes revealed that in coniferous forests flat nests of *F. rufa* are located in brighter areas ($P < 0.05$) compared to nests of other shapes. For *F. rufa* in other forest types and *F. polycтена* in all forest types, such difference is not significant ($P > 0.05$).

According to the proposed model, heat loss and generation calculations for various mound sizes and shapes were performed for two cases: *i*) when the mound has the shape of a hemisphere, the ratio of mound diameter (D) to its height (H) is $D/H = 2$ and *ii*) when the mound has the shape of a spherical segment, the ratio of mound diameter to its height is $D/H = 3$.

To ensure comparability of the calculations, the dimensions of the inner cone [diameter (d) and height (h)] were considered to be dependent on the height of the mound: the diameter $d = 0.6 h$, and the height $h = 1.3 d$.

Figure 6 shows the results of calculations of heat release in the nests and heat loss of the nests depending on the diameter of the mound.

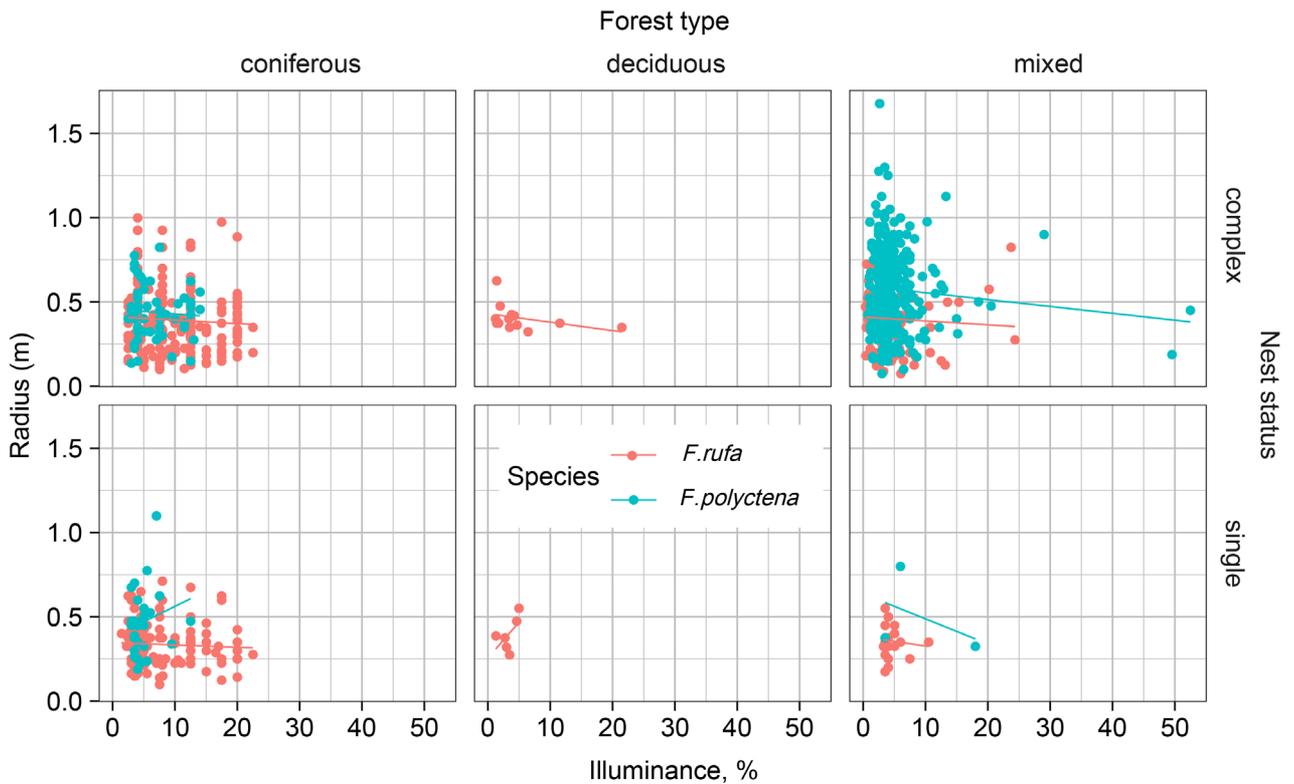


Figure 3. Dependence of the radius of the nest of *F. rufa* and *F. polycтена* on the illumination of the space under the foliage. Points – primary data; straight lines are regression lines. The linear regression equations are not given, because for all data groups, the coefficient of determination $R^2 < 0.01$.

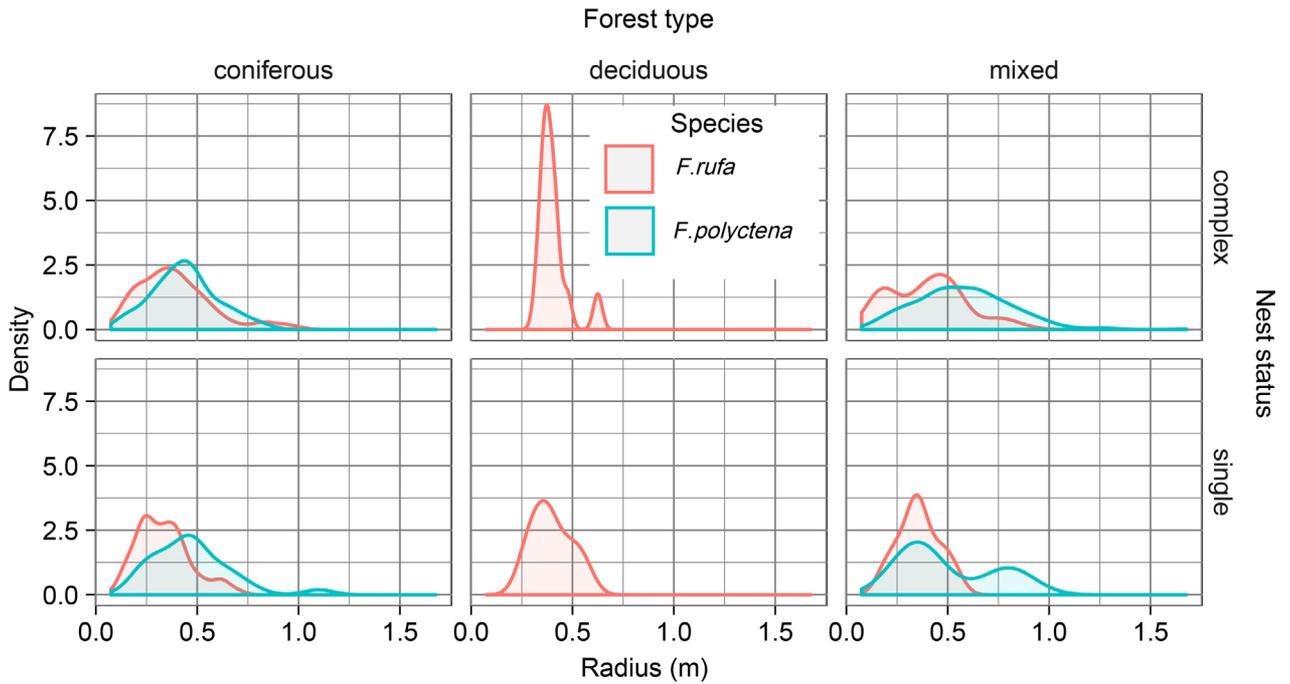


Figure 4. Kernel density estimation of *F. rufa* and *F. polyctena* nest illuminations.

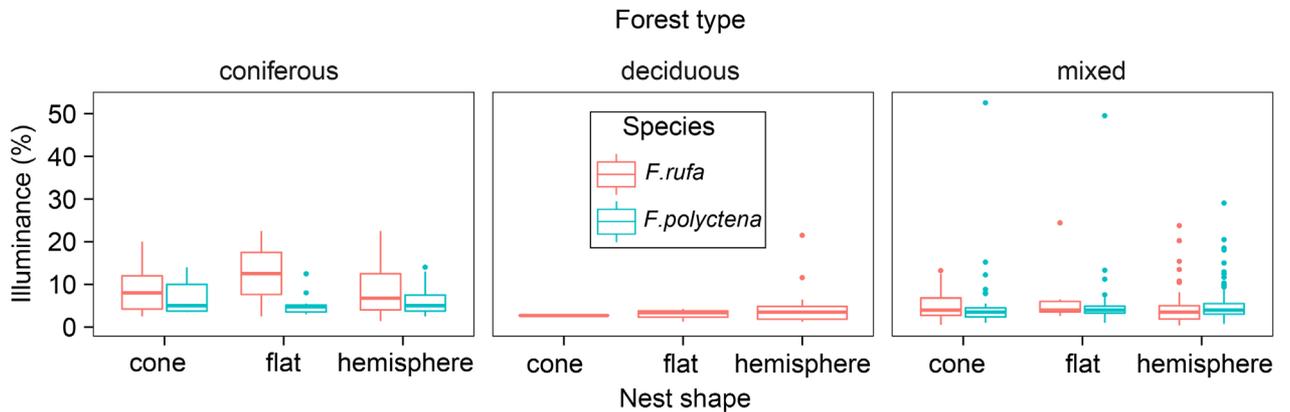


Figure 5. Diagram of the range of illumination of nests of different shapes for *F. rufa* and *F. polyctena* in different types of forests.

As can be seen in Figure 6, the amount of heat released in the nest is characterized by a pronounced exponential dependence and it has a positive correlation with the colony size (diameter of the mound).

The heat loss of the nest also depends on its size, the ratio of the volume of the nest and the mound, and the state and material of the cover layer. The exponential dependence observed in this case is less pronounced.

It can also be seen in Figure 6 that the lines on the graphs intersect at some “critical” points with coordinates D_{cr} , which divide the range into two parts: to the left of D_{cr} , the heat loss Q_{hl} is higher than Q_{met} , and to the right it is lower.

In practice, this means that if $D_x > D_{cr}$, then in such a nest, given the thickness of the cover and the condition of the mound, it is impossible to maintain an acceptable temperature during the day. The nest is completely dependent on external factors.

In the case of $D_x > D_{cr}$, the colony is dependent slightly on external conditions and is capable of active thermoregulation particularly by controlling the temperature of the filtered air.

When $D_x > D_{cr}$, we can talk about unstable equilibrium, with the slightest disturbance being able to cause a shift of the mound thermal state in one direction or another. Thus, there is a certain critical nest size, less than which the mound is not able to maintain its thermal state.

In our case, for nests with a spherical mound shape (*F. rufa*), the critical diameter was found to be 1.15 m (Figure 6), while for spherical segment mounds (*F. polyctena*) this value is 0.90 m (Figure 6).

To find out the effect of ambient temperature on the fundamentally achievable temperature in a nest of the given size, we calculated the total nest-environment heat transfer coefficients by the expression (Equation 8):

$$k_{n-en} = \frac{Q_{hl}}{(t_n - t_{amb})} \text{W/K} \quad (8)$$

where Q_{hl} – heat loss, W (Watts),
 Q_{met} is the metabolic heat of ants, W
 t_n is the nest temperature (°C),

t_{amb} is the outside temperature (°C),
 k_{n-en} is the “nest-environment” heat transfer coefficient, W/K

It turned out that the heat transfer coefficient depends linearly on the diameter of the nest, and increases with increasing diameter of the above ground part. The range of change is 0.05–0.55 W/K.

After that, the theoretically achievable temperature in the nest was determined based on the amount of heat that a nest of known mass can produce in the mound of the corresponding class. The results of our calculation are presented in Figure 7.

Figure 7 shows the nests temperature lines for mounds (*F. rufa*) of various size classes. It is shown that for

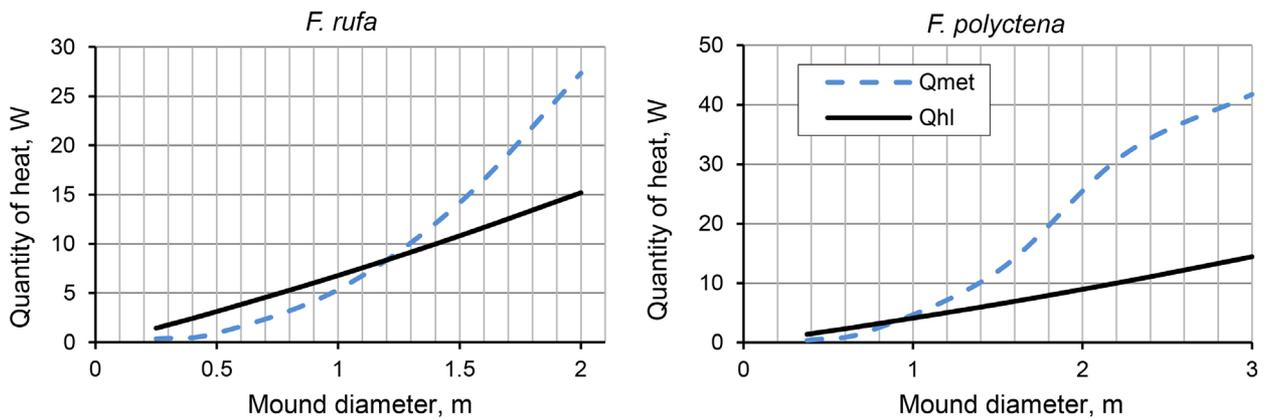


Figure 6. The dependence of heat fluxes on mound sizes in *F. rufa* and *F. polyctena*.

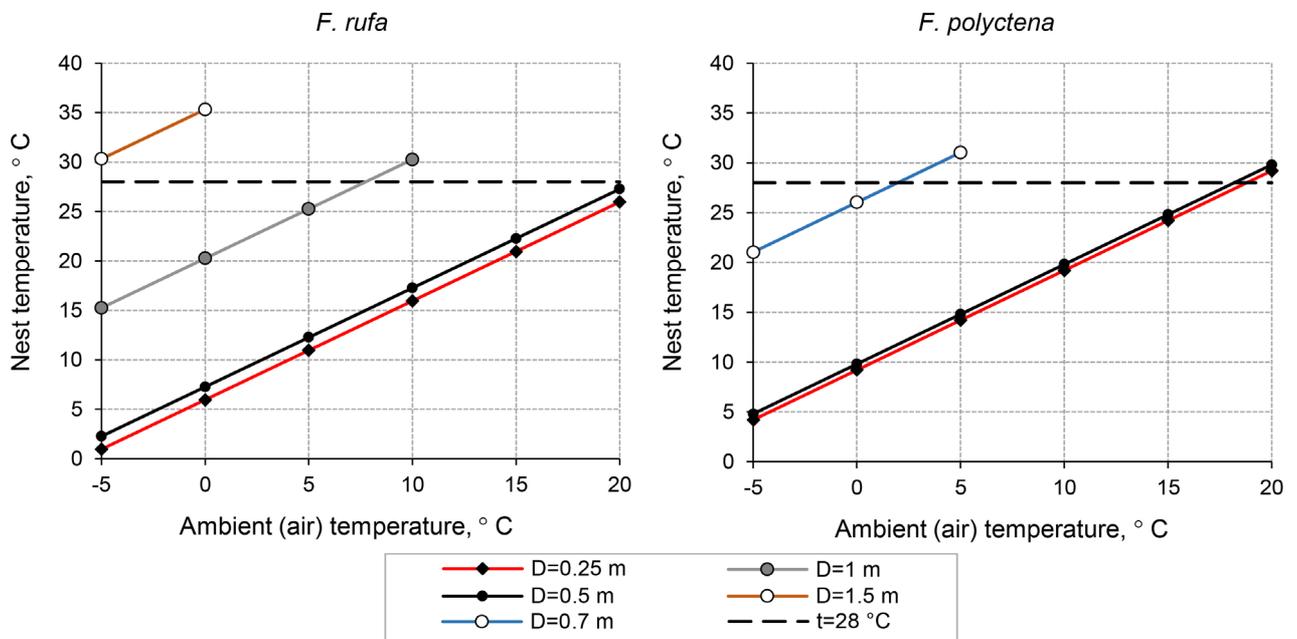


Figure 7. The dependence of nest temperature of *F. rufa* and *F. polyctena* on ambient temperature.

diameter of mounds up to 0.5 m, the temperature in the nest cannot reach +28 °C even if it is +20 °C outside, because the heat dissipation capacity of the nest is insufficient to compensate for the heat loss from the mound. Mounds with a diameter of 1.0 m can theoretically provide a nest temperature of +28 °C even if outside temperature is as low as +7 °C. When the diameter is 1.5 m, we can talk about the complete autonomy of the nest. So, even with frosts up to -8 °C, a temperature of +28 °C is achievable in the nest. However, this will not last long, because insect energy reserve is limited.

In general, a similar picture is observed for *F. polyctena* nests (Figure 7). Mounds with a diameter of less than 0.5 m are not autonomous at air temperatures up to +18 °C, nests of 0.7 m in diameter can function normally at air temperature above +2 °C, and almost complete autonomy is observed for nests with a diameter over 0.8 m.

When our model is compared with temperature measurements in nests, the temperature in the mound is higher in nests of size class 3 and 4 compared to smaller nests, classes 1 and 2 (Table 3).

The larger the nest, the higher the temperature in its inner cone. According to our observations, in large nests of size classes 3 and 4, brood develops faster in spring; there are larvae and pupae of sexual individuals in such nests as early as April. At the same time, in the nests of classes 1 and 2, brood was either at the egg stage or absent altogether. Large nests, therefore, outpace the small ones in the rate of reproduction of the population.

At high air temperatures, temperature inside large nests of 3 and 4 size classes can be 3–6 °C higher than in nests of 1–2 size classes. However, such differences are not significant for the latter, which indirectly indicates their dependence on ambient temperature. The data obtained, thus, are consistent with our model and the calculated critical dimensions of the nests.

Nevertheless, the humidity is independent of the nest size; it is always more humid inside nests than in the environment.

We have not found high correlation between the considered features at +19 °C air temperature. An exception was the correlation between the size of the nest and the

temperature of the inner cone (0.62), and that between soil temperature and the temperature of the inner cone (0.54). At air temperature of +6 °C, higher correlation coefficients were obtained: 0.82 between the size of the nest and the temperature of the inner cone, and 0.95 between the air temperature and the temperature of the soil. Thus, at lower air temperatures, the heating effect is more pronounced. No significant correlations were found for the summer and autumn periods.

Moreover, during the season, a gradual attenuation of the spring heating effect is observed (Table 4), which is apparently due to the lack of need for such high temperatures.

The difference between inside and outside temperature can reach 10 °C in large nests of 3rd size class in early spring. During warm months, when the air warms up to 20 °C and above in the afternoon, the effect of spring heating disappears. In late spring (second half of May), summer, and autumn it is completely absent. Apparently, the top temperature values of nest heating, as shown in the model calculations, cannot exceed +28 °C. These temperature values seem sufficient for brood development. The disappearance of the spring warming effect is characteristic of nests of all sizes. Probably, in larger nests, warming up ends earlier, after sexual individuals exit the pupae. And further warming up may not be necessary, since sexual individuals have already hatched. In smaller nests, lagging behind large ones in brood development, heating can continue further, until sexual individuals exit the pupae. The lower temperature of the inner cone in the nests of size classes 1–2 is obtained both from data collected in nature and calculated using the example of the model.

4. Discussion

The phenomenon of vertical seasonal polydomy (Stukalyuk, 2017), which is known in *F. rufa*, is a reflection of the critical lack of internal heating. The migrations of the ant colony in this case are associated with the characteristics of the brood growing strategy. The issue of brood rearing strategies was discussed in detail in a number of studies (Gösswald and Bier, 1953, 1954; Gösswald, 1955; Otto, 1962; Schmidt, 1974; Kipyatkov, 2007). In terminology of

Table 3. Average temperatures and humidity in mounds of different size classes.

Size class mound, m	t of the air, °C	t of the soil, °C	t dome surfaces, °C	t inner cone, °C	Air humidity, %	Humidity in the nest, %
I (up to 0.5 m)	19.3 ± 0.4	12.5 ± 0.3	20.3 ± 0.3	20.6 ± 0.3	45.6 ± 0.7	69.6 ± 8.4
II (0.51–1.0)	19.0 ± 0.3	12.3 ± 0.2	22.3 ± 1.0	21.6 ± 1.1	45.6 ± 0.3	74.0 ± 4.6
III (1.01–1.5)	19.1 ± 0.3	12.5 ± 0.2	20.7 ± 1.2	23.2 ± 0.5	45.2 ± 0.2	73.7 ± 7.7
IV (1.51–2.0)	19.3 ± 0.2	12.7 ± 0.1	23.2 ± 0.7	26.3 ± 0.6	45.2 ± 0.2	77.3 ± 1.7

Table 4. Nest temperatures during the season.

Size class mound, m	Season	t of the air, °C	t of the soil, °C	t dome surfaces, °C	t inner cone, °C	Air humidity, %	Humidity in the nest, %
I (up to 0.5 m)	Spring	6.0	6.0	6.0 ± 0	7.7 ± 0.9	47.0 ± 0	66.0
II (0.51–1.0)				6.1 ± 0.4	14.4 ± 0.6		
III (1.01–1.5)				6.5 ± 0.8	16.2 ± 0.6		
I (up to 0.5 m)	Spring	19.0	12.0	20.3 ± 0.3	20.6 ± 0.3	45.6	72.0
II (0.51–1.0)				22.3 ± 1.0	21.6 ± 1.1		
III (1.01–1.5)				20.7 ± 1.2	23.2 ± 0.5		
I (up to 0.5 m)	Summer	25.0	17.0	21.6 ± 0.3	23.7 ± 0.7	55.0	83.0
II (0.51–1.0)				21.8 ± 0.2	26.2 ± 0.3		
III (1.01–1.5)				22.0 ± 0.5	26.8 ± 0.2		
I (up to 0.5 m)	Autumn	24.9	18.0	25.6 ± 0.4	24.6 ± 0.4	50.0	70.0
II (0.51–1.0)				24.9 ± 0.7	25.6 ± 0.5		
III (1.01–1.5)				25.6 ± 0.5	25.4 ± 0.5		

Kipyatkov (2007), this option is known as the strategy of spring cultivation of reproductive individuals with autumn accumulation of resources.

When winter ends, the queen rises into the heat core of the nesting dome and begins to lay eggs (the so-called winter eggs), from which females and males later develop. Summer eggs are laid in the summer, when the oviposition resumes (Kipyatkov, 2007). The serial structure of the reared brood is characteristic for red wood ants. Such a cycle largely determines the annual development cycle of red wood ants. In spring, oviposition is intense at the nest temperature of +20–30 °C, and after its completion queens move into chambers with a temperature of up to +18 °C (Horstmann, 1975; Kipyatkov and Shenderova, 1986).

According to Dlussky (1975), the nest of red wood ants is heated by the heat generated by the ants. Sugar reserves accumulated from last fall can serve as the heat source. Over a 12 h period, the temperature in the nest can increase from +7–10 °C to + 20–25 °C, which favors the development of brood and oviposition, as demonstrated by our data and model. These data are also confirmed by more recent studies of lipolysis in the bodies of ants located on the surface of nests and in passive workers (Kadochova et al., 2017). Our present results also confirmed the findings of Zakharov (1972) that there is a certain critical size of the nest under which internal heating is insufficient for autonomous thermoregulation.

It is known that stable nests have a hemispherical shape while actively growing nests are conical (Zakharov, 2015). Concerning flat nests, their shape may be due to the fact that the main part of the nest (IC) is located under the soil surface. It is also known that in the shade, under the dense forest foliage, mounds are usually higher, while in open

places they are flat (Zakharov, 2015). We found that among the Kyiv population of red wood ants, hemispherical nests prevail, which indicates their stable state and location in places with a moderate level of illumination during summer and autumn months.

F. rufa prefers to locate their nests on the edge of the forest and on glades heated by the sun (Czechowski et al. 2002). This provides the necessary optimal mode for brood development as the nest quickly and rather easily warms up in the spring. Moreover, the shape of the nest, the angle of its surface inclination, and its height indicate that ants can rearrange their nest depending on the insolation regime (Chauvin, 1960). In most well-lit places, one should expect the prevalence of flat nests, which is confirmed by our data for *F. rufa* in pine forests. Our model covers the aspect of the nest heating in spring, when the temperature regime is most relevant for the ant colony. In summer, this need disappears. According to our data, there is no dependence of the location of the nest on the level of illumination, although there is a certain range in which most nests are located.

In spring, there is still no foliage on the trees in the forest, or it is not completely developed. Therefore, during this period, when the nest warms up from the inside by ants, its location relative to the lighting mode does not play a noticeable role since illumination is almost the same everywhere. In spring, red wood ants come out to the surface of the nest, but in summer, on the contrary, they avoid illuminated areas where the temperature can rise above +40°C, which is lethal for them (Kadochova et al., 2019). Insolation does not lead to heating the inner parts of the nests greater than the temperature of the soil at the same depth (Gorny et al., 2015).

In underground nests, the microclimate practically does not differ from that in the soil, while in above ground mounds the temperature can be higher due to heating by sun, which favors the development of broods (Dlussky, 1980).

The microclimate inside red wood ants' nests is determined primarily by factors such as nest size, intranesthumidity (moisture capacity), and the degree of shading. The ants themselves are capable of regulating the temperature during the day, closing or opening and expanding the ventilation holes in the nesting dome (Horstmann and Schmid, 1986). Thermoregulation in small nests located in well-lit places occurs mainly due to capture of solar radiation and the insulating properties of the nest material (Galle, 1973; Brandt, 1980; Frouz, 1996; Kadochova and Frouz, 2013). For large colonies, in addition to these factors, new ones are added: the metabolic activity of ants, including those associated with spring heating of the nests by workers (Horstmann, 1987, 1990; Horstmann and Schmid, 1986), as well as heat generation by microorganisms that decompose the nesting material (Coenen-Stass et al., 1980; Frouz et al., 1997). The latter factor was not taken into account in our model. Our study indicates the specific sizes of small nests that are not capable of autothermoregulation, and large ones with this property. The reasons for such differences are analyzed (by the example of the model and the collected data). In addition, we found, as reported earlier (Frouz, 1996), that small nests are not always located in places well-heated by the sun, as other authors point out. Probably this is due to the fact that some of the colonies studied were located in the region more to the north of Ukraine (in Finland). In Kyiv, a zone favorable for nests of all size classes is within 4% of insolation in an open area. It is possible that at geographically different points this parameter may vary.

During spring time, the number of workers heating the nest increases, and their contribution to the nest heating becomes the main factor of thermoregulation (Horstmann, 1975, 1987; Horstmann and Schmid, 1986). According to Frouz and Finer (2007), the thermal conditions of the nest in spring also depend on its humidity and the region of study. The authors compared populations of *F. polyctena* in Czech Republic and Finland, on the northern and central boundaries of the habitat range. In Finland, the temperature increase in the nests of the local population began simultaneously in all the nests studied, while in the Czech Republic the temperature of dry nests began to rise earlier than that of wet ones. Given the geographical proximity of Ukraine and the Czech Republic, we see this feature as more preferable. Also, according to these authors, in dry nests, the temperature reached its peak in the evening and decreased during the night, while in wet nests, a marked increase in temperature was delayed

until night hours. Over the course of a day, temperatures fluctuate much more in dry nests than in wet ones. These differences are caused by different heat capacities of dry and wet nests. More marked temperature fluctuations indicate less independence of dry nests from external factors.

There is evidence that after sunset and the closing of ventilation openings in the mound, the surface area of the mound cools down. As a result, moisture condensation begins and additional heat is released (Gorny et al., 2015). In our study, when constructing a model, the effect of changes in humidity was not taken into account, in view of the assumption that the process is stationary.

The seasonal temperature dynamics inside the nest are also well studied (Kadochova and Frouz, 2014). Using 12 nests of *F. polyctena* as an example, it was found that the temperature difference between the depths of 10 and 5 cm in the nest was on average positive, which indicates the heat flux from inside the nest, emphasizing the importance of internal heat sources. The highest temperature of the IC was reached in June and the lowest was found in September. Linear models showed a significant difference in the thermoregulatory pattern between September and the rest of the year. From April to August, weather (air temperature, precipitation, and solar radiation), nest properties (humidity, number of nests, nest affiliation) and ant activity (number of foragers entering a nest) influenced the temperature of the inner cone. In September, the only significant factors were precipitation and nest properties (humidity, number of nesting holes, nest affiliation). Kadochova and Frouz (2014) suggest that during the period of ants' activity (April–August) the thermoregulation of the nest is actively supported, while later in autumn, ants switch to passive thermoregulation of the nest. This is also confirmed by our data. Measurements of the nest temperature in September did not show significant differences from air temperature. Spring warming up after wintering can be carried out rather quickly, within two days from the awakening of the population and the nest reaches constant temperature values (Gorny et al., 2015). Reaching the value of 22 °C in a large nest (more than 1 m in diameter) can occur in 13 h (Dlussky, 1975). During this time period, ants spend insignificant amount of stored carbohydrates, up to 2.5% of the mass of ants (Gorny et al., 2015). Our model has clearly demonstrated the possibility of such heating, however, with the specification of the nest size. As shown by the modeling and data collected in nature, small nests of size classes 1–2 are not capable of heating, while large ones (3–4 and higher classes) are capable of it. Of decisive importance is the population size of the nest; the larger it is, the faster the spring warm-up occurs. In summer and autumn, warming up is not used, since the ambient temperature is already sufficient for the full development of the brood.

Frouz (2000) reported a relationship between the size of the nest population and the ability of red wood ants of active thermoregulation. This is quite consistent with our modelling and data about the mechanism of spring heating. According to Zakharov (1978), nests of red wood ants with a diameter of up to 0.6 m and a population of up to 100,000 working individuals are not capable of independent thermoregulation and are in the risk zone, thus about 3/4 of them die in a short time. This size is critical for further development and is confirmed by our model as well as collected evidence. The data we obtained slightly exceed the critical size of the nest found by Zakharov (1978), but conditions in a particular research area may matter. The heating mode in such nests is similar to that of earthen mound nests and depends on solar radiation. Larger nests with autonomous thermoregulation are the basis for forming new nests by budding, i.e., for enlargement or restoration of the nesting complex (Zakharov, 1991). For red wood ants, autonomous thermoregulation in the nest is a prerequisite for further colony growth and brood development.

According to our data, the nests that make up the complexes are larger than single ones, and, therefore, have greater autonomy of thermoregulation. Most of the large nests are combined into complexes. The exchange of population between them enhances their adaptive capacity. In addition, we found for *F. polyctena* a greater percentage of large nests and nests included in complexes. This indicates the advantage of this species over *F. rufa* in terms of nest size, their aggregation into complexes, and, therefore, the autonomy of thermoregulation. The

main factor providing the possibility of autonomous thermoregulation is the colony size (population), which was shown by the example of the model and our data.

5. Conclusion

Thermoregulation in the nests of red woodants (at least in *F. rufa* and *F. polyctena*), the ability to maintain a constant high temperature throughout the spring season, is one of the most important adaptations that allowed ants to populate the vast territory of Eurasia and exist in different, contrasting climatic conditions, from southern foreststeppes to northern taiga and foresttundra. For example, the ability of ants to rebuild the mound actively and quickly, changing its shape due to changes in external conditions, in particular lighting, can play a significant role (Dlussky, 1967; Zakharov, 2015). Our model represents an idealized case of the mound of the most common shape under fairly favorable conditions. By changing the initial data, we can continue studying this phenomenon, making calculations for various natural zones and comparing the results to real data, we can study the phenomenon of thermoregulation with a much greater degree of detail, and identify new, previously unknown aspects of the life activity of ants.

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