

Phenology and causation of nest heating and thermoregulation in red wood ants of the *Formica rufa* group studied in coniferous forest habitats in southern Finland

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The inner nest temperature in field colonies of ants of the *F. rufa* group was studied with thermograph recordings and spot sampling. The observations indicate that in colonies with a worker complement exceeding 1 million, nest-warming after winter could start as an autocatalytic process and hence may not require triggering by sunning behaviour. In the colony studied with the thermograph the intranest temperature remained at a stable level, near 30°C in late spring and summer, even when the outside temperature temporarily dropped below freezing point. A slight “overshoot” or increase in inner nest temperature, was evident, however, when the outside temperature dropped below the threshold for ant activity in spring. It was found that nests later producing sexuals maintain a significantly higher inner temperature in spring than nests later producing only worker broods. The nest-warming effect of insolation is considered more important in small or weak colonies, whereas endogenous nest heating, based on the metabolism of the ants and their clustering behaviour, is more compatible with the observations in the case of vigorous colonies. The recordings suggest that a capacity for social thermoregulation is a cause of thermal stability in red wood ant nests.

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1. Introduction

One reason for the success of social insects is their ability to maintain climatic conditions favourable for brood development within their nests (Wilson 1971). In a cold climate, this ability may include mechanisms for warming the nest and maintaining thermal homeostasis. Social thermoregulation is renowned in the case of honeybees (Seeley & Heinrich 1981, Seeley 1985). It may be less known that red wood ants of the *Formica rufa* group possess an impressive ability to maintain a high temperature within their large mound nests (Steiner 1924, Raignier 1948, Heimann 1963, Kneitz 1964, 1969, 1970). The results of early studies, especially the detailed investigation of Kneitz (1964), suggested that metabolic heat production has a significant role, but this does not seem to have gained general acceptance. A recent review by Seeley & Heinrich (1981) places the main emphasis on the red wood ant mound

as a solar collector, mentioning the “Wärmeträgertheorie” of Zahn (1958), and threats the part played by metabolic heat production as rather uncertain. Brandt (1980a, b), who studied the thermal diffusivity of the building material of red wood ants, came to the conclusion that “there is no need to introduce ants with a physiological heat production”. Coenen-Stass et al. (1980), on the other hand, considered microbial activities in the nest material to be the main source of heat production and assumed that the start of heat production in spring is connected with the building activity of ants collecting fresh plant material after the winter. One source of these discrepancies may be that the thermal behaviour of red wood ant nests has hitherto been studied in Central European lowland habitats, characterized by fairly high ambient temperatures. We here present results obtained with Fennoscandian red wood ants, in the hope that the colder climate of that region may bring the so far blurred picture into focus.

2. Material and methods

2.1. Ant species

Our main material is a common Finnish *Formica rufa* species hitherto classified as *Formica polyctena* Förster (Rosengren 1977a, b, Rosengren et al. 1979), but distinct from Central European material of that species with respect to the micropuncturing of the queen gaster (Rosengren 1977a, Collingwood 1979). This species or subspecies was recently described under the preliminary name *Formica "grankullensis"* (Collingwood & Agosti 1986), tentatively included in the *Formica aquilonia* complex, although not showing the taxonomic worker characters for *Formica aquilonia* Yarrow. Previous reports of *F. polyctena* Förster from southern Finland (e.g. Hölldobler 1960) or adjacent areas of the Baltic probably refer to *F. grankullensis* (Collingwood personal communication). In addition we studied nests of *F. aquilonia* occurring in the same area and habitat type but not in the same forest patches as *F. grankullensis*. Both *F. aquilonia* and *F. grankullensis* live in regularly shaped, often large, polygynous mound nests, which are frequently agglomerated into polydomous "supercolonies" (Rosengren & Pamilo 1983).

2.2. Study areas and habitats

The mound nests studied occurred in a coniferous forest dominated by pine and spruce. The main study area for *F. grankullensis* was situated in Sunnanvik in Sjundeå rural district, about 30 km west of Helsinki, but smaller nest groups of the species were studied in Grankulla and Esbo (Karabacka and Kilo) about 10 km west of central Helsinki. Our study nests of *F. aquilonia* were located in a spruce-forested 9-ha area containing about 150 nest mounds of the species and situated in Träskända (Esbo), about 15 km west of central Helsinki. The habitats belonged to the *Myrtillus* or *Oxalis-Myrtillus* types (classification in Rosengren et al. 1979) and thus moderately rich rather than poor forest.

2.3. Sampling procedures

The temperature within the mound nests was measured with several 40–60 cm long mercury thermometers or with an electric thermometer (technoterm® 5500), the bimetal sensor of which constituted the terminal point of a 120 cm long, thin stiff plastic tube. We were chiefly interested in measuring the temperature within the movable thermal centre of each nest, rather than the temperature at a fixed depth in the nests. The thermometers were consequently used for two purposes:

- 1) searching for the thermal "heart" of the nest and
- 2) measuring the temperature of that part.

The thermoelectric device was superior, especially in searching and sampling large mounds, and we used the mercury thermometers mainly for smaller nests. The sampling data given here (Table 2) do not include the depth at which the warmest point was found because the depth varies with the size and shape of the nest, and thus is not a useful parameter in population studies summarizing information from several nests. We tried to sample the nest temperatures at a low air

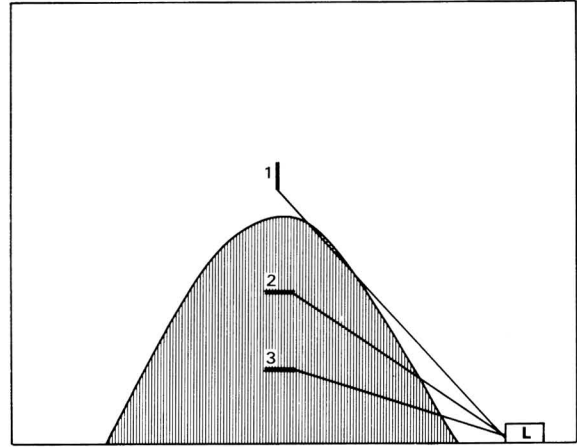


Fig. 1. Nest M with the location of the 3 "sensors" (1–3) connected to the thermograph (L). Sensor 1 was situated in the air 10 cm above the apex of the mound, sensor 2 in the mound 30 cm below the apex and sensor 3 60 cm below the apex. Before winter, sensor 1 was transferred to the earth nest below the mound, where the ants overwintered, but after the spring melt it was put back in its original position.

temperature under overcast skies but in some cases the latter condition was not fulfilled. In these cases the within-nest temperatures are corrected by subtracting the subsequently measured surface temperature (Table 2).

2.4. The main observation nest

The nest temperature of one particular nest (nest M) of *F. grankullensis* was continuously recorded throughout the 5-year-period 1975–1979 with a Lamprecht® ("Fern") thermograph equipped with 3 mercury "sensors" (Fig. 1). The sensor situated above the surface of the mound was moved to the earth nest before winter (and back again in early spring).

Nest M (94 cm high and 750 cm in circumference) is identical with "mound B", described previously with respect to habitat characteristics and foraging area (Rosengren 1977a, b). It is possible to give a crude estimate of the size of the worker population inhabiting nest M although the forager traffic was too intensive to be counted during the peak of the season. The method used was as follows. As described previously (Rosengren 1977a), the forager population of a rather small nest in the vicinity was estimated in mid August 1975 by a Lincoln index procedure combining capture-mark-recapture and traffic counts. The nest contained 93 000 foragers (Rosengren 1977a). In late autumn of the same year traffic counts were carried out on the same day at both the mound nests (overcast sky, virtually even temperature around 10° C during the hours of counting).

The number of foragers leaving nest M (per time unit) was 10.5 times the number departing from the small nest. Extrapolating this to the number of foragers gives nearly 1 million foragers in nest M during summer. According to Horstmann (1982), the forager population constitutes 43 % of the total

worker population in *F. polyctena*. This would give a total of about 2.3 million workers in nest M. The size of the worker population of nest I (Table 1) was estimated in 1981 with the Lincoln index method for traffic counts. The estimate gave about 400 000 foragers, which corresponds to a total worker population of nearly 1 million (Rosengren et al. 1985). The observations of early heating in that nest (Table 1) were, however, made in spring 1986 at a time when the size of the forager population had grown to a point which precluded traffic counts during most conditions suggesting that the population size at that time must have been still larger. A crude approximation of worker densities per litre nest material (based on estimates of population size combined with knowledge of the nest size) indicated an average density of 2000–2500 workers/litre. The worker population is, however, not evenly distributed within the nests and worker densities within the centre of the nest mounds are likely to be higher.

3. Results

3.1. Monthly average of intranest temperature

Fig. 2 gives the pooled, monthly average temperatures for the 5-year recording period in nest M (Fig. 1). Throughout the period April–November, the within-nest averages are marked higher than the monthly averages for the ambient temperature. The thermal centre of the nest is situated deeper in early spring and autumn than in late spring-summer (Fig. 2). It can be seen from the original recording sheets (unpubl.) that the winter temperature within the mound nest changed slowly with the ambient temperature, but that a stable level of 1–2°C was maintained in the hibernation chambers of the earth nest.

3.2. The start of nest warming in spring

The temperature of the earth nest was still below +3°C when the temperature in the still snowcovered mound nest 60 cm from the apex suddenly began to rise on the night of 7.4.–8.4.1977 (Fig. 3). A similar, though less dramatic, jump in mound temperature was evident in other years and has recently been ob-

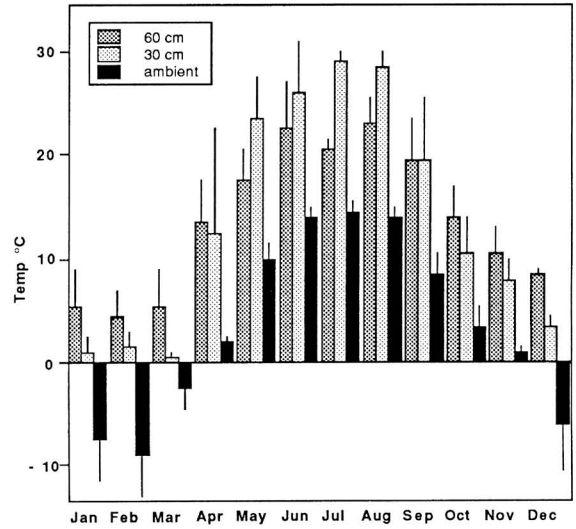


Fig. 2. Monthly averages of within-nest temperatures (data taken from thermograph recordings at 6-hour intervals) based on pooled data for the 5-year period 1975–1979. Standard deviations for within-nest temperatures (30 cm and 60 cm) are based on the total number of readings (every 6th hour over the different years for each month). The ambient temperatures are based on data from Vichtis meteorological station. In this case standard deviations are given for the monthly means ($n = 5$).

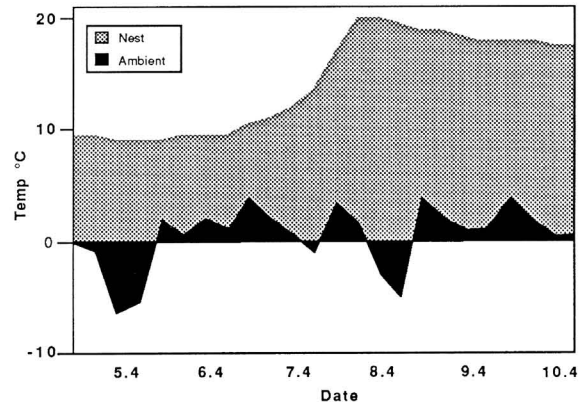


Fig. 3. Inner nest temperature at a depth of 60 cm (grey areas) and air temperature (black area) above the top of the nest (sensor 1 in Fig. 1) during the period 5.4.–10.4. 1978, based on thermograph recordings.

Table 1. Inner nest temperature in 16 *F. grankullensis* mounds in the same area (Sunnanvik, Sjundeå) at the end of March 1986 before the springmelt. Individual readings from the warmest point found are given for nests I and II (the “hot spots” situated about 40 cm from the surface in both cases). Means and standard deviations are given for the other 14 mound nests, which gave no indication of within-nest heating at this time of the year (range of warmest points: -0.6°C to +2.5°C).

| Nest | Date | % Snow cover | Snow layer (cm) | Ice layer (cm) | Ambient temp. °C | Nest temp. °C |
|------|---------|--------------|-----------------|----------------|------------------|---------------|
| I | 28.3-86 | 100 | 5–15 | 10 | +0.5 | +24.6 |
| II | 28.3-86 | 100 | 20–25 | 8 | +0.3 | +27.0 |
| 1–14 | 28.3-86 | 25–100 | variable | variable | -0.1 ± 2.5 | +1.1 ± 0.9 |

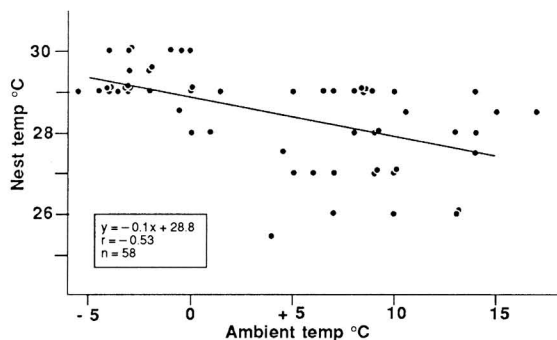


Fig. 4. The regression of inner nest temperature (sensor 2, Fig. 1) on outside air temperature (sensor 1, Fig. 1) for May 1978. Data points for internal and external temperatures for noon and midnight taken from the thermograph recordings. The negative correlation is statistically significant ($P < 0.001$).

served in recordings from *F. aquilonia* too (Fortelius unpublished). The temperature measured within some other *F. grankullensis* nests after the cold and snow-rich winter of 1986 confirmed that intranest heating may start when the surface layer of the nest is still hard frozen and completely covered by snow and the ants thus prevented even from brief visits on the surface (Table 1). The phenomenon, although occurring only in a minority of nests studied, need not be quite exceptional. When observing *F. grankullensis* nests throughout several spring periods, we have now and then encountered larvae or pupae of sexuals, or even alatae, in partly snow-covered nests still completely surrounded by snow (Fortelius & Rosengren unpubl.). Those cases suggest that intranest warming may already have started in late winter, because the development from egg to pupa requires some weeks and cannot take place in a cold nest (Kneitz 1964).

3.3. Diel variations in intranest temperature

During summertime diel variations in intranest temperature were very weak in the case of nest M (one-week July recording from this nest published in Rosengren et al. 1979). More obvious diel fluctuations occurred in nest M in spring, but to our surprise these correlated negatively with the external temperature (Fig. 4). A long period of frost may decrease intranest temperature or at least shift the thermal centre to a deeper level within the nest (unpubl.), but short spells of frost may temporarily increase inner

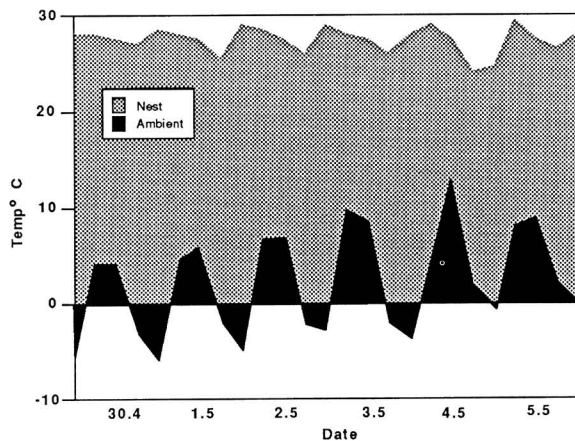


Fig. 5. The relation between diel variation in inner nest temperature (sensor 2, Fig. 1) and outside air temperature (sensor 1, Fig. 1) at the beginning of May 1978 according to thermograph recordings. It can be seen that a decrease in the external temperature regularly coincides with an increase in temperature within the mound.

nest temperature, while warm weather has the opposite effect (Fig. 5). Fig. 6, based on May recordings in nest M during one of the years, indicates that the ants may be able to maintain a high degree of thermal homeostasis which even may include compensation of air temperatures below 0°C . (note that $b = 1.1$)

3.4. Correlation between nest temperature and production of sexuals

Luther (1985) found that red wood ant nests producing sexuals had a higher mean temperature in spring than nests producing only a worker brood. Our present results confirm this for both *F. aquilonia* and *F. grankullensis* (Table 2). The difference was observable before any brood was present in the mound nest and thus cannot be explained as a result of the actual presence of the brood. The data of Luther (1985) indicate furthermore that the thermal difference between nests producing sexuals and nests producing only workers persists after the alatae have disappeared from the nests and can actually be traced throughout the season, including the autumn period. *F. aquilonia* nests later producing only workers showed a significant positive correlation in spring between within-nest temperature and temperature measured at the surface of the nest ($r = 0.283$, $n = 81$, $P < 0.02$), thus suggesting that the degree of in-

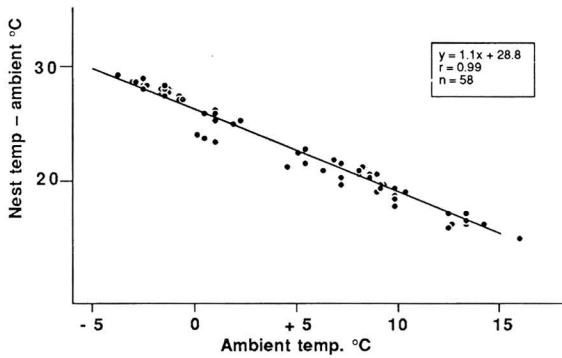


Fig. 6. Regression of inner nest temperature (30 cm) minus the corresponding external temperature (sensor 1, Fig. 1) on external temperature (sensor 1, Fig. 1). Data obtained from readings of thermograph recordings at noon and midnight during May 1978.

solation may contribute to the inner nest temperature, as commonly assumed (Seeley & Heinrich 1981). Nests later producing sexuals did not, however, exhibit, such a correlation ($r = -0.069$, $n = 38$, NS).

4. Discussion

4.1. Is intranest heating caused by insolation or metabolism?

The "Theory des Domes" of Forel (references in Seeley & Heinrich 1981) considers the nest mound as a solar collector. Another hypothesis stressing the importance of insolation is the "Wärmeträgertheorie" of Zahn (1958). Those theories presuppose that direct solar radiation is either absorbed in the physical mound structure or "carried" by ants moving from the nest surface to the inside. They are supported by the observation that red wood ants often select sunny forest openings as nesting sites and that the shape and orientation of the nest mound may reflect its presumed role as a solar collector. Alternative or complementary explanations are based either on the hypothesis that the ants may generate significant heat through their metabolism (Kneitz 1964, 1969, 1970) or on the hypothesis that microbial activity in the nest material could account for observed intranest temperatures (Coenen-Stass et al. 1980).

The results presented here are difficult to explain unless we attribute a significant role to metabolic heat

Table 2. Means and standard deviations of inner nest temperatures measured in mid-May in nests later producing sexuals and nests later producing only workers ("non-sexual" mounds). In *F. grankullensis* the comparison was carried out in two different areas inhabited by polydomous colonies (Gp = Kasaberg, Grankulla, Äp = Änkans skog, Sunnanvik, Sjundeå). The *F. aquilonia* material is from Träskända in Esbo. In the case of *F. grankullensis*, but not *F. aquilonia*, the temperature was measured under heavily overcast skies. The data for *F. aquilonia* were corrected by subtracting the surface temperature of each nest (about 10°C) from the inner temperature (warmest point). P = significance of t -test.

| Species and colony | Mound-type | Mean | SD | N | P |
|-------------------------|------------|-------|------|-----|--------|
| <i>F. aquilonia</i> | | | | | |
| TR | non-sex | 6.14 | 4.54 | 66 | |
| | sex | 13.38 | 5.78 | 33 | <0.001 |
| <i>F. grankullensis</i> | | | | | |
| Gp | non-sex | 14.88 | 6.31 | 10 | |
| | sex | 22.67 | 6.66 | 15 | <0.01 |
| Äp | non-sex | 17.27 | 5.25 | 13 | |
| | sex | 21.60 | 3.62 | 15 | <0.02 |

production by red wood ant workers, although we do not wish to deny a complementary role of other mechanisms. Our arguments in favour of endogenous or metabolic heat can be summarized as follows:

1. Horstmann (1983), reporting nest temperatures very close to those observed by us, remarked that the temperature difference between the inside of nests and the ground is about 10°C. Maintenance of this difference through the night could perhaps be explained by insolation combined with excellent heat storage capacity of the nest material, as suggested by Seeley & Heinrich (1981). The nest observed by us in southern Finland, however, had a temperature of 25–30°C in late April when the ground temperature was still close to or below 0°C (the ground of forest habitats even when free from snow, regularly contains ice at this time of the year) and the air temperature frequently dropped below freezing point in the night (Fig. 5). It does not appear possible to attribute persistence of a temperature difference of 25°C and even more (see also Fig. 6) to physical heat storage in the nest material.

2. The insolation hypothesis does not explain why the inner nest temperature may increase with decreasing external temperature (Fig. 5). These phenomena are easily explained, however, by assuming that ant workers producing metabolic heat, cluster to-

gether in the centre of the nest when the ambient temperature drops below a given threshold.

3. It has been shown that the red wood ant species *F. truncorum* Fabr., a xerothermic builder of irregular nest mounds on open cliffs, relies much more strongly on insolation for warming its nests than *F. rufa* L., which builds regular domes of the type discussed here (Rosengren et al. 1985). We find it likely that the relative importance of insolation for nest warming may also vary within a species, depending, for example on the age, volume and population size of the nests (see also Kneitz 1964) or on the type of habitat. The small mound nests of *F. grankullensis* and *F. aquilonia* found in very dry habitats, such as sparsely pine clad rocks, appear to have poor thermoregulation and may rely more on insolation for nest warming than mound nests of the same species found in richer forests (unpubl.). Even in these cases, however, nests totally lacking endogenous heating, like those observed by Brandt (1980a), appear to be rare. It is easy to observe that even *F. aquilonia*, a species also frequent in closed stands of spruce, selects sunny patches as nesting sites whenever possible (Luther 1985). Although preferred as nesting sites, if the ants have the choice, sunny openings do not seem to be obligatory in the case of nests with a worker population exceeding 1 million (estimates above). The largest and most populous red wood ant nest ever observed by the senior author was situated in a stand of *Prunus padus* surrounded by tall spruce trees, the nest and its vicinity being completely shielded from direct insolation, and less extreme cases of the same phenomenon are not uncommon in our study area. Strongly shaded nests, although sometimes awakening from hibernation rather late, and producing male biased broods, may maintain a high temperature, between 28 and 30°C (Rosengren, unpubl. point measurements). Such cases are not compatible with explanations based on insolation alone.

4.2. The microbial hypothesis

Some of the observations mentioned above are not necessarily explainable only by assuming heat produced in the bodies of the ants. The nest material could, through the activity of microbes, generate considerable amounts of heat (Coenen-Stass et al. 1980), a hypothesis implicating that the ants use the needles and twigs collected by them as "fire-wood".

Coenen-Stass et al. claims that intranest temperatures reach a high level in spring because the ants collect fresh material and reorganize nest architecture after the winter, thus creating favourable conditions for heat-generating, aerobic microorganisms. Our observation that intranest heating may start before the snow melts seems, however, to disprove the above hypothesis because the ants are during those conditions unable to collect new material and the sudden jump in heat production (Fig. 3) cannot coincide with a major reorganization of nest architecture improving ventilation. It is even more difficult to explain the negative correlation between outside temperature and inside temperature (Fig. 5) as a microbial effect. Why should the microorganisms increase their metabolism when the outer temperature drops below freezing point? And why should their activity result in the maintenance of a fixed target temperature buffered against external fluctuations over a long timespan (Fig. 6)? The result that nests producing sexuals maintain a higher temperature than nests producing only workers (Table 2) is also very difficult to understand if microbial activity is assumed to be the main source of heat production, but becomes intelligible if production of sexuals and production of heat are both assumed to depend on the amount of chemical energy stored in the fat-bodies of overwintering workers (Kneitz 1964, Schmidt 1974, Martin 1980b).

We do not question the calorimetric data of Coenen-Stass et al. (1980), but wish to point out that the nest studied by those authors was exceptional if compared with those generally occurring in our habitats. The authors report a maximum worker density of 575 ants/litre in the centre of their study nest. Corresponding samples taken from our study nests of both *F. grankullensis* and *F. aquilonia* had several times higher worker densities (data in methods and Luther 1985). The conclusion of Coenen-Stass et al. (1980) that the metabolic activity of the ants is a negligible heat source compared with the microbes could thus be true for their study nest, but misleading in the cases studied by us. Horstmann (1983), while accepting the basic claims of Coenen-Stass et al., reached a very similar conclusion with regard to *F. polyctena* nests from southern Germany.

4.3. Triggering of intranest heating in early spring

The "sunning" behaviour of red wood ants in which dense clusters of workers (sometimes includ-

ing also queens) appear to sun-bathe on the exposed nest surface in early spring is considered an almost ubiquitous feature of ants of this species group. It has been suggested that a phase of sunning not only precedes intranest heating but that sunning by activating the lipid reserves of young workers could function as a physiological trigger causally connected to intranest heating (Kneitz 1964, Martin 1980b). Marked sunning behaviour is common also in the red wood ant habitats studied by us but appears characteristic of poor nests containing ground frost for a long time after the end of hibernation (unpubl.). We have, however, never observed any evidence of sunning in some repeatedly observed vigorous nests characterized by a high worker density. It has in some cases been observed by us that workers may cluster on the nest surface under a thin layer of melting and therefore transparent snow, a phenomenon interpretable as a kind of hothouse effect. This could implicate that sunning may easily escape detection. The cases of early nest heating listed in Table 1 can not, however, have been preceded by "sunning under the snow" because the nest surfaces were not only covered with snow, but frozen to a depth of about 10 cm. The ice layer must have prevented all visits of ants to the surface, since it had to be penetrated with a sharp tool before the thermometers were inserted. The layer of ice may have enhanced accumulation of heat within the nest by reducing heat loss to the environment but this "igloo" effect must also have prevented transfer of heat from the environment to the nest. This is further evidence that theories based on insolation, although not completely wrong, may be insufficient to explain nest warming in red wood ants.

Both sunning and migration of workers from the earth nest to the mound nest within still snow-covered nests is explainable by thermotaxis, in which workers move along a gradient from lower to higher temperatures (Kneitz 1964). Sunning on the heated nest surface could well function as a metabolic trigger activating the metabolism of the ants after the dormancy period (Martin 1980b). Our present observations (see also the sudden jump in intranest temperature recorded in Fig. 3) indicate that this physiological activation, known to depend on heat rather than light (Schmidt 1969) can take place within the nest and thus resembles an autocatalytic process. The threshold for this "spontaneous combustion" may be determined both by the number of workers and by the amount of chemically stored energy in their fat bodies.

4.4. Thermal nest homeostasis – social regulation or humidity effect?

The diel oscillations illustrated in Fig. 5 could be interpreted as overshoot in an underdamped control mechanism based on negative feed back (Mc Farland 1971). It would, following this analogy, be tempting to consider the oscillations as representing one mechanism by which a thermoregulative social system maintains a given degree of homeostasis. This is, however, only one interpretation and Raignier (1948), observing that the temperature in red wood ant nests increases on cold nights, actually suggested a quite different mechanism for his finding.

Raignier (1948) postulated that a layer of mist, due to condensation of water vapour above the mound, could hinder heat loss and thus increase temperature inside the nest, but we find it unlikely that this is the only cause or even the main cause of the phenomenon. Red wood ant foragers may spend the night outside during summer, but in spring they usually return to the nest if the ambient temperature drops below a threshold of about 5–7°C (Rosengren 1977a). During this season, it is thus obvious that the population disperses at high temperatures and gathers at low temperatures and the beginning of the rise in nest temperature coincides rather well with a fall of the ambient temperature below the activity threshold (Fig. 5). Such strong aggregation of the population cannot be observed in summer-autumn (aphid tenders, in particular, may stay with their aphids even during brief spells of frost). This, in contrast to Raignier's hypothesis, fits the observation that the negative correlation between inner and outer temperature is much less obvious in summer-autumn. It is furthermore evident in Fig. 5 that the rise in inner nest temperature, if not delayed by high day-temperature (e.g. on 4.5 in Fig. 5), started long before evening. During the light period, the air close to the ground is likely to be in a state of turbulence which makes it unlikely that the isolating humidity shield postulated by Raignier (1948) can be sufficiently stable during the day. When opening a large number of nests in search of sexual pupae in spring, we gained the impression that the worker population aggregates more strongly in the central part of the nest (and at nest openings) during cold than during warm days. Clustering behaviour is known to regulate hive temperature in honey bees (Seeley 1985) and according to recent results it also appears to be important in red wood ant thermoregulation (Horstmann & Schmid 1986). We therefore find it fairly parsimonious to as-

sume that the diel fluctuations observable in intranest temperature (Fig. 5) are connected with temperature-dependent variations in worker density and clustering behaviour in the central part of the nest.

4.5. Nest temperature and colony fitness

An ant colony cannot contribute to the gene pool of the population by producing sterile workers. Production of workers is thus only the means by which a colony improves its ability to produce sexual progeny. Young workers storing lipids in their fat-bodies through winter transform those reserves into glandular nutrients that can be used for raising the sexual brood in early spring (Kneitz 1964, Schmidt 1974). The present observations (above) confirm that raising of the sexual brood to maturity does not require any external input of food brought to the nest from the habitat by foragers of the same season. It has furthermore been suggested that metabolic heating of red wood ant nests in spring may rely on utilization of the lipid reserves present in the store animals (Martin

1980b). The total amount of energy present in the fat bodies of workers could thus be a common denominator both for the ability to maintain a high temperature within the nest and for the capacity to produce sexual progeny in spring. If these assumptions are true, we would expect a positive correlation between production of sexuals and high spring temperature within red wood ant nests, which would mean that colony fitness, as suggested by the data of table 2, could be measured with a thermometer.

There is strong circumstantial evidence that the sex-ratio in red wood ants may depend on the nutritive condition of the colony, but a correlation between sex-ratio and inner nest temperature has so far not been demonstrated (Rosengren & Pamilo 1986). The nests starting heat production exceptionally early in spring (Table 1), without a sunning period, have indeed produced a one-sex female brood in all the cases observed by us so far. But this does not constitute conclusive evidence, because most of the nests producing sexuals in the habitats studied here have female-biased sex ratios (Luther 1985, Rosengren & Pamilo 1986).

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