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Characteristics of thermal processes in ant nests built under stones (Hymenoptera: Formicidae)

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Abstract
Ants prefer to nest under stones. This is due to temperature regimes favorable to the development of ant broods. In this paper, we investigated the influence of stone and ambient parameters on ant nests and created a model of thermal processes in ant nests under stones. The simulation results were compared with temperature measurements. Temperature was measured under 20 stones under different illumination conditions (sun, penumbra and shade) for 3 ant species (*Myrmica rubra*, *Formica cinerea*, *Lasius niger*) in Ukraine from April to August 2021. Stones were categorized as hot, warm and cold. Each stone was checked once a week for the number of workers and brood. Under two stones, temperature was measured using loggers. The number of workers under hot stones in spring increased three weeks earlier than under cold and warm ones. In May-June, the maximum number of workers was recorded under hot stones. In July, the number of ants was minimal under all categories of stones. Larvae appeared under hot stones two weeks earlier than under other categories of stones. In August, the number of pupae under cold and warm stones was greater than under hot ones. Number of larvae and pupae was positively influenced by the diameter of the stone, whereas stone height did not exert an important role. Ants preferred to inhabit nests under large flat stones, which are easily heated in spring and warm the soil under them. Another important characteristic was the location of the stones. The highest brood development was noted in nests under stones in open areas well lit by the sun in the daytime. In summer ants migrated from under hot stones, because soil under it dry and warmed. Stones and their position may be important factors in accelerating the development of brood in colonies of ant species that do not have active thermoregulation.

Key words: ants, stones, nesting, rate of brood development, illumination conditions.

Introduction

Ants build their nests in a wide variety of substrates. In the case of a high density of nests in the territory, the nest-building activity of ants can significantly change the microclimatic conditions of the landscape, and even the physicochemical properties of soils, thereby affecting other groups of organisms. including plants and microbiota (Frouz & Jílková 2008; Jílková et al. 2010). At the same time, there is also an inverse relationship: microrelief conditions influence the nest preferences of different ant species (Pedersen & Boomsma 1999). Some species (for example, *Myrmica rubra* (Linnaeus, 1758) and *Temnothorax* spp.) prefer shaded habitats, while others (*Cataglyphis* spp., *Formica cinerea* Mayr, 1853) nest in open habitats (Radchenko 2016). Other species, for example *Colobopsis truncata* (Spinola, 1808), *Temnothorax* spp., *Leptothorax* spp., can inhabit ready-made passages of bark beetles in the wood, while the nest does not undergo major changes. Some species of ants nesting in the wood can significantly modify it (*Crematogaster* spp., *Camponotus vagus* (Scopoli, 1763)) (Zakharov 2015).

The nest-building activity of ants nesting in the soil is usually seasonal. So, after wintering, the underground part of the nest is restructured in the fall, whereas the chambers are prepared for wintering. To a lesser extent, rebuilding of the nest (mainly exits) can be observed after heavy rains in summer. Of course, in the case of a colony moving from one nest to another, a maximum of nest building activity is also observed (Zakharov 2015). The scale of burrowing activity of ants can be judged from the following facts. Passages and chambers can make up to 12% of the total volume in the nest of the sand ant *Formica cinerea* (Baxter & Hole 1967), and up to 20% of the volume of the anthill in *F. exsectoides* Forel, 1886 (Salem & Hole 1968).

For most ant species that dig nests in the soil, nest construction is associated with passive regulation of microclimatic conditions, which is provided by various environmental factors (illumination regime, soil moisture, temperature fluctuations in the upper part of the substrate during the day). Some species, such as *Lasius niger* (Linnaeus, 1758) and *L. flavus* (Fabricius, 1782), build nests in the form of earthen mounds, which are heated by the sun. Some species of ants (*Formica rufa* group), when they reach a large colony size, become autonomous and build nests in which the temperature is always 2-6 °C higher than in the environment (Dlussky 1975; Frouz & Finer 2007; Stukalyuk et al. 2020). This allows the brood to develop faster in the spring, the number of individuals in the colony grows faster, and the red wood ants can have up to 4-5 generations of workers per year, while other species (*Formica cunicularia* Latreille, 1798, *Lasius alienus* (Foerster, 1850), *L. niger*, *Myrmica* species) have no more than one or two (Zakharov 2015). Some other species are also capable of active thermoregulation, building cardboard nests in in old hollow trees (*Lasius fuliginosus* (Latreille, 1798)) (Kravchenko 1973). However, the number of ant species with active thermoregulation is largely inferior to the number of those with passive thermoregulation. For ant species that do not have active thermoregulation, the issue of successful brood development is addressed in several ways. First, ants, depending on their habitat, can settle in different types of substrate, which determines their high ecological plasticity: in the ground, under the bark of fallen trees, in stumps, and under stones (Czechowski et al. 2002). A typical example is *L. niger*, which has successfully established itself in many urbanized habitats (Ihnatiuk & Stukalyuk 2015). It is known that some ant species build different types of nest in habitats with different microclimatic conditions, as was shown for species of the genus *Lasius* (Gaspar 1971, 1972)., Some ant species build earth mounds in shaded habitats, whereas in insolated habitats they only have underground nests (*L. alienus*, *L. niger*, *Tetramorium caespitum* (Linnaeus, 1758)) (Zakharov 2015). Another way is to build chambers that protrude somewhat above the ground, for example, in earthen hummocks reinforced with stems of herbaceous plants, as observed in *L. niger*, *L. flavus*, and *Myrmica* species (Radchenko 2016). Such chambers contain broods, which, as a result of warming up a thin layer of soil, develop faster. These species of ants regulate the temperature in the nest passively, only by changing the shape of the mound (Dlussky 1980). Finally, the last way is to build nests under stones, or solariums (Zakharov 1999). Thus, the characteristics of ant nesting, at least in the temperate climate zone, are directly related to the brood rearing strategy. Ants occupy those parts of the microrelief that will be most conducive to the rapid development of their brood.

The nest building of ants under stones is practically not studied. In many works, there are references to the fact that ants nest under stones, especially in cold climatic regions or in high mountains (Czechowski et al. 2002). Some ant species successfully colonize small rocky islands (*Myrmica* spp., *Camponotus ligniperda* (Latreille, 1802), *Lasius niger*; Vepsäläinen & Pisarski 1982). There is evidence that the nests of these species of ants may coincide with the stones between which the tunnels are laid. However, there is no physical justification for this method of nesting. It can be assumed that the heating of the stone affects the temperature of the soil area adjacent to it, but there are no descriptions or measurements of such processes. Thus, we can suppose that the presence of stones can significantly accelerate the development of ant brood, if there is a nest under the stones in a suitable habitat. In some habitats (forest areas, steppes), there are few stones, while in others (mountains, anthropogenic habitats such as cities, fields, quarries, etc., local outcrops of rocks - limestones, sandstones, basalts, granites) they can be abundant (Kilpeläinen et al. 2011).

In our work, for the first time, it is shown how the thermal processes occurring in the stone as a result of heating from the rays of the sun affect the microclimatic conditions in the nest. To do this, we took into account stones of different sizes and different degrees of immersion, located in different habitats according to lighting conditions. Short-term and long-term measurements of the physical parameters of stones were carried out, under which nests of ants of three species were found. Based on the obtained data, for the first time, a mathematical model of thermal processes occurring in stones and in the soil under them is proposed. The authors suggest that the heat-accumulating role of stones is relevant for ants building nests under them in illuminated or partially illuminated habitats during the second half of spring and the first half of summer.

Material and methods

Research region

The study was conducted in April-August 2021 on the territory of the Litky village (Kyiv region, Ukraine). The section of the Desna River at its confluence with the river Lubych was chosen for sampling (Fig. 1). In this place, the river bank is reinforced with granite embankments, i.e., a large number of stones of different sizes are everywhere present. During the fieldwork, stones were carefully lifted, and the presence or absence of ants and their chambers was recorded. If ants were found, the stone was marked with a serial number using a marker as suitable for further research. The physical parameters of 20 stones selected for further measurements are given in Table. 1. Of these: (1) stones 1, 3-5; 7-12 were in shaded habitats; (2) stones 14; 18-20 were in habitats illuminated by the sun at least part of the daytime (morning, evening); (3) stones 2; 6; 13; 15-17 were in places illuminated by the sun constantly.

Fig. 1 – Place of research at the confluence of the rivers Desna and Lyubich (Litky village, Kyiv region, Ukraine); **1**, location of stone **2**; **2**, location of stones **1**, **3-12**, **19-20**; **3**, location of stones **13-18**.

Study design

Stones pre-selected for further analysis in April 2021 were then inspected once a week, so that the disturbed ants would not move to another place due to too frequent lifting of the stone. The process of counting the number of ants took no more than 1 minute, while photographing was carried out. Each time the stone was carefully returned to its place. The counts of the number of ants continued from April to August 2021. According to the average temperature between the morning (10:00) and evening (17:00) measurements in June, the stones were divided into 3 categories: (1) hot (the maximum temperature under the stone was 35-39 °C, and most of the daytime under the influence of direct sunlight); (2) warm (temperature was 30-32 °C, part of the daytime in the shade); and (3) cold (temperature was 26-28 °C, all the time or most of the day in the shade). Accordingly, further analysis was carried out in two directions: (1) searching for possible differences between the number of workers, larvae and pupae of the three ant species nesting under stones (*Myrmica rubra*, *Lasius niger*, *Formica cinerea*) for the period April-August 2021; and (2) the same, but without taking into account the species, but taking into account the category of stones (hot, warm, cold stones).

First, the parameters of stones inhabited by different ant species were compared. Then we compared number of workers, larvae and pupae nesting under stones during the study period for the different species. Next, we compared the number of ants, regardless of species, nesting under stones with the three different temperature regimes. Finally, to confirm the results obtained, real data were compared with the results of mathematical modeling of thermal processes occurring in stones and soil under them.

Research methods

Weather. During the observation period (April-August 2021), the spring was rather cool, with a large amount of precipitation (Table 1). The maximum precipitation occurred in April and May, the minimum in July. Cloudy days were the minimum in July, clear days were also the most in July.

Short-term measurements

Measurements of the physical parameters of stones. Soil temperature was measured under the stone itself, where there are passages, and on the soil nearby. The air temperature was also recorded (at a level of up to 0.5 m). We recorded stone measures (length, width, and thickness, in cm) and type (limestone, granite or asphalt). Also, we recorded how deep the stone was immersed in the soil.

Table 1 – Climatic conditions in the study area in April-August 2021.

Month	Average temperature during the day, °C	Average temperature at night, °C	Clear days	Cloudy days	Days with precipitation
April	11	5	7	16	7
May	18	11	6	15	10
June	26	17	7	15	8
July	29	19	17	9	5
August	25	17	13	12	6

In order not to distort the temperature and humidity values in ant nest under the stone, the probe of the thermometer was advanced from the side under the surface of the stone (at an angle of about 5 degrees), before counting the number of ants. As a result, after processing the measurement results, we obtained the microclimatic conditions under the stone and the average values of the size of the stone under it the three species of ants build nests.

Ants-related measurements. We took into account what area (or volume) the passages under the stone occupied. According to Baxter & Hole (1967), the volume of passages and chambers of ants under stones can reach 12%. The diameter of passages and chambers under the stone was measured. To do this, immediately after opening the stone, we photographed the ants in it until they all ran away, so that it was possible to establish their approximate number at the time of opening from the photo. The cameras were photographed separately, against the background of the ruler, in order to know their width and length.

Considered parameters. As a result, we considered the following groups of parameters:

1. Ant species.
2. Parameters of the stone (see), which included: (a) air temperature near the stone and the conditions of illumination by the sun (in the shade, partial shade or in open space); (b) dimensions of the stone; (c) stone surface temperature (pyrometer Testo 830-T1); (d) soil temperature and moisture under the stone (bayonet thermometer model 4 in 1 Soil Survey Instrument); (e) temperature and moisture content of the soil around the stone at a depth of 5-10 cm from the soil surface(f) material of the stone; (g) type of soil (loam, sandy loam, etc.)

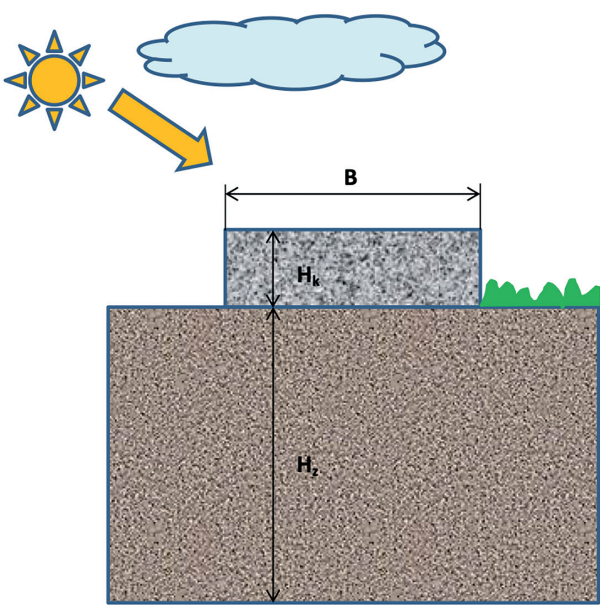

Fig. 2 – Schematic representation of the experimental setting: B: width of the stone; Hk: height of the stone; Hz: thickness of the soil layer under the stone.

3. % of the area under the stone occupied by ants (this can be determined from the photo, either in % or in cm^2).
4. Parameters of the nest itself (i.e., number of ants under the stone at the time of the first opening, and temperature and humidity of the soil under the stone).
5. These observations were repeated 4 times a month, at the same time, in sunny weather. Data analysis was carried out between different species of ants and categories of stones for each of the weeks of the period April-August 2021.

Temperature and humidity of the soil under the stone were determined before making photographs to record the number of ants.

Long-term measurements. For long-term measurements, we chose two stones, No. 2 and No. 20, which were quite large and were located on the surface of the soil. Under these stones, a large number of ants belonging to the same species *F. cinerea* were found (Table 1), which facilitated further measurements. A data logger (model TZ-TempU02, manufacturer TZone, Taiwan) was placed under each stone from June to the end of August, to measure the temperature every 15 minutes. The total number of measurements was 7251 and 6965, respectively. The logger was placed in such a way that it was directly under the stone, in chambers dug by ants. At the end of the measurement period, the logger was removed and connected to a PC to download the data. Such long-term measurements were needed to adapt the mathematical model of thermal processes occurring in and under the stone. The remaining measurements were carried out by the standard methods mentioned above (pyrometer, bayonet thermometer, dimensions, number of ants).

Building a mathematical model

To determine the thermal state of nests located under stones, a mathematical method was used to calculate heat transfer in the "stone-soil" system. The use of the finite difference method made it possible to take into account the change in heat transfer parameters (air temperature, solar radiation intensity, thermophysical properties of stones and soil) during daily cycles. The two-dimensional differential equation of heat conduction was written as:

$$C \cdot \frac{\partial t(x,y,\tau)}{\partial \tau} = \lambda \left(\frac{\partial^2 t(x,y,\tau)}{\partial x^2} + \frac{\partial^2 t(x,y,\tau)}{\partial y^2} \right), \qquad (1.1)$$

where C is the specific heat capacity of the material, J/($m^3 \cdot$ K);

l is the thermal conductivity of the material, W/(m K);

$t(x,y,\tau)$ indicates temperature field of stone (soil), °C.

x, y are spatial coordinates, m;

τ is the current time of the process, s.

Boundary conditions were set for the stone surface, which took into account convective radiant heat exchange with the environment and directed radiant heat flux from the sun. The soil temperature at a depth (1 meter below the surface of the stone) was assumed to be constant, according to the geographical location of the area and the season.

The transformation of the differential equation to a system of algebraic equations was performed according to the method of heat balance of the calculation unit (Brovkin, 2014). According to the method, the heat balance of the calculated volume attributable to this node was recorded. After that, having performed algebraic transformations, an expression was obtained for calculating the node temperature at the next time step. In particular, for a point located on the outer horizontal surface of a stone, we obtained:

$$t_{i,j}^{k+1} = t_{i,j}^{k} + \frac{\Delta Fo_{i,j}}{\lambda_{i,j}} \cdot \left(2t_n \cdot \alpha_{\Sigma} \cdot \Delta + 2q_s \cdot \Delta + t_{i-1,j}^{k} \cdot \frac{2\lambda_{i-1,j} \cdot \lambda_{i,j}}{\lambda_{i-1,j} + \lambda_{i,j}} + t_{i+1,j}^{k} \cdot \frac{2\lambda_{i+1,j} \cdot \lambda_{i,j}}{\lambda_{i+1,j} + \lambda_{i,j}} + 2t_{i,j+1}^{k} \cdot \frac{2\lambda_{i,j+1} \cdot \lambda_{i,j}}{\lambda_{i,j+1} + \lambda_{i,j}} - t_{i,j}^{k} \cdot \left(2\alpha_{\Sigma} \cdot \Delta + \frac{2\lambda_{i-1,j} \cdot \lambda_{i,j}}{\lambda_{i-1,j} + \lambda_{i,j}} + \frac{2\lambda_{i+1,j} \cdot \lambda_{i,j}}{\lambda_{i+1,j} + \lambda_{i,j}} + 2\frac{2\lambda_{i,j+1} \cdot \lambda_{i,j}}{\lambda_{i,j+1} + \lambda_{i,j}} \right) \right), \quad (1.2)$$

where a_a is the total heat transfer coefficient from the stone surface, W/(m^2 K);
q_s is the heat flux density from the sun to the stone surface, W/m^2;
i is the node number along the x coordinate;
j indicates node number along the y coordinate;
Δ indicates spatial step, m;
$\Delta Fo_{i,j}$ is an analogue of the Fourier number of the node with the number i,j :

$$\Delta Fo_{i,j} = \frac{\lambda_{i,j} \cdot \Delta\tau}{C_{i,j} \cdot \Delta^2}, \quad (1.3)$$

here Δτ is the time step, s;
$l_{i,j}$ indicates thermal conductivity coefficient of node i,j, W/(m K);
$C_{i,j}$ indicates specific heat capacity of the material of node i,j, J/(m3 K).

The values of the thermophysical properties of the objects necessary for the calculations (the specific heat capacity of the material, the thermal conductivity of the material, the heat flux density from the sun to the stone surface) were taken according to literature data (Kazantsev 1975; Romanko et al. 2016).

The developed mathematical model was applied using data obtained from two loggers, field measurements and weather data for the village of Litky, Kyiv region (website https://world-weather.ru/pogoda/ukraine/litky_1/).

The results of the control calculation for stone No. 2, under which one of the loggers was located, is shown in Fig. 3.

Calculated and measured soil temperatures under the stone demonstrated satisfactory agreement, with an absolute error is no more than 1-3 °C.

Statistical analysis

Because of deviation from normality and unequal variances, non-parametric analyses were used. Differences between groups (number of workers, larvae and pupae under stones) were tested using the Kruskal-Wallis (KW) test for equal medians followed by Mann-Whitney (M-W) tests. Linear regression models and ANCOVA anal-

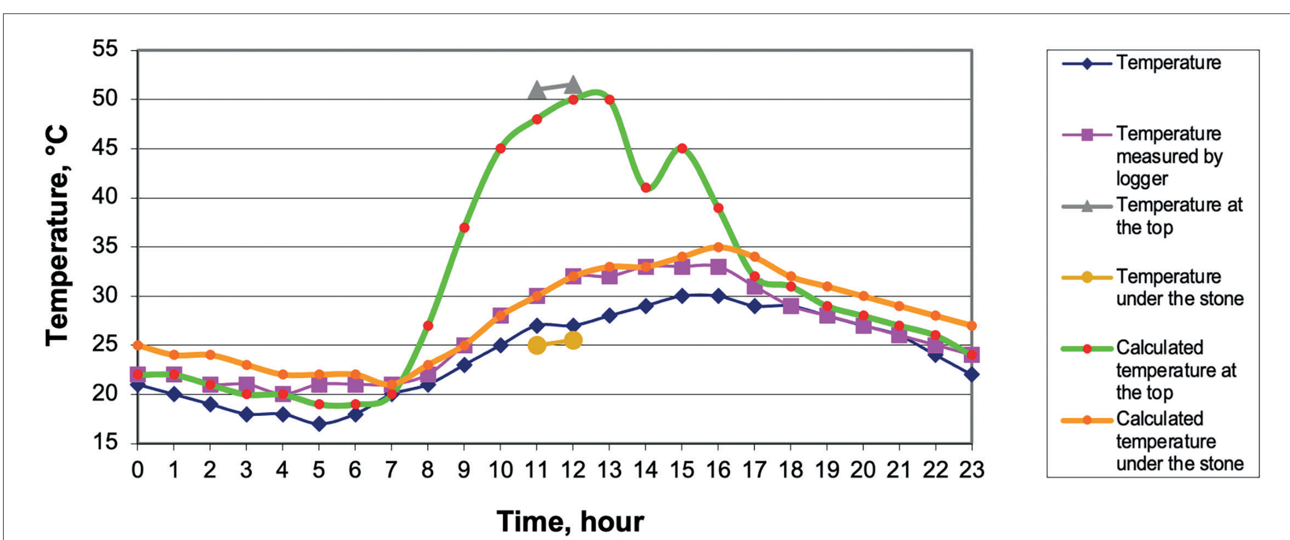

Fig. 3 – Temperature distribution for stone No. 2 on 06/19/2021.

ysis were used to identify the relationship between the linear dimensions of the stone and the number of ants and their brood. We considered the average between the two diameters, as well as the height, as two parameters that could affect the number of ants and their brood. For workers, two time periods were taken: (1) mid-June, when they were at a maximum, and (2) the end of July, when they were at a minimum. For larvae, we took the middle of May (the period of maximum abundance), and for pupae the middle of June (also the peak of abundance). Statistical calculations were performed using Past software 4.03.

Variations in the values (size of the stones, number of workers, larvae, pupae) of the studied parameters are shown in the form of box plots obtained using Origin 2021b program.

Results

Stone sizes. We did not find a significant difference in the size (diameters and height) of the stones under which *Myrmica rubra*, *Lasius niger*, and *Formica cinerea* are nested (Fig. 3). However, the stones under which *Formica cinerea* nested were somewhat larger in both diameters (Fig. 3). Significant differences were however found between height and longer diameter, i.e. the stones were flat in shape, as diameter always exceeded height (K-W: p=3.138E-05). This form of stone can be convenient for heating by sunlight. The mean number of ants under stones at first examination was about the same (K-W: p=0.1385).

Differences between ant species in terms of the number of workers and brood under stones during April-August 2021.

Workers. For *Myrmica rubra*, significant differences were found in the number of workers (Table 2) among different months. The smallest number of ants was recorded in April and July, and the largest in May and June (Fig. 5A; Table 2). In August, the number of ants increased slightly again, but still to a lesser extent compared to June (Fig. 5A, Table 2).

For *Lasius niger*, the number of ants at different times also differed significantly (Fig. 5D, Table 2). Population growth began in May, peaked at the end of June, and declined in July (Table 2). In August, there was a slight increase in the number of ants, but to a much lesser extent compared to April (Table 2).

For the number of *Formica cinerea* workers, the differences were also significant (Fig. 5G, Table 2). The population growth continued throughout May, attaining in June the maximum number of workers, then the decline began to a minimum in July (Table 2). In August, there was a more significant increase in the number of workers compared to other ant species, the average number of ants being comparable to that in early May (Table 2).

Thus, in all ant species, the maximum number of workers was recorded in May-June, and the minimum in July. In August, workers increased again, especially in *Formica cinerea*. The number of *Formica cinerea* workers in the peak weeks of June exceeded that of the other two species by 2-3 times. May, June and August were the most favorable months for finding worker ants under stones.

Larvae. The number of *Myrmica rubra* larvae also changed significantly among months (Fig. 5B, Table 2). Larvae were observed only during May-June, and their number was highest in May (Fig. 5B, Table 2). For *Lasius niger*, larvae were also found in May, and only a small number of them were found in the first week of June (Fig. 5F, Table 2). The maximum was observed in mid-May (Fig. 5F). For *Formica cinerea*, there were also significant differences between months in the number of larvae (Fig. 5H, Table 2), while the first larvae appeared already at the end of April, and the maximum occurred in the second week of May (Fig. 5H); by the end of May its number has dropped significantly (Table 2).

In all three species of ants, larvae under stones were present for a rather small period of time - from May to June (for *Myrmica rubra*, *Lasius niger*), or from April to May (for *Formica cinerea*). The larvae do not have a protective shell, so the impact of high temperatures or low soil moisture (which was 75% in May and dropped to 60% in July) is fatal for them and they possibly moved inside the nest. *Formica cinerea* showed a faster larval development compared to the other two ant species.

Pupae. *Myrmica rubra* pupae were found under stones in June and August, with more pupae in August (Fig. 5C, Table 2). *Lasius niger* pupae also had different numbers in different months (Fig. 5F, Table 2): they began to appear at the end of May, with two packs, one in mid-June and the other in August (Table 2). *Formica cinerea* also showed differences in the number of pupae among months (Fig. 5I, Table 2). The period of presence of pupae under stones in this species was much wider. The first pupae appeared in the second half of May, and their number reached a maximum in the first half of June; in July there were practically no pupae, but in August their number increased again, becoming comparable to that of June (Table 2).

Thus, in *Myrmica rubra* pupae appeared later than in other species. *Myrmica rubra* pupae do not have a protective cover (cocoon); therefore, they are more vulnerable to negative factors (high temperature and low humidity). In addition, this species nests in shaded habitats more often than the other two (all 5 colonies were found in the shade, under cold stones; for *Lasius niger* 5 colonies were found under cold stones and one under hot stone; for *Formica cinerea* 4 colonies under warm stones, the rest 5 under hot).

Table 2 – Results of statistical tests on the number of workers, larvae and pupae of three ant species living under stones in different months.

Species	Category	K-W test	Compared months, higher value vs. lower value	M-W test
Myrmica rubra	Workers	K-W: p=3.695E-05	June vs April	<0.0001
			May vs April	0.001
			June vs July	<0.0001
			May vs July	0.004
			June vs August	0.011
Lasius niger		K-W: p=1.831E-10	May vs April	0.004
			June vs May	0.007
			June vs July	0.005
			April vs August	0.008
			August vs July	0.004
Formica cinerea		K-W: p=5.504E-09	May vs April	0.002
			June vs May	0.214
			June vs July	<0.0001
			August vs May	0.046
Myrmica rubra	Larvae	K-W: p=0.005046	May vs June	0.011
Lasius niger		K-W: p=0.01399;	May vs June	0.004
Formica cinerea		K-W: p=6.616E-05	May vs April	0.003
			May, 2nd week vs May, 4th week	0.020
Myrmica rubra	Pupae	K-W: p=0.01923	August vs June	0.036
			June vs May	0.030
Lasius niger		K-W: p=1.225E-06	May, 3rd week vs May, 4th week	0.024
			June vs May	0.003
			August vs May	0.003
Formica cinerea		K-W: p=1.287E-06	June vs May	0.001
			June vs July	<0.0001
			August vs July	<0.0001
			August vs June	0.108

Differences in the number of adults and brood of ants nesting under stones of different categories.

Cold stones. Under cold stones, ants had different numbers of individuals at different times of the year (Fig. 6A, Table 3). In April, the average number of ants was minimal, in May there was a continuous increase in the number of workers, and the maximum was recorded in the second half of June (Table 3). A decline was observed in July, with a slight increase in August (Table 3).

There are significant differences in the number of larvae under cold stones (Fig. 6B, Table 3): they appeared in early May, there was a maximum in the second week of May, and they were practically absent in June (Table 3).

Pupae were found in different numbers from the end of May to the end of June, as well as in August (Fig. 6C, Table 3). At the same time, their maximum number was recorded in the second half of June and at the end of August (Table 3); in July they were practically absent.

Warm stones*.* Under warm stones, the number of ants also underwent significant changes according to the month (Fig. 6D, Table 3). The increase in the number of workers began at the end of April and continued in May. The maximum occurred in the first half of June; in July there was a decline, but in August the number of workers increased again becoming comparable to that observed in June (Table 3).

Under warm stones, the number of ant larvae did not differ significantly (Fig. 6E, Table 3). The larvae were found exclusively in May, with a maximum in the second week of May (Table 3).

Pupae varied in their number during the observation period (Fig. 6F, Table 3). The pupae appeared at the end of May and reached their maximum number in the middle of June; they were practically absent in July, but a second peak of abundance was observed in August (Table 3).

Hot stones*.* The largest changes in the number of workers were recorded under hot stones (Fig. 6G, Table

3). The first workers began to appear under the stones in early April. Their number increased in May, up to a maximum in June (but the average number of ants are comparable with May, Table 3). In July, there was a decline, but in August the number increased slightly again (Table 3).

Under hot stones, the number of larvae varied significantly (Fig. 6H, Table 3), since they were found here from the end of April to the end of May. There was a minimum in April, with maximum values in the second week of May (Table 3).

The number of pupae under hot stones underwent significant changes during the study period (Fig. 6I, Table 3). The first pupae appeared at the end of May, and their number increased until mid-June (Table 3). In July, there were practically no pupae; they began to appear again in the second half of August (Table 3).

Overall, the number of worker ants under hot stones begins to increase earlier than under cold or warm ones. Under the hot stones, the maximum number of workers was recorded in May-June. In July, we found the minimum number of workers under all categories of stones. Under hot stones, larvae appeared earlier, as early as the end of April, while under warm and cold stones they appeared in May. Accordingly, pupae appeared under all categories of stones at the end of May; however, their number in August under cold and warm stones exceeded the number of pupae under hot ones. Consequently, in August, when the soil became wetter after the rains began, part of the brood moved again under the stones, especially under the cold and warm ones. The maximum variation in ant numbers under stones occurred among workers, especially in the hot stone category.

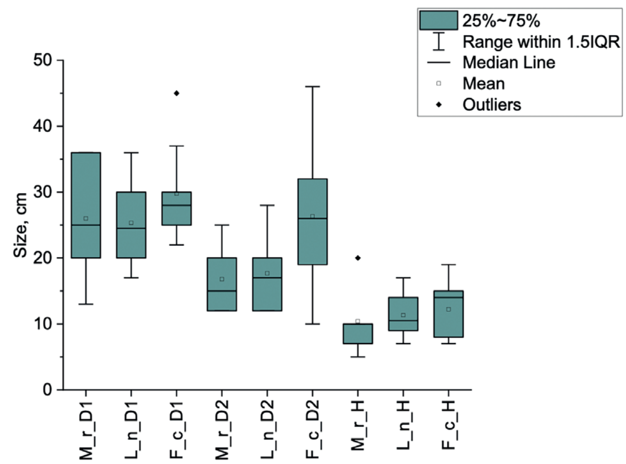

Fig. 4 – Linear dimensions of stones with *Myrmica rubra* **(M_r),** *Lasius niger* (**L_n**), *Formica cinerea* (**F_c**) nests. **D1** and **D2** are diameter **1** and **2**; **H** is height. All measures are in cm.

Table 3 – Results of statistical tests on the number of workers, larvae and pupae of ants living under stones with different temperature conditions.

The temperature regime of the stone	Category	K-W test	Compared months, higher value vs. lower value	M-W test
Cold stones	Workers	K-W: p=4.931E-16	May vs April	0.001
			June vs May	0.002
			June vs July	<0.0001
			August vs July	0.012
	Larvae	K-W: p=7.286E-05	May, 2nd week vs May, 1st week	0.021
			May vs June	<0.0001
	Pupae	K-W: p=7.354E-13	June vs May	0.040
			August vs July	<0.0001
Warm stones	Workers	K-W: p=0.0208	June vs April	0.030
			July vs June	0.029
			June vs August	0.113
	Larvae	K-W: p=0.06092	May, 1st week vs May, 2nd week	0.112
	Pupae	K-W: p=0.009957	May vs June	0.030
			June vs July	0.026
			August vs July	0.029
Hot stones	Workers	K-W: p=4.789E-07	May vs April	0.037
			June vs May	0.065
			July vs June	0.004
			August vs July	0.015
	Larvae	K-W: p=0.004047	May vs April	0.004
	Pupae	K-W: p=0.00115	June vs May	0.008
			June vs July	0.015
			August vs July	0.007

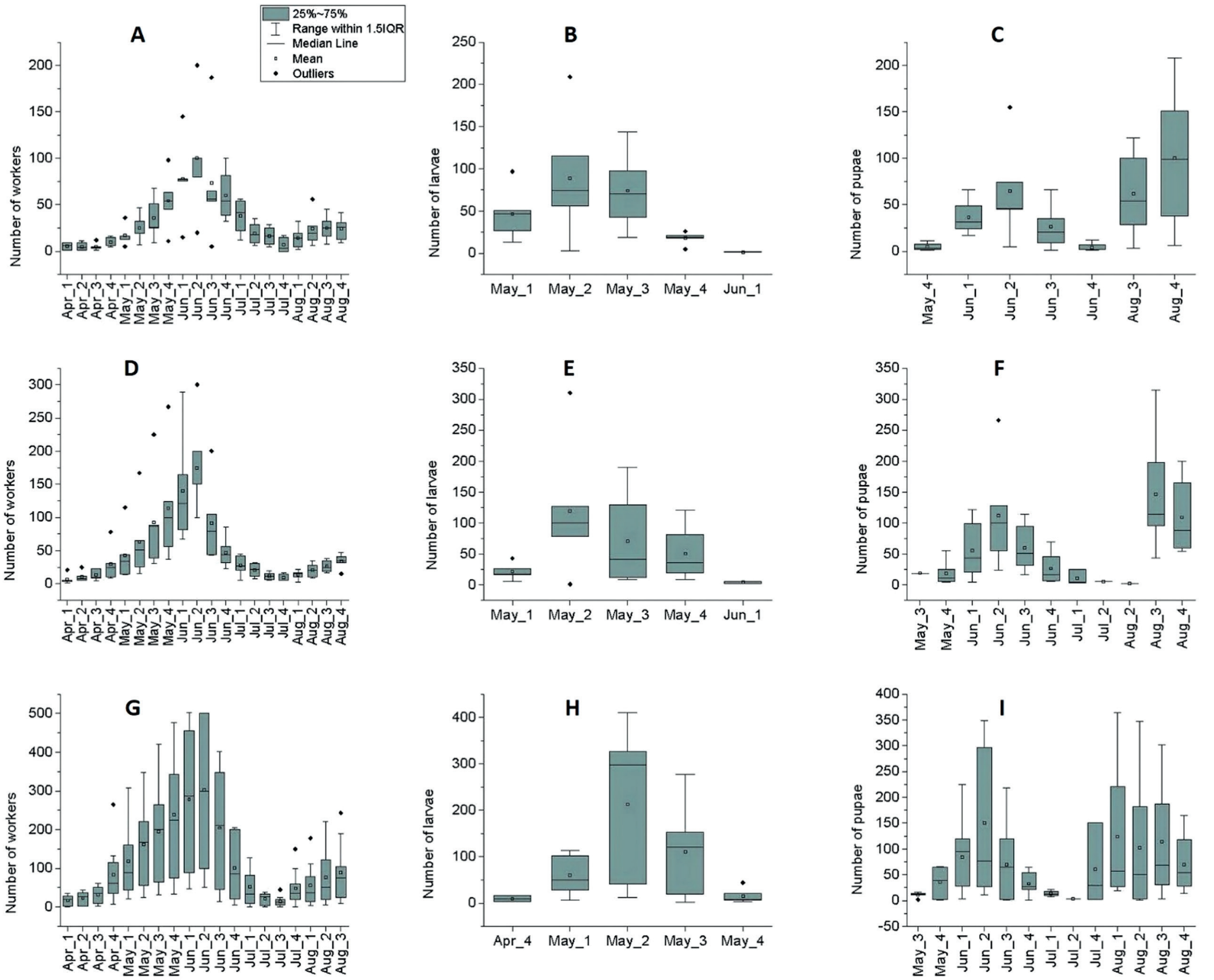

Fig. 5 – Number of workers, larvae and pupae found under stones in the nests of three ant species (**A-C**, *Myrmica rubra***;** **D-F**, *Lasius niger*; **G-I**, *Formica cinerea*) during April - August 2021. **A**, **D**, **G**: workers ; **B**, **E**, **H**: larvae; **C**, **F**, **I**: pupae. **1-4** indicates the number of week in each month.

Relationship between the linear dimensions of the stone and the number of workers and brood

The size of the stone can have a significant effect on the number of ants and their brood (Fig. 7, Table 4). At the same time, the height of the stone has a lesser effect on the number of ants or their brood than the average diameter (Table 4). Thus ants prefer to settle under stones covering a large area of the surface above the nest, i. e. under the large flat stones. Number of workers, pupae and larvae increased with stone diameter, and for workers this increase was steeper in June than in July (Table 4).

Large stones provide a comfortable temperature for early pupal development.

In July, the relationship is weaker than in June, since workers were not present under all the stones (Fig. 7A, B, Table 4). For larvae and pupae, a similar dependence was established - there were more of them under large stones (Fig. 7C, D). In July, the number of pupae under stones also decreased (Table 4). This indicates that the ants move their brood, depending on the temperature regime under the stones. The greatest effect of overheating seems to be experienced by the larvae. Settling the soil under large stones gives an advantage in the timing of the start of colony growth. However, settlement under deeply submerged stones is apparently unprofitable for ants, since the soil under such stones heats up much later, because the openly located part of the stone receives less heat from the environment (air and the sun).

Simulation of thermal processes in ant nests under stones

With the help of the developed model, a simulation of heat transfer in nests under stones was carried out. To test the assumption about the fundamental influence on the heat

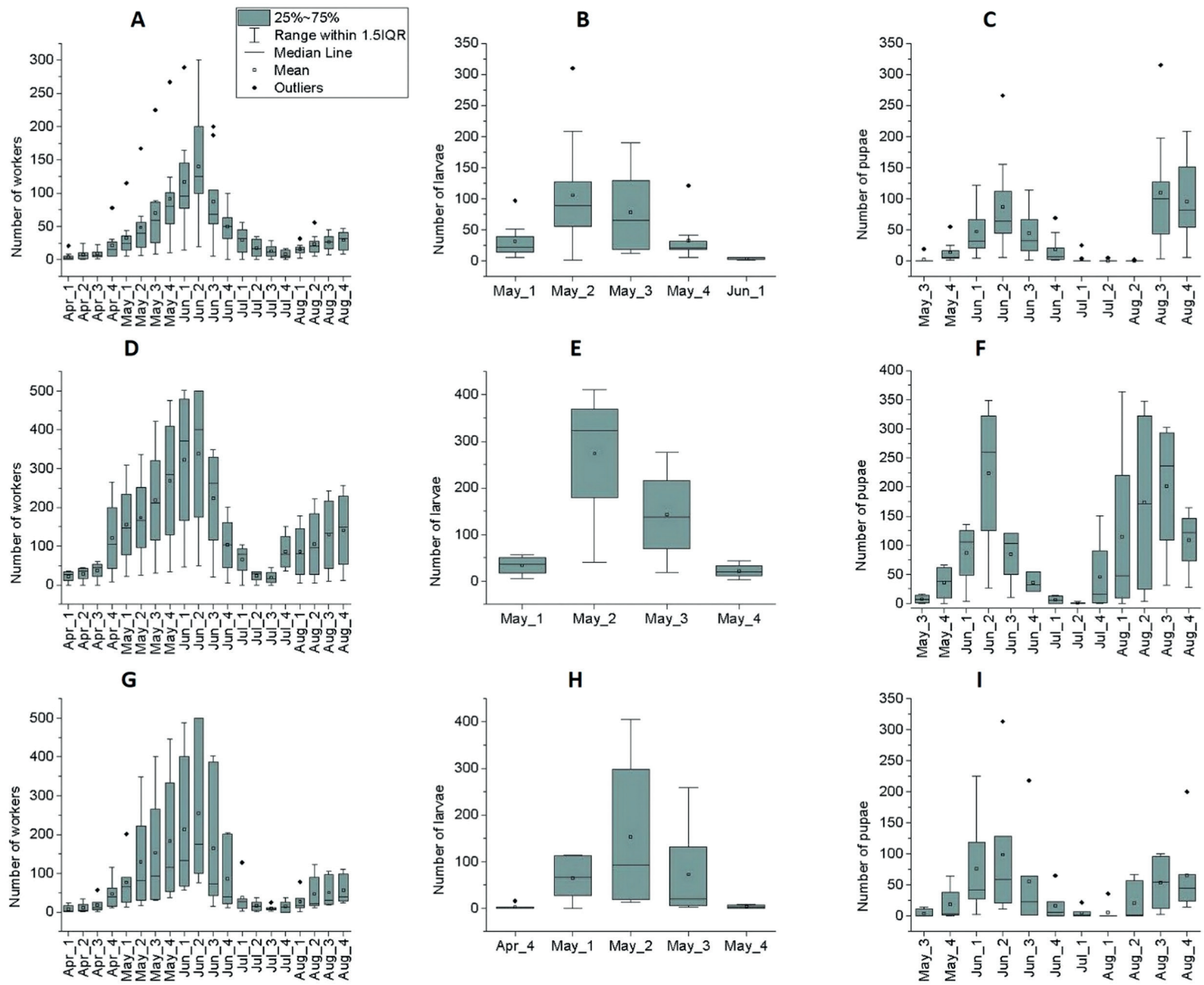

Fig. 6 – Number of workers, larvae and pupae found under stones (**A-C**, cold; **D-F**, warm; **G-I**, hot) during April – August 2021. **A**, **D**, **G**: workers; **B**, **E**, **H**: larvae; **C**, F, **I**: pupae.

transfer, several series of calculations were performed for various conditions. First of all, the stones were grouped into two groups according to their thickness: (1) thin (flat) - up to 7 cm; (2) thick (massive) - over 7 cm and up to 18 cm. According to the illumination, three types of conditions were considered: (1) open solar space; (2) penumbra; (3) solid shadow.

Figures 8A-C show the simulation results of massive stone heating for the three types of lighting conditions. Daily temperature changes are shown at characteristic points (surface of the stone, under the stone).

Figures 8D-F show the results of calculations for a thin stone.

Figures 9A-C show the temperature distribution over the thickness of a massive stone and in the soil under it at certain times of the day (6 am, 2 pm, 9 pm). The temperature distribution in a thin stone and under it is shown in Figures 9D-F. Two-dimensional visualization of the temperature field in the "massive stone-soil" system for 10 am and 2 pm is shown in Figure 10.

Results from the model confirmed the assumption about the fundamental influence of the stone illumination conditions on the thermal regime of the nest located under it. For open conditions, the temperature under the stones exceeds the air temperature throughout the day; for penumbra, temperature is higher at night - early morning hours and follows the air temperature during the day and in the evening; for the shadow, temperature is also higher at night - early morning hours and significantly lower in the daytime and in the evening.

The massiveness (thickness) of the stone also affects the temperature conditions under the stone. Under illuminated thin stones, the soil warms up to a higher temperature than under thick ones. However, in partial shade and shade, temperature is somewhat lower for thin stones than for massive ones. Apparently, this is due to the influence of

Table 4 – Regression results for the relationships between stone characteristics and ant numbers in different periods.

Stone characteristics	Category	Time	Intercept	Slope	One-way ANCOVA, homogeneity of slopes
Height	Workers	Mid June	76.593 (-156.13, 273.72)	11.927 (-4.8108, 30.128)	F=1.522, p=0.2253
		End of July	8.4347 (-25.292, 48.263)	1.5013 (-2.8483, 4.9869)	
Average diameter	Workers	Mid June	-156.24 (-363.63, 6.1926)	15.148 (9.312, 24.454)	F=9.945, p=0.003248
		End of July	-40.395 (-79.69, 6.5478)	2.7061 (0.29361, 4.8525)	
	Larvae	The end of May	-50.51 (-183.97, 87.678)	5.7384 (0.51718, 11.592)	-
	Pupae	Mid June	-31.726 (-221.33, 128.97)	6.1218 (-0.18237, 14.145)	F=3.319, p=0.0768
		End of July	-1.3145 (-17.172, 13.557)	0.23191 (-0.35334, 0.87069)	

the outflow of heat into the soil, the temperature of which at a depth of 1 meter was taken equal to 16 °C.

At the same time, it was not possible to establish a noticeable stabilizing effect of the size of the stone on the temperature in the nests. For comparison, data reported in Table 5 show the temperature at the main design points of the "stone-soil" system of stones of various massiveness.

It should be noted that the natural moisture content of the soil, which largely determines its heat capacity and thermal conductivity, affects the processes of heat transfer under the stone. Within the framework of the developed mathematical model, the influence of soil moisture under the stone was taken into account by correcting the heat capacity and thermal conductivity of the soil according to field measurements. Therefore, the heat capacity and thermal conductivity were changed depending on soil moisture.

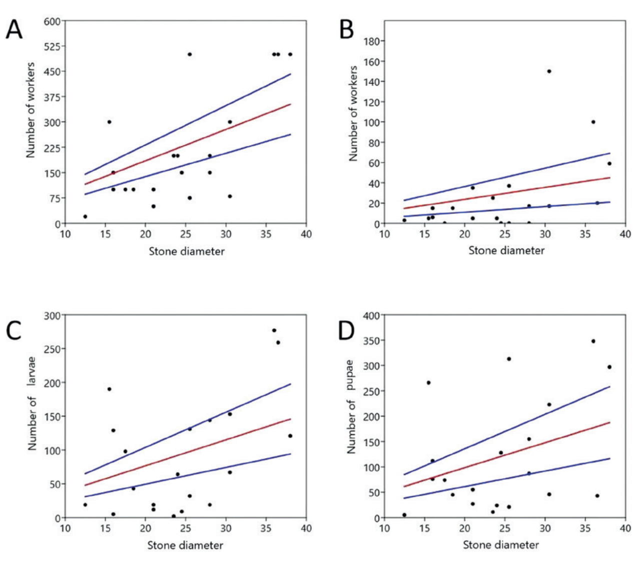

Fig. 7 – Relationship between the number of ants and their brood and the linear dimensions of the stone (average diameter, cm). **A**, workers in mid-June (R2 = 0.46788, p = 0.00088136); **B**, workers at the end of July (R^2 = 0.27579, p = 0.017422); **C**, larvae at the end of May (R^2 = 0.25457, p = 0.023286); **D**, pupae in mid-June (R^2 = 0.16688, p = 0.073735).

Discussion

Adaptative significance of nesting under stones

Ants that do not have active thermoregulation of the nest are characterized by various adaptations to microclimatic conditions. So, in shaded habitats, under a canopy of dense grass, many species of the genus *Myrmica* build nests in the form of earthen hummocks (Radchenko 2016). These bumps can be reinforced with grass stalks. The porosity of the bumps allows for rapid heating, but also causes rapid heat loss at night. Therefore, the ants move their brood to the lower chambers when it gets cold. Such a response to temperature changes has been also shown for the fire ants *Solenopsis invicta* Buren, 1972 (Penick & Tschinkel 2008). When the temperature rises above the optimal value (32.8 °C) for brood development, ants move to the lower chambers of the nest (Penick & Tschinkel 2008). Apparently, this also happens in ant nests under stones investigated in our study. If in spring and early summer such movements are quite rare, then with the onset of a hot period at the end of June they become more frequent, and, in the end, the brood moves to the lower chambers completely. Drying of the soil under the stone can also contribute to this. This is confirmed by the reappearance of pupae in *Formica cinerea* in August under stones. Thus, the larvae were developing in the inside of the nest while it was too hot in July. Penick & Tschinkel (2008) found that for fire ants temperature changes are a more important factor than circadian rhythm. At the same time, even mounds in the shade heated up more than the ground, as they had a lower heat capacity, possibly due to their porosity (Penick and Tschinkel 2008). The greatest heating of the mound occurs on the sunlit side (Kadochová 2017).

Other ant species build earth mounds: *Formica picea* (Collingwood 1961) in swamps, *Lasius niger* in suburban habitats (fields, pastures), and *Lasius flavus* in meadows (Radchenko 2016). Many ant species nest under stones, at least in part. These species include, for example, *Tetramorium caespitum* and *Tapinoma erraticum* in the

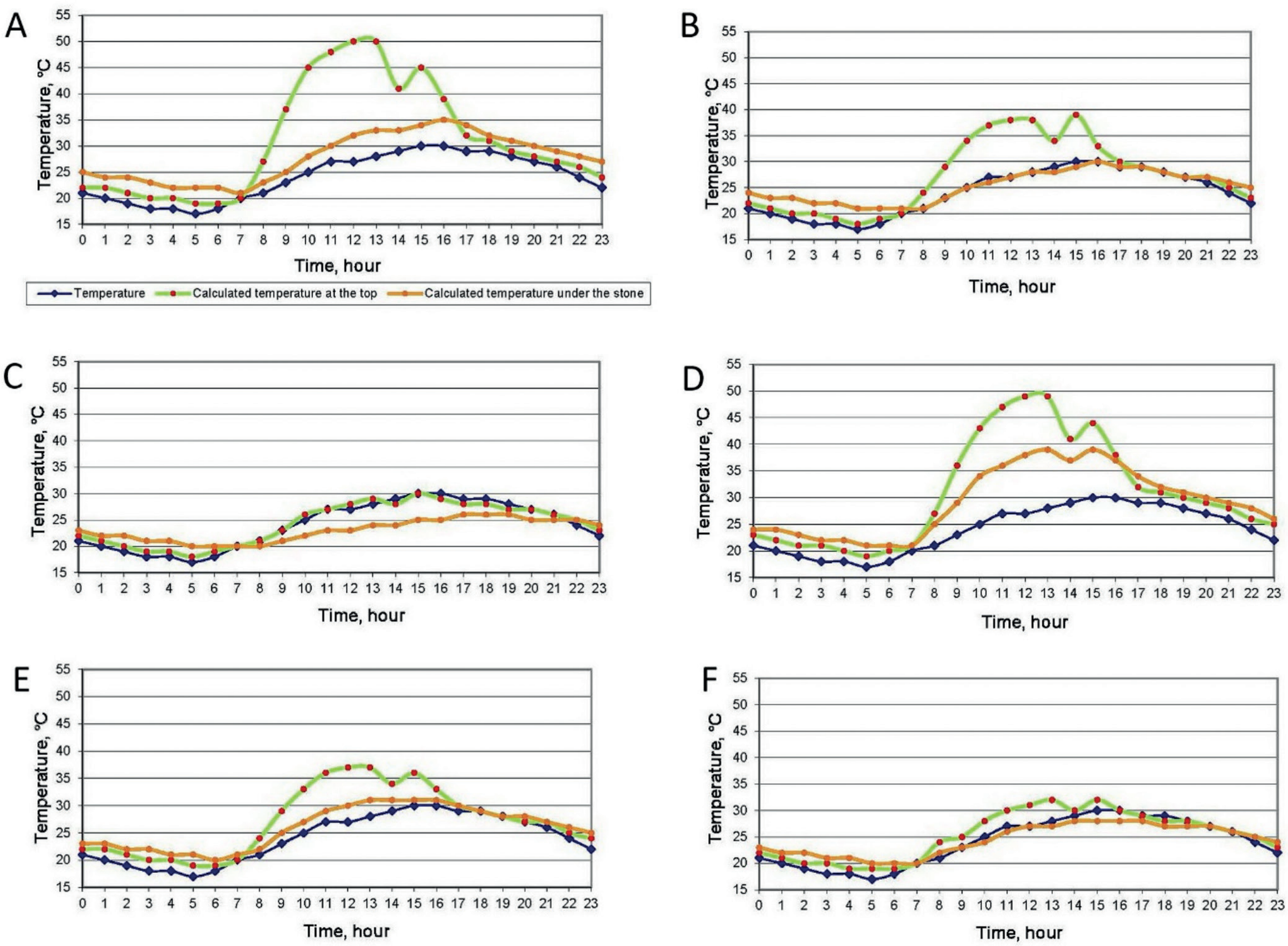

Fig. 8 – Daily temperature changes at characteristic points of the system for thick stone (**A**, open space; **B**, penumbra; **C**, shadow); Same, for thin stone: **D**, open space; **E**, penumbra; **F**, shadow

Crimean mountain steppes (Stukalyuk & Radchenko 2011). The stones favored by ants can include quartzite, sandstone, tillite, and dolerite (Dean & Turner 1991). In our work, almost all the examined stones (18 out of 20) were of granite. It can be assumed that the rock of which the stone is composed does not play such a big role as its size (primarily diameter) and location (in the shade or in the sunlit area). But on the other hand, the material of the stone can affect the accumulation and retention of water in the soil below it, and this can be important in steppe and desert conditions. For example, quartzite is more effective at retaining water in the soil than sandstone because sandstone is more porous. Dean & Turner (1991) consider the following benefits from the colonization of the soil under the stones: (a) protection from predators; (b) smooth temperature variations compared to areas with open soil; (c) higher soil moisture under the stones which allows for faster digging here. However, these benefits apply only to the topsoil adjacent to rocks (Dean & Turner 1991). Dean & Turner (1991) found that the temperature fluctuates less under stones than in exposed soil. The reason for ant settlement in the soil under the stones, according to these authors, may be not only the optimum temperature, but also that the stones provide shelter for the nest foundress queens.

The shape of the stone also matters. In our work, we found an effect of the stone diameter, whereas height was not important. Other authors have already noted that ants prefer to settle under flat stones, which are better illuminated by the sun (Brian 1977; Pontin 2005). Species of ants preferentially colonize areas with stones, compared with areas devoid of stones (*Leptothorax acervorum*, *Formica fusca*; see Brian 1956). Some data indicate a positive relationship between the total number of ants and the stone coverage of an area (Catarineu et al. 2018). Most temperate ant species in the Northern Hemisphere can build nests under stones (Kadochová & Frouz 2013). Thus, we can conclude that the presence of stones is extremely important for ants, since it enables them to develop broods more quickly. This was shown in our work: the brood of ants nesting under hot stones appeared earlier compared to ants nesting under cold stones.

The presence of vegetation around the nest can also affect the temperature regime of the nest. The more vegetation, on a dry weight basis, the lower the nest temperature (Véle & Holuša 2008). Most of the nests investigated in our study were under stones located in areas with sparse patches of grass or completely devoid of it. However, in arid conditions, ants can nest under stones around which dense grass grows (Espadaler 2007). Also, cutting down trees can increase the temperature of *Formica aquilonia* Yarrow, 1955 nest mounds, causing them to overheat (Sorvari & Hakkarainen 2005).

Ants nesting under stones

The very presence of stones or rock outcrops may be favorable for summer nests of ants such as *Formica truncorum* Fabricius, 1804 (Elias et al. 2004). This may be due to the fact that in rocky areas, where the soil layer is thinner, the outflow of heat into the soil is difficult, so the heating of the soil, as well as the anthill, is faster. Stones, especially in northern regions, may be an important factor in accelerating brood development in ant species without active thermoregulation. Therefore, many ant species nest under them, such as *Camponotus ligniperda* in Finland (Collingwood 1961) or *Formica sanguinea* Latreille, 1798 in Scotland (Hughes 2006). Under one stone, several ant species can settle independently of each other, such as *Pachycondyla harpax* (Fabricius, 1804) and *Camponotus fumidus* Roger, 1863 (Wheeler 1901).

The features of nesting of ants under solarium stones are considered most fully in the work of Zakharov (1999). One nest of *Formica sanguinea* on the south side of the mound had 6 tanning stones connected to the central nest by tunnels. As the sun moved, the ants moved their brood under the currently lit stone. A well developed system of solarium stones was also found in the large colony of *Manica rubida* (Latreille, 1802). Ants of this species used the solarium for 5-7 hours on a sunny day (Zakharov 1999). A similar situation, with a long stay of the brood under a stone, is possible in our case, although we did not observe such a developed solarium network, with the exception of stones 18-20, under which one *Formica cinerea* colony lived. Apparently, the number of solariums indicated by Zakharov (1999) is not the limit, and in large colonies of *F. cinerea* their number can be dozens.

Development cycles of ants

Ants of different species may have different temperature optimums for brood development. Thus, for *Myrmica punctiventris* Roger, 1863 it is 16-21 °C (Banschbach et al.

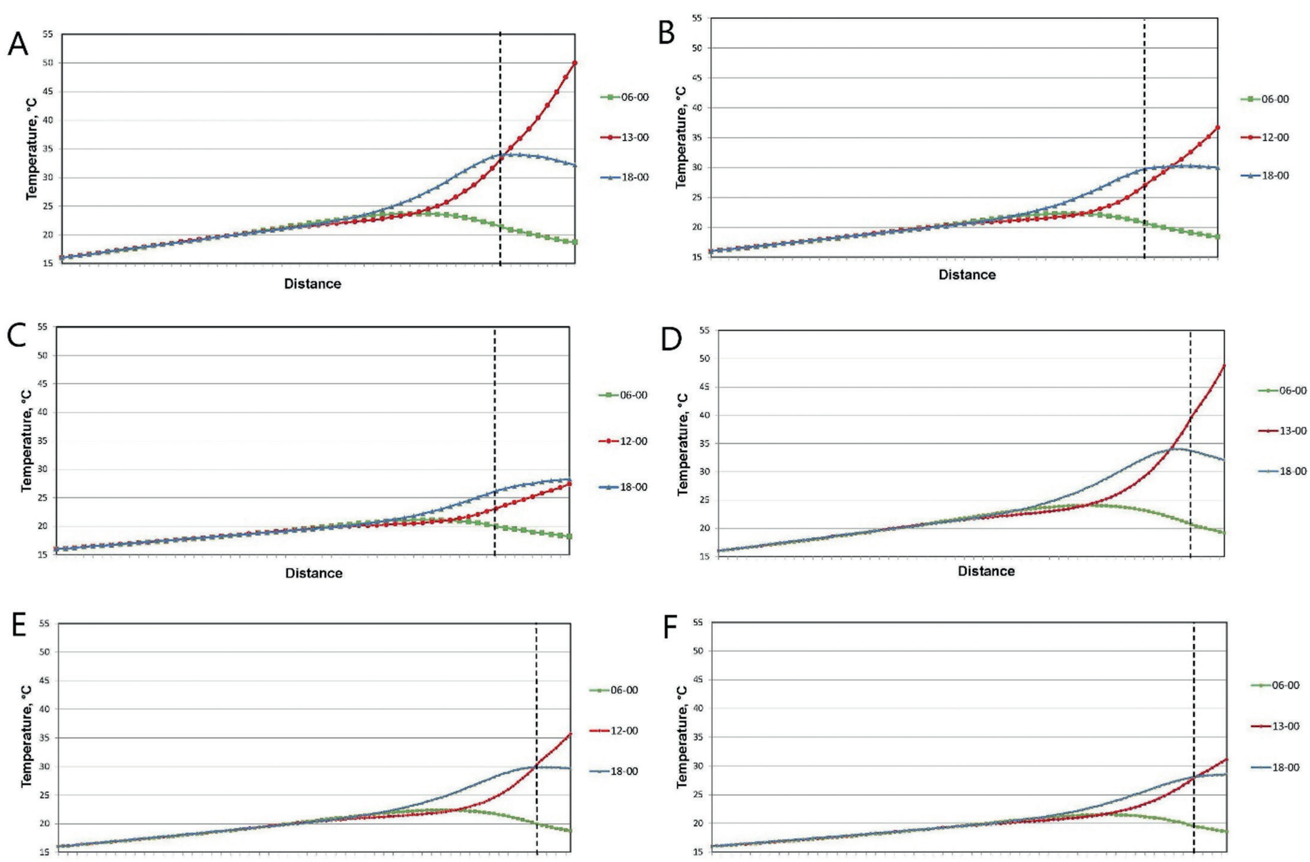

Fig. 9 – Temperature distribution along the height of a thick stone and in the soil under the stone (**A**, open space; **B**, penumbra; **C**, shadow) and for a thin stone (**D**, open space; **E**, penumbra; **F**, shadow).

Table 5 – Values of calculated temperatures for stones of different massiveness for different location conditions on the hottest day of July.

Location of the stone	Stone type					
	Thick			Thin		
	Sun	Penumbra	Shadow	Sun	Penumbra	Shadow
maximum stone top temperature	50	39	30	49	37	32
maximum temperature under the stone	35	30	26	39	32	28
temperature under the stone at 00-00 at night	25	24	23	24	23	23
temperature under the stone 06-00 am	22	21	20	21	20	20

1997), while *Formica cinerea* can develop at temperatures in the range of 20-28 °C. At the same time, workers that developed from pupae at a temperature of 28 °C foraged more often, but for a shorter time compared to workers developed at 20 °C (Ślipiński et al. 2021). In our case, most of the *Formica cinerea* pupae had already completed their development under the stones at the end of June, so high temperatures (over 30 °C) did not affect them. Apparently, the same is typical for *Myrmica rubra* and *Lasius niger*, but these species nest in less illuminated areas than *Formica cinerea* (Radchenko 2016; Czechowski 2002). Because of this, the stones under which these two species nested did not heat up so much, although the development of these species took place at a later time compared to *Formica cinerea*. High temperatures under stones only persist during the heat of the day, and the ants are able to regulate the temperature of the brood by moving it up under stones or down into the ground, as shown for *Camponotus mus* Roger, 1863 (Roces & Nunez 1995).

Developmental cycles of ants were studied in detail by Kipyatkov (2001). For *Formica* ants (including *Formica cinerea*), he singled out a peculiar development cycle, characterized by wintering of workers with queens, but without brood. *Myrmica* ants, on the contrary, overwinter with larvae, from which pupae emerge in late May-early June; by mid-July, the number of pupae decreases. The second generation of larvae occurs in the second half of July, and they pupate until mid-August. This agrees with our data, except for the cases when larvae or pupae were not observed in the second half of July, as they were moved from under the stones deep into the nest. A generation of alates emerges from the spring larvae of *Formica cinerea*; workers develop until August-early September. This time coincided with the discovery of a second peak of pupae under the stones. The same was observed for *Lasius niger*. Thus, in the three species of ants nesting under stones studied in our research, at least one generation of winged and one generation of workers emerge per season. The temperature optimum for oviposition is within 23-28 °C; pupae can withstand high temperatures (up to 29-30 °C), since in two out of three species (*Lasius niger* and *Formica cinerea*) they are protected by a cocoon. We have found that solarium stones in sunlit places accelerate the development of ants by at least one to two weeks. Therefore, these species of ants do not have to build complex nests, like the red wood ants; their needs are fully met by stones that can increase the temperature of the soil under them by 2-6 °C compared to the adjacent areas.

Conclusions

It has been established that the number of workers under hot stones increases two to three weeks earlier in spring than under cold and warm ones. The maximum number of workers was observed in May-June under hot stones. The minimum number of ants was observed iIn July, under cold, warm and hot stones. Larvae were found under hot stones two weeks earlier than under other categories of stones. On the contrary, in August the number of pupae under cold and warm stones was greater than under hot ones.

The number of larvae and pupae were influenced by stone diameter, whereas its height was not important; in other words, ants preferred to settle under large flat stones, which easily heat up in spring and warm the soil under them.

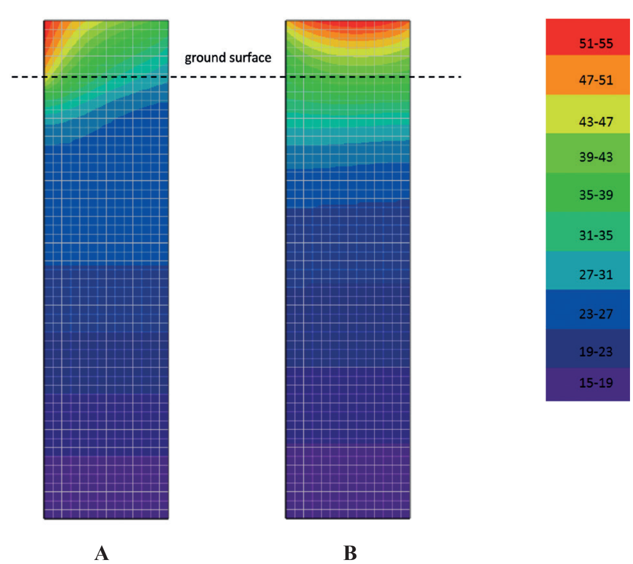

Fig. 10 – Two-dimensional temperature field of the "thick stone-soil" system for open space: **A**, time **10-00**; **B**, time 14-00: Temperature scale in °C. The heights of rectangles are: the height above the sole (for the part above the dashed line) and the depth below the soil (for the part below the dashed line).

Another important characteristic is the location of the stones. The highest rate of development was found in nests under stones in open areas that are well illuminated by the sun during the day.

In summer, when the soil dries up and heats up, ants migrate from nest chambers under the stones to deeper parts of the soil layer. Thus, stones may be an important factor accelerating the development of brood in colonies of ant species that do not have active thermoregulation.

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