SUNNING CLUSTERS OF ANTS CONTRIBUTE SIGNIFICANTLY, BUT WEAKLY TO SPRING HEATING IN THE NESTS OF THE RED WOOD ANTS, *FORMICA POLYCTENA*

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ABSTRACT

Red wood ants perform sun-basking behavior in the spring. This very conspicuous behaviour consists from densely packed bodies of ants, forming sunning clusters, which expose themselves to sun radiation. This led to rapid increase in ant body temperature. The expectation was that the ants so heated that return to the nest may bring heat from outside, which heats the nest. Although this was postulated a long time ago, the effect of sun-basking behaviour on nest heating has not been tested. Filling this gap is the subject of this study. To do this the presence of sunning clusters on 10 *Formica polyctena* nests was recorded using camera-traps, which recorded presence of sunning clusters on the nest surface daily from March 10 to June 3, 2016 in the south of the Czech Republic. Camera traps also recorded external air temperature. At the same time, internal nest temperatures were measured by thermometers located inside the nests, which continually recorded nest temperature over the same period. Comparison of consecutive days without and with sunning clusters of ants revealed an increase in internal nest temperature occurred when clustering was recorded. This, however, was only recorded for nests in which the temperature did not go above 20 °C. Frequency of daily occurrence of sunning clusters (proportion of days on which clusters were observed) was significantly positively correlated with daily increase in the internal temperature of the nests. This holds even when the increase in the internal temperature of the nests is corrected for increase that occurs at the same external temperature, but in the absence of clustering. This statistical evidence clearly indicates that sun-basking contributes to the heating of nests in spring, but it is very low. This is supported by the fact that nests that differ substantially in the frequency of occurrence of sunning clusters do not differ significantly in internal nest temperature in spring.

Keywords: red wood ants; social behaviour; sun-basking behaviour; sunning clusters; thermoregulation

Introduction

Red wood ants, *Formica rufa* group, are important keystone species in boreal and temperate forests in Eurasia, where they are important predators and ecosystem engineers (Hölldobler and Wilson 1990). Their importance is associated with their building large nest mounds from soil, needles and other organic material, which serve both as a shelter for adults and an incubator for the brood (Wilson 1971; Jones and Oldroyd 2006). One nest can contain up to a million workers and last for decades (Dlusskij 1967; Hölldobler and Wilson 1990; Stockan and Robinson 2016). The structure of their nests, together with various behavioural adaptations, enable wood ants to maintain a stable temperature in their nests above 20 °C during spring and summer, which enables faster development of their brood and a continuous production of sexual offspring and workers (Kneitz 1964; Rosengren et al. 1987; Frouz 2000; Jones and Oldroyd 2006), which contribute to their ecological success. The temperature regulation in the nest starts by a great increase in temperature in March and April and a high temperature is maintained until September when thermoregulation stops, even though workers continue to forage and are active. This is most likely related to the reproduction period of queens (Kipyatkov and Shenderova 1990; Kadochová and Frouz 2014a).

Thermoregulation in red wood ants is a complex process. The structure of the nest provides excellent insulation and is a collector of solar energy (Brandt 1980; Frouz 1996; Frouz 2000; Kasimova et al. 2014). However, during the period of active thermoregulation inner heat sources are crucial. There are three internal heat sources: 1) heat generated by microbial activity of material inside the nest (Coenen-Staβ et al. 1980), 2) metabolic heat produced by the ants (Kneitz 1964; Martin 1980; Horstmann and Schmid 1986; Rosengren et al. 1987; Kadochová and Frouz 2014a) and 3) heat transported by ants in their bodies (Zahn 1958). The latter mechanism is based on the absorption of solar radiation by ants when they are outside the nest. When they return to the nest, this heat is dissipated as they cool down and as a consequence the inner temperature of the nest increases. This may occur during the whole year and be greatly enhanced by the heat transfer of sunning clusters.

Sun basking or formation of dense thick clusters of ants on the surface of nests is frequently reported (Zahn 1958; Rosengren et al. 1987; Frouz 2000) in spring, when an increase in nest temperature occurs. Exposure to solar radiation is widely used by both solitary and social insects to increase their body temperature (Heinrich 1995; Challet et al. 2005). However, sun basking in red wood ants is reported to make the increase in body temperature much more efficient (Kadochová et al. 2017). This is likely to be due to the fact that clustering results in a mass that is much greater than that of single ant and hence a much lower surface to volume ratio, which results in much smaller thermal loses for clusters than individual ants and faster warming of ants in clusters. Zahn (1958) postulated that formation of sunning clusters is a means of transporting heat. However, although this was widely accepted (Rosengren et al. 1987; Frouz 2000; Kadochová

Chanas, P., Frouz, J.: Sunning clusters of ants contribute significantly, but weakly to spring heating in the nests of the red wood ant, *Formica polyctena*
European Journal of Environmental Sciences, Vol. 15, No. 1, pp. 28–33
https://doi.org/10.14712/23361964.2025.4

and Frouz 2014b; Kadochová et al. 2019), to the best of our knowledge, it has never been tested.

The aim of this study is to determine the relationship between occurrence of sunning clusters and increase in red wood ant's nest temperature in spring. The following three hypotheses were tested: 1) During days when the presence of sunning clusters is recorded the internal temperature of the nests increases more than when no clusters were recorded and the daily increase in the internal temperature will be higher on days when clusters occur more frequently. 2) The efficiency of sunning clusters for heating nests will be highest in spring. In early spring the efficiency of clusters may be limited by the fact that not all the ants are active and the number of workers that can participate in clustering is limited, whereas later, when spring internal heat production has started, relative importance of clustering will be less. Finally, 3) it is also expected that forming clusters more often will heat up nests faster during summer. In addition to testing these hypotheses the relative contribution of sunning clusters to spring temperature increase will be estimated.

Materials and Methods

Study site

This study was carried out in the southern part of the Czech Republic at Batkovy near Tabor (724 m a. s. l.) in a forest dominated by Norway spruce (*Picea abies*). Ten nests of *Formica polyctena* were selected that were about 1 m^3 in size and located at the edge of the forest or up to 20 m from the edge. This site was chosen as several previous studies on ant thermoregulation were done here (Frouz 2000; Frouz and Finer 2007).

Data collection

To record the occurrence of clusters of ant workers on the surfaces of nests during spring, 10 infrared digital scouting cameras (UV565 HD) were mounted on trees at a height of about 2 m and each focused on a nest. The cameras took pictures every day from 7:00 a.m. to 8:00 p.m. at 20-minute intervals (40 photographs per day) from 10th March to June 3, 2016. At the same time, cameras recorded external temperature. To record internal nest temperature one digital thermometer attached to a data logger (Testo 174T, Germany) was placed in each nest. Thermometer sensors were placed in the middle of each nest 20 cm below the surface of the mound (near the heat core: Coenen-Staβ et al. 1980; Frouz 2000; Frouz and Finer 2007; Kadochová and Frouz 2014b; Kadochová et al. 2019) in the middle of November 2015 in order to avoid disturbing the structures of the nests at the beginning of the spring when ant activity begins to increase. Temperature was measured every hour. The occurrence of clusters was evaluated manually from camera photographs. For analysis of the incidences of two categories: cluster present and cluster absent were recorded. For sunning cluster to be classified as present, ants have to be densely packed, forming a continuous mass of ants in a way that the surfaces of the nests were not visible and the clusters were at least 100 cm^2, which is about the size of human hand, which is similar to the size of clusters described by other authors.

Data processing

The main parameter evaluated was daily changes in the internal temperature of nests, which was calculated for each nest and date of observation as the difference in the internal temperature measured at 8:00 p.m. minus temperature measured at 7:00 a.m. on the same day.

Because daily changes in the internal temperature can be affected by the external temperature in addition to presence of clusters, a linear regression between external temperature and daily changes in nest temperature, using all 589 daily observations when no clusters were recorded. This linear regression was used to calculate expected daily temperature changes for each day of observation when only influenced by the external temperature. Daily changes in the internal temperature corrected for the effect of external temperature were calculated based on temperature changes minus those predicted for average external temperature on a given day based on the external temperature recorded near each nest.

The difference in internal nest temperature was correlated with daily frequency of the occurrence of sunning clusters, which was based on the number of records of when sunning clusters were present on a given day, divided by total number of observations made daily on each nest (here 40).

To evaluate the effect of sunning clusters on nest temperature during whole period of observation, the average frequency of daily sunning clusters was calculated for each nest and the average calculated for all the days they were recorded. Likewise, average internal temperature was calculated as average of all temperatures recorded in each nest during whole observation period. All data processing and handling was done using MS Excel.

Results

Comparison of the results for consecutive days with and without occurrence of sunning clusters reveals that temperatures were higher on days when cluster were recorded and increases during the day, that is, between 7:00 a.m. and 8:00 p.m. (Fig. 1A, B). This, however, was not the case for nests in summer when the temperature in the nests exceeded 20 °C (Fig. 1C).

The correlation between frequency of cluster occurrence and daily temperature changes (i.e., difference between temperatures at 8:00 p.m. and 7:00 a.m.) (Fig. 2A) over the whole period of observation reveals that the daily internal temperature increased significantly with increasing occurrence of sunning clusters. This holds for

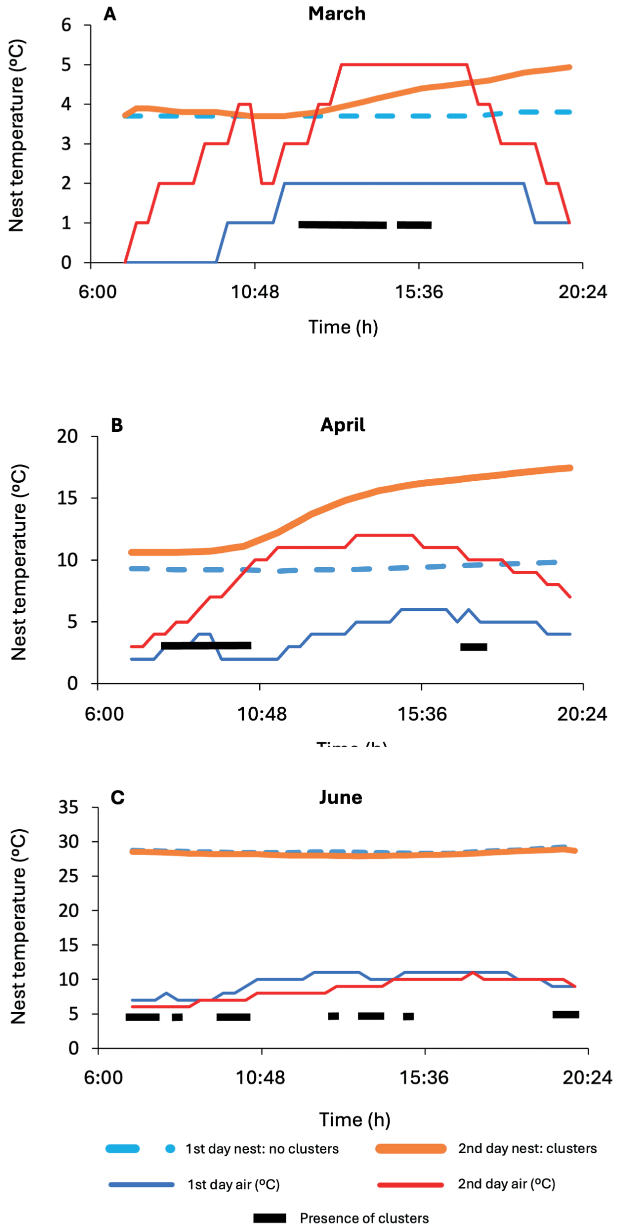

Fig. 1 Comparison of the changes in nest temperature that occurred on two consecutive days in which on the first day there were no sunning clusters and on the second day there were. Horizontal bars indicate presence of clusters on the second day. Line represents air temperature on 1st and 2nd day, which in A) was March, B) April and C) June, respectively.

the whole observation period as well as for observations done on nests with internal nest temperatures below 10 °C and between 10 °C and 20 °C. However, for nests with a temperature over 20 °C there was no significant relationship between occurrence of sunning clusters and daily changes in the internal temperature of nests. Comparison of the daily changes in the internal temperature of nests without and with sunning clusters revealed that temperature increased more in nests without sunning clusters (t-test, $p = 0.0103$).

However, as depicted in Figs 1A and 1B, days on which sunning clusters were recorded may be warmer than on days when they were not recorded. Thus, the recorded temperature increase may not be due to presence of sunning clusters, but that sunning clusters indicate warmer days. To compensate for this the daily increase in the internal temperature of nests was expressed as the average external temperature for all days when sunning clusters were not recorded. This relationship, as expected, indicates that weather conditions affect the increase in nest temperature. To correct for this effect, expected daily temperature changes based on external temperature was calculated and subtracted from the recorded daily changes in temperature These changes in temperature were then correlated with the frequency of occurrence of sunning clusters as above. This also indicates that an increasing frequency in sunning clusters is also associated with a significantly higher daily increase in the internal temperature of nests, based on data recorded over the whole observation period (Fig. 3A). When evaluated separately for data for nests with various internal temperatures, this relationship was significant only for nests with internal temperatures between 10–20 °C. For temperatures below 10 °C this relationship was positive but only marginally significant (Fig. 3B). As above, no effect of sunning clusters on daily temperature changes was recorded for nests with temperatures over 20 °C. In contrast, for the results that were not corrected for the effect of the external temperature there were no statistically significant difference in the temperature in nests on days with and without sunning clusters (Fig. 3D). In both cases the highest effect of sunning clusters (based on the slope of regression) was for nests with an internal temperature between 10 °C and 20 °C (Fig. 2C, Fig. 3C). This also corresponds with the records depicted in Fig. 1.

The effect of sunning clusters on changes in the internal temperature of nests, despite being significant, was very weak. Based on the R^2 values in Figs 2A–C and Figs 3A–C sunning clusters account for less than 10% of the variability in daily changes in temperature (whether corrected for the effect of external temperature or not). The slope of the regression in Fig. 2 and Fig. 4 also indicate that if sunning clusters were present throughout a day the increase in nest temperature would be at most 5 °C. This is quite a lot for one day and the example in Fig. 1B indicates that this may occur on some days, but sunning clusters are not present every day and usually not for a whole day. As the average daily frequencies of sunning clusters for the whole observation period vary for individual nests between 0.02 to 0.1 (Fig. 4), the average effect on daily temperature increase would be less than 0.5 °C. Therefore, it is not surprising that there were no significant differences in the average internal temperatures of nests studied, despite the several fold difference in occurrence of sunning clusters on different nests (Fig. 4).

Discussion

As cited above, many authors who have studied sunning clusters in red wood ants (Zahn 1958; Rosengren et al. 1987; Frouz 2000; Kadochová and Frouz 2014b;

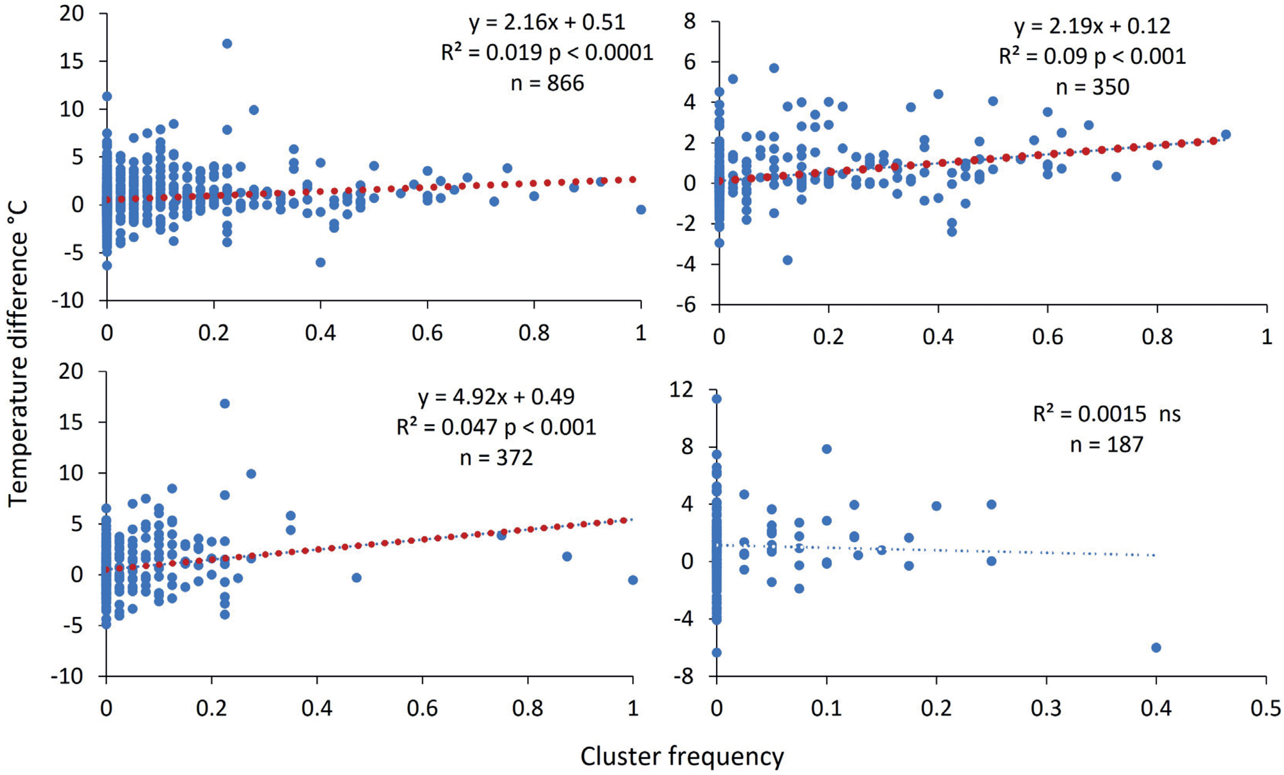

Fig. 2 Relationships between daily differences in internal nest temperature and daily frequency of cluster occurrence A) for all the data, B) for internal nest temperature below 10 °C, C) for internal nest temperature between 10 °C and 20 °C, and D) for internal nest temperature above 20 °C. Text on figures is the equation of the linear regression R^2 and p value and number of observations. Regression line and equation were omitted if correlation was not significant.

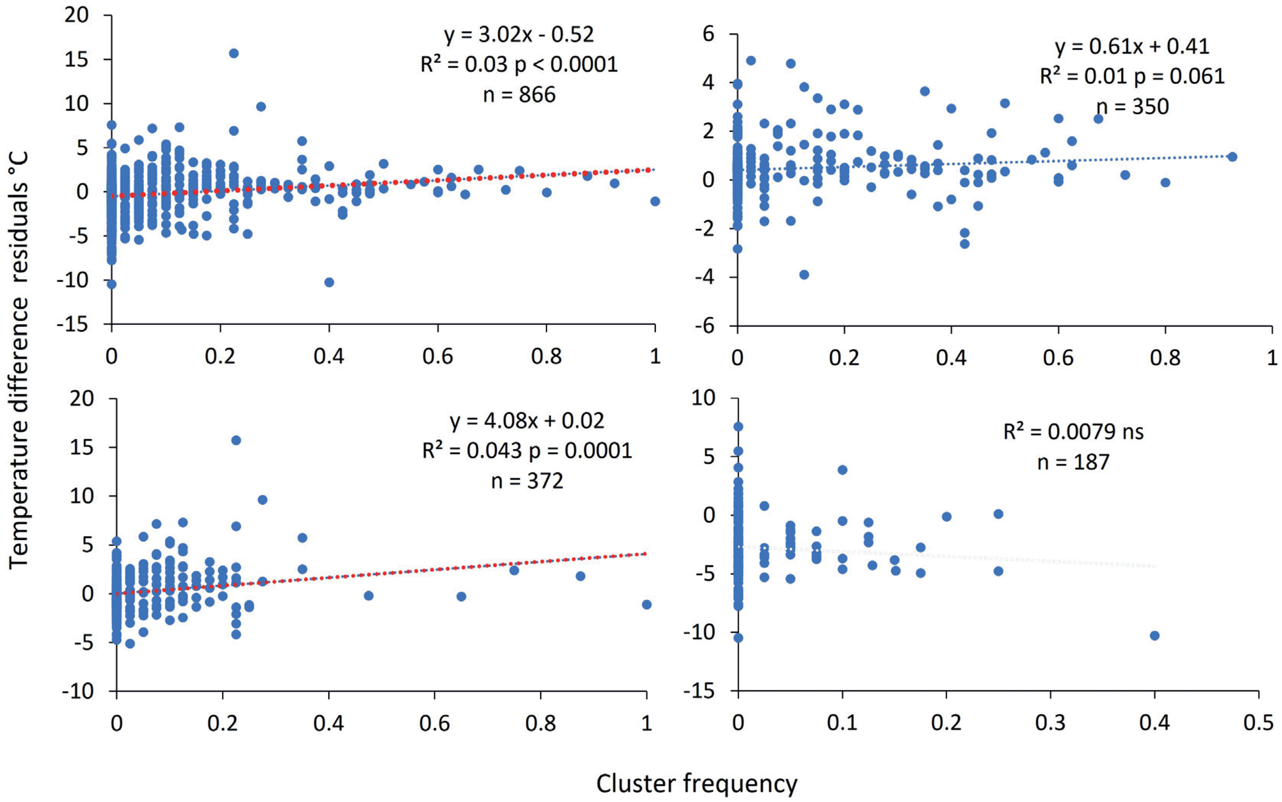

Fig. 3 Relationship between daily differences in internal nest temperature corrected for predicted daily temperature difference, when clusters were not present at the same temperature and daily frequency of cluster occurrence A) for all available data, B) for internal nest temperatures below 10 °C, C) for internal nest temperatures between 10 °C and 20 °C, and D) for internal nest temperatures above 20 °C. Text on figures is the equations of linear regression R^2 and p value and number of observations. Regression line and equation were omitted if correlation was not significant. Red line is used for correlations that are significant at $p < 0.1$.

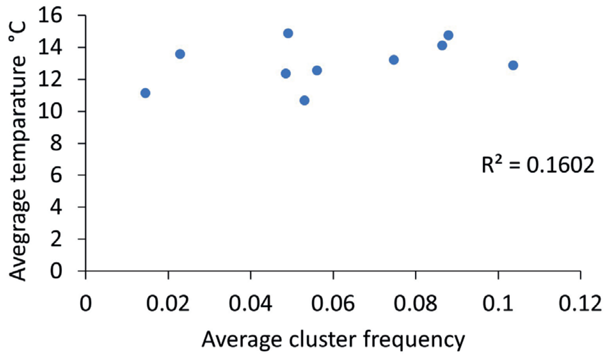

Fig. 4 Relationship between the average temperature of nests over the whole observation period in spring 2016 and average cluster frequency recorded for the same nests. R^2 value indicates non-significant relationship.

Kadochová et al. 2019) suggest that this behaviour helps to transfer heat accumulated in bodies of workers into the nest and in so doing increases the temperature inside nests. The current study revealed that increase in frequency of sunning clusters results in an increase in the internal temperature of nests over course of a day even if corrected for the effect of external temperature (Fig. 3). To the best of our knowledge, this is first quantitative support for the assumption that sunning clusters helps in the heating of nests in spring.

In accordance with hypothesis 2 proposed above, the effect of sunning clusters on the internal temperatures of nests is highest early in spring, when nest temperature is between 10 °C and 20 °C (Fig. 2 and Fig. 3). The expectation was that in early spring, when temperatures in nests are low, the transfer of heat may be limited by the fact that not all the workers are active and most are in hibernation. In addition, solar declination changes during the course of a year (Rueda et al. 2024), which affects solar irradiation that is lower in early spring than in late spring or summer. More detailed measurements, however, would be needed of the heat capacity of clusters and solar radiation to test these assumptions. In contrast, when nest temperature is over 20 °C, internal nest temperature is maintained by the heat produced by ants and decomposition of nest material (Martin 1980; Frouz 1996, 2000; Jílková and Frouz 2014) and the role of sun basking is limited.

However, despite the effect of sunning clusters in increasing the internal temperatures of nests it is relatively weak compared to other factors. That is, contrary to the proposed hypothesis 3, there was no significant relationship between average frequency of sunning clusters and nest temperature over the whole period of observation. This is rather surprising considering the fact that ants in the clusters can become very warm (Kadochová et al. 2019) with the heat capacity of ant bodies two orders of magnitude higher than that of nest material (Frouz 1996). There may be several reasons for this, one factor could be the frequency of clusters is relatively low, with averages over the whole spring of up to 0.1, which means clusters were recorded in 10% of the observations. Relationship between cluster frequency and daily temperature increase indicates that when clusters occur throughout a day the temperature may increase by up to 5 °C. But when clusters are only recorded in 10% of the observations, the daily increase in temperature is only about 0.4 °C. Another important factor is the low thermal conductivity of nest material (Frouz 1996), which means that when ants return to a nest, they may form a hotspot, which may not be recorded as an increase in temperature in the centre of a nest, which has been reported in similar systems (Albdour et al. 2022).

This, however, also may indirectly be the result of higher body temperatures of the ants in nests as ant respiration increases with temperature (Kadochová et al. 2017), which may result in an increase in worker's respiration, which is an important source of heat for maintaining the internal temperature of nests (Frouz 1996, 2000; Jílková and Frouz 2014). In this way sunning clusters may contribute to an increase in the internal temperature of nests in spring by a process that was not considered in the current study. This is indirectly supported by the record that the highest effect of sunning clusters on the temperature in nests occurred when the temperature was between 10 °C and 20 °C and the nest material was already slightly warm and the ants inside the nest remain warm for longer and their respiration may then also contribute to nest heating.

Production of hotspots within nests may also have other positive effects in being attractive to queens, which may start laying eggs (Kipyatkov and Shenderova 1990), which may result in an earlier first generation of offspring (Porter 1988; Roces and Núñez 1989). Formation of these hotspots may also terminate diapause in workers and result in earlier onset of activity in the colonies. The results complement those of other studies that indicate that nest temperature is influenced by many factors that vary throughout a year (Coenen-Staß et al. 1980; Rosengren et al. 1987; Frouz 1996; Frouz and Finer 2007; Kadochová and Frouz 2014b; Kadochová et al. 2019).

Conclusions

This study shows that sunning clusters formed by red wood ants contribute to the spring increase in the internal temperature of their nests. The direct effect of sunning clusters on temperature increase is, however, relatively small. It is likely that sunning clusters contribute to the start in ant colony activity in spring by other indirect mechanisms. These results complement those of other studies indicating that nest temperature is influenced by many factors and varies throughout a year.

Acknowledgements

This work was supported by the Ministry of Education, Youth, and Sports of the Czech Republic – MEYS (project nos. LM2015075, EF16_013/0001782), and Div-Land project provided by Czech technological agency. We would like to thank J. Kukla and V. Jílková for their help with the installation of cameras. Thanks also go to J. Hanzelka for his help with the preparation of raw data from data loggers.

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