



REVIEW

**REVISED** Thermoregulation strategies in ants in comparison to other social insects, with a focus on red wood ants (*Formica rufa* group) [v2; ref status: indexed, <http://f1000r.es/35p>]

**Previously titled:** Thermoregulation strategies in ants in comparison to other social insects, with a focus on *Formica rufa*

Štěpánka Kadochová<sup>1</sup>, Jan Frouz<sup>2</sup>

<sup>1</sup>Department of Ecology, Charles University, Prague, CZ12800, Czech Republic

<sup>2</sup>Institute for Environmental Studies, Charles University, Prague, CZ12800, Czech Republic

**v2** First published: 19 Dec 2013, 2:280 (doi: [10.12688/f1000research.2-280.v1](https://doi.org/10.12688/f1000research.2-280.v1))  
 Latest published: 21 Mar 2014, 2:280 (doi: [10.12688/f1000research.2-280.v2](https://doi.org/10.12688/f1000research.2-280.v2))

**Abstract**

Temperature influences every aspect of ant biology, especially metabolic rate, growth and development. Maintenance of high inner nest temperature increases the rate of sexual brood development and thereby increases the colony fitness. Insect societies can achieve better thermoregulation than solitary insects due to the former's ability to build large and elaborated nests and display complex behaviour. In ants and termites the upper part of the nest, the mound, often works as a solar collector and can also have an efficient ventilation system. Two thermoregulatory strategies could be applied. Firstly the ants use an increased thermal gradient available in the mound for brood relocation. Nurse workers move the brood according to the thermal gradients to ensure the ideal conditions for development. A precise perception of temperature and evolution of temperature preferences are needed to make the correct choices. A second thermoregulatory strategy used by mound nesting ants is keeping a high temperature inside large nests. The unique thermal and insulation properties of the nest material help to maintain stable conditions, which is the case of the Wood ant genus *Formica*. Ants can regulate thermal loss by moving nest aggregation and alternating nest ventilation. Metabolic heat produced by ant workers or associated micro organisms is an important additional source of heat which helps to maintain thermal homeostasis in the nest.

**Open Peer Review**

Referee Status:

	Invited Referees		
	1	2	3
<b>version 2</b> published 21 Mar 2014			 report
<b>version 1</b> published 19 Dec 2013	 report	 report	 report

- 1 **Jouni Sorvari**, University of Eastern Finland Finland
- 2 **Haitao Wu**, Chinese Academy of Sciences China
- 3 **Clint Penick**, North Carolina State University USA

**Discuss this article**

Comments (0)

**Corresponding author:** Štěpánka Kadochová ([stepanka.kadochova@natur.cuni.cz](mailto:stepanka.kadochova@natur.cuni.cz))

**How to cite this article:** Kadochová Š and Frouz J. **Thermoregulation strategies in ants in comparison to other social insects, with a focus on red wood ants ( *Formica rufa* group) [v2; ref status: indexed, <http://f1000r.es/35p>] *F1000Research* 2014, 2:280 (doi: [10.12688/f1000research.2-280.v2](https://doi.org/10.12688/f1000research.2-280.v2))**

**Copyright:** © 2014 Kadochová Š and Frouz J. This is an open access article distributed under the terms of the [Creative Commons Attribution Licence](#), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited. Data associated with the article are available under the terms of the [Creative Commons Zero "No rights reserved" data waiver](#) (CC0 1.0 Public domain dedication).

**Grant information:** The author(s) declared that no grants were involved in supporting this work.

**Competing interests:** No competing interests were disclosed.

**First published:** 19 Dec 2013, 2:280 (doi: [10.12688/f1000research.2-280.v1](https://doi.org/10.12688/f1000research.2-280.v1))

**First indexed:** 03 Mar 2014, 2:280 (doi: [10.12688/f1000research.2-280.v1](https://doi.org/10.12688/f1000research.2-280.v1))

**REVISED Amendments from Version 1**

In this second version of our review paper we have incorporated comments and changes suggested by referees. Those changes include a change of title suggested by Dr. Sovary, which now better captures the range of ants described in the paper.

Other changes include broadening of the introduction to include the main idea that two thermoregulatory strategies can be found in mound building ants, more detailed description of nest moisture changes during natural forest succession (gradual increase of shading and change from dry thermoregulation strategy in young nests to wet nest strategy in big mature colonies), and the addition of information regarding exchange of respiratory gases in the paragraph about *Atta* nest ventilation systems.

We also shortened and rewrote some of the paragraphs about thermoregulation in *Formica rufa* group as suggested by the referees to make the main message of the review more clear. There have been minor changes (namely formatting) in the reference list and one reference was replaced.

In Table 1 a thermoregulatory strategy column was added to divide the species into "brood movers" and "stable temperature nest". Also the description of the thermoregulatory characteristics in the *Formica rufa* group was improved.

The authors thank the referees for their review and comments to our paper. Most of suggested changes have been included in the latest version of the paper. For more details and explanation of the changes included and omitted please see the referees' comments and authors' replies.

**See referee reports**

## Introduction

Temperature is an important factor for all ectothermic organisms, including ants. Their rate of development is accelerated with high temperatures<sup>1</sup>, the movement rate speeds up<sup>2</sup> and the rate of food and oxygen consumption also increases<sup>3</sup>. Higher temperatures can be advantageous for colony fitness as it can increase reproduction rate though at the same time can be disadvantageous due to higher energy expenditure<sup>4</sup>.

Most insect species have a solitary mode of life in adulthood; these individuals are able to regulate their body temperature through behavioural reactions such as sunning or seeking cool shelter<sup>5</sup>. More sophisticated forms of thermoregulation can be found among social insects. They are able not only of regulating their own body temperature but also the temperature of the immediate surroundings. This ability is due to the large number of individuals in the society, their behavioural interactions and nest construction<sup>6</sup>. The nest protects the whole colony and serves as a shelter for adults and, more importantly, as an incubator for the brood. Improved colony homeostasis could even be one of the reasons why insect sociality evolved<sup>5</sup>. Thermoregulation, however, requires the expenditure of energy and so comes with costs as well as benefits.

The level of nest thermoregulation depends on many other factors, e.g. nest size, population size, and the moisture and thermal conductivity of the nest material. Among mound building ants two

main thermoregulatory strategies can be distinguished: 1) moving the brood according to thermal gradients (natural or induced) and 2) keeping stable temperatures inside their nests. This paper's objective is to provide an overview of nest thermoregulation strategies occurring among ant societies, with a focus on thermoregulation in the red wood ants (*Formica rufa* group), in comparison to other social insects.

## Nest architecture and properties of nest material

Ants nest in wide range of materials; in soil, under stones, in leaf litter and even in living trees (see Table 1). Some of them build above-ground nests, usually from soil or organic material, called ant hills or mounds. These nests show an advanced ability in regulating inner temperature.

The red imported fire ant *Solenopsis invicta* and members of the genus *Pogonomyrmex* build soil mounds from excavated soil<sup>7,8</sup>. These nests gain heat through solar radiation and the brood is moved along an increased thermal gradient<sup>1,9</sup>. Weaver ants from the genus *Oecophylla* construct their nest from living leaves, with the help of their own larvae, which produce a special "glue" from their salivary glands<sup>10</sup>.

Red wood ants from the genus *Formica* build large nests from organic material that is based on a mixture of soil, twigs, coniferous needles and pebbles<sup>3,11-13</sup>. In these nests a stable heat core can be maintained thanks to the good insulation properties of these materials and the metabolic heat produced by the ants or their associated microflora<sup>14,15</sup>.

The composition of the organic material is not the same throughout the whole nest volume<sup>3,16</sup> and the mound structure is not rigid either. The ants loosen and renovate the nest structure and the organic material is continuously moved from the inside to the outer layers<sup>3</sup>. Nest structure and architecture plays a vital role in nest thermoregulation. The tunnels and passages build by ants are important mainly for ventilation and humidity control, which affect the nest temperature. Pieces of tree resin are often incorporated into the *Formica* nest material because of its antimicrobial effect<sup>17</sup>. The resin inhibits the growth of potentially pathogenic bacteria and fungi in the nest.

Thatch ants, *Formica obscuripes*<sup>18</sup> and *Acromyrmex heyeri*<sup>19</sup>, use plant fragments as a building material and arrange them in a thick compact surface layer called "thatch" which has a lower thermal diffusivity than the surrounding soil. The thatch prevents nest overheating by the incoming solar radiation and avoids losses of the accumulated heat into the cold air during night<sup>19</sup>.

Nest moisture can have two different and opposite thermoregulatory effects: 1) moisture can support microbial heat production (i.e. increase the temperature)<sup>3,15</sup>; 2) it can decrease the insulating properties of nest material (i.e. decrease the temperature)<sup>11</sup>. A study of the relationship between daily temperature regime and moisture in *Formica polyctena* nests revealed two possible thermoregulation strategies which differ between dry nests and wet nests<sup>15</sup>.

**Table 1. Examples of thermoregulation and nesting strategies in social insects.**

Thermoregulation characteristic	Thermoregulation strategy	Nest type	Taxa and species involved	References
Temperature is stable, same as the temperature of the soil	Brood translocation	Underground nests only	Ants: <i>Tetramorium tsushimae</i> , genus <i>Lasius</i> and <i>Myrmica</i> , <i>Pogonomyrmex</i> ; Termites: genus <i>Coptotermes</i>	Hölldobler & Wilson (1990) <sup>23,47</sup> , Sanada - Morimura & al. (2005) <sup>59</sup>
Temperature is not stable, nest follows microhabitat temperature - oscillations can be buffered by insulation properties of microhabitat, sometimes natural structures can be used as heat accumulators	Brood translocation	Nests in wood (logs or stumps), in leaf litter, and under stones	Ants: <i>Acromyrmex ambiguus</i> , <i>Camponotus mus</i> , <i>C. vicinus</i> , <i>Myrmica punctiventris</i> Roger, <i>Onychomyrmex hedleyi</i> , <i>Polyrhachis simplex</i> Termites: <i>Kalotermitidae</i> , <i>Hodotermitidae</i> , <i>Rhinotermitidae</i> , <i>Termopsidae</i>	Banschbach & al. (1997) <sup>32</sup> , Bollazzi & Roces (2007) <sup>30</sup> , Roces & Nunez (1989) <sup>39</sup> , Chen & al. (2002) <sup>56</sup> , Hölldobler & Wilson (1990) <sup>23,47</sup> , Miyata & al. (2003) <sup>58</sup> , Ofer (1970) <sup>57</sup>
Temperature oscillates, the thermal gradient could be greater than the ambient temperature because the mound surface serves as a solar collector	Brood translocation	Underground nest with aboveground crater or similar structure + above ground soil (soil and fecal pellets mixture) or thatch mound	Ants: <i>Acromyrmex heyeri</i> , genus <i>Lasius</i> , <i>Myrmica rubra</i> , <i>Pogonomyrmex occidentalis</i> , <i>Solenopsis invicta</i> , Termites: <i>Cephalotermes rectangularis</i> , <i>Microceretermes edantatus</i> , <i>Thoracotermes macrothorax</i>	Weir (1973) <sup>39</sup> , Bollazzi & Roces (2002) <sup>38</sup> , Cassil & al. (2002) <sup>69</sup> , Cole (1994) <sup>60</sup> , Hölldobler & Wilson (1990) <sup>23,47</sup> , Lüscher (1961) <sup>62</sup> , Nielsen (1972) <sup>57</sup>
Energy is accumulated by spatial structure - silk caps of pupal cells storing sun energy	Stable temperature	Paper nest	Hornet: <i>Vespa orientalis</i>	Ishay & Barenholz-Paniry (1995) <sup>64</sup>
Energy is accumulated by sun bathing ants and is transported into the nest	Stable temperature	Underground nest + above ground organic mounds	Wood ants: <i>Formica rufa</i> , <i>F. polyctena</i>	Coenen-Stass (1985) <sup>14</sup> , Frouz (2000) <sup>15</sup> , Zahn (1958) <sup>51</sup>
Nest is heated by the sun (temperature of peripheral layers oscillates) + inner core with more stable temperature, heated by metabolism of termites or ants	Stable temperature (?)	Aboveground nest in wood (living trees)	Termites: <i>Coptotermes acinaciformis</i> , <i>C. frenchi</i>	Greaves (1964) <sup>65</sup>
	Stable temperature (?)	Underground nest + aboveground soil mound	Termites: family <i>Termitidae</i> , <i>Macrotermes bellicosus</i> , <i>Amitermes merionalis</i> ; Ants genus <i>Atta</i> - <i>Atta texana</i> , <i>A. vollenweideri</i>	Kleineidam & al. (2001) <sup>27</sup> , Hölldobler & Wilson (1990) <sup>23,47</sup> , Korb & Linsenmair (1998, 2000) <sup>25,42</sup> , Grigg (1973) <sup>26</sup>
Nest is heated by sun (temperature of peripheral layers oscillates in small nests or stable in big ones) + inner core with stable temperature, heated by metabolism of ants + decay of organic material	Stable temperature	Underground nest + above ground organic mounds	Wood ants: genus <i>Formica</i> - <i>Formica aquilonia</i> , <i>F. rufa</i> , <i>F. polyctena</i>	Coenen-Stass (1985) <sup>14</sup> , Frouz (2000) <sup>15</sup> , Rosengren & al. (1987) <sup>46</sup> , Zahn (1958) <sup>51</sup>
Stable temperature inside the cluster is maintained by ant metabolism	Stable temperature	No stable nest - bivouacs	"Army ants" <i>Eciton burcheli</i> , <i>E. hamatum</i>	Franks (1989) <sup>48</sup> , Schneirla (1971) <sup>41</sup>
Active heating by members using contractions of muscles	Stable temperature	Wax or paper nest in air or various cavities	Honey bees, Stingless bees, Bumble bees, Wasps: <i>Apis mellifera</i> , <i>A. florea</i> , <i>A. dorsata</i> , <i>Bombus sp.</i> , <i>Trigona denoiti</i> , <i>Vespa simillima</i> , <i>V. xanthoptera</i> , <i>V. crabro</i>	Fletcher & Crewe (1981) <sup>61</sup> , Heinrich (1981) <sup>20</sup> , Ishay (1973) <sup>63</sup> , Martin (1988) <sup>50</sup> , Morse & Laigo (1969) <sup>66</sup> , O'Donnell & Foster (2001) <sup>68</sup>

Dry young nests are usually located in sunny open places<sup>12</sup>. Solar radiation heats up the nest and keeps the nest material dry, with low heat capacity and conductivity. The thermal losses of dry nests are estimated to be 0.15–4.3 W per nest<sup>15</sup>. The temperatures of dry nests are usually the highest in the evening and they drop during the night. Thermoregulation in dry nests is based on a combination of metabolic heating from the ants, the insulating properties of the nest and solar heating<sup>15</sup>.

During forest succession, ant nests become more shaded and gradually switch to a wet thermoregulation regime<sup>12</sup>. In the evening the temperature in these nests is low and it increases during the night. The high night temperature at the nest surface indicates substantial heat loss, about 24–30 W per nest. The wet nests have a high thermal capacity; increasing the temperature by 1°C requires a thermal input of 35 W<sup>15</sup>. This means that maintaining a sufficient temperature in a wet nest requires a heat source beyond the metabolic heat produced by ants and the heat obtained from solar radiation. The additional heat source in wet nests is provided by microbial activity<sup>3,15</sup>. Both of these two types of thermoregulation strategies are applied in natural populations, but in different stages of nest development. The microbial community in *F. polycetena* nests differs from that in the surrounding soil in part because of differences in pH and food availability and quality<sup>13</sup>. Thermoregulation via microbial heating was first proposed in 1915 by Wasmann<sup>3</sup>. In 1980 the existence of microbial heating in *F. polycetena* mounds was confirmed in an experiment showing that in the absence of ants non-sterilized nest material generated a substantial amount of heat but sterilized nest material generated almost no heat<sup>3</sup>.

Microbial activity can be estimated by calculating the respiration rate of the nest material, which is used as a proxy for the respiration rate of the microbes living in it<sup>3,15</sup>. There are detectable seasonal changes in the respiration rates of nest material with the highest rates found in summer. The mass-specific heat production of ants is higher than that of the nest material but, when considering the total mound volume, microbial heat production is more than seven times higher than the heat evolved by ants<sup>3</sup>. Ants can affect microbial activity via nest material aeration, supply of fresh plant material and their own metabolic heat production. Since the microbial activity of wet nest material depends strongly on temperature<sup>3</sup>, a temperature increase in some small parts of the nest (due to ant metabolism or sun radiation) results in an increase in microbial activity and consequently in a subsequent overall increase of nest temperature.

As first mentioned by Forel in the early 1920s the ant mound often serves as a solar collector<sup>20</sup>. Solar energy can both increase the metabolism of ants and help heat the nest mound<sup>21</sup>. Compared to underground nests, mounds absorb heat more quickly both in the direct sun and in the shade<sup>9</sup>. Ants in the Northern Hemisphere usually remove shading grass from the south side of the mound so that the temperature increases quickly on that side. This creates a temperature gradient that many species use for brood displacement<sup>9</sup>. Other species decorate the mound surface with small pebbles or dead vegetation, which can work as heat collectors or as radiation reflectors<sup>22</sup>.

Mounds of some *Formica*, *Solenopsis* and *Lasius* species are asymmetric, with the main axis oriented in a south-north direction<sup>23,24</sup>. In *S. invicta* the angle of the south slope of the mound is negatively correlated with the maximal sun angle<sup>22</sup>. Sun-influenced thermoregulation in termites has also been documented, for example in fungus-growing members of the genus *Macrotermes*<sup>25</sup>. The amount of intercepted sunlight influences the shape of termite mounds and leads to great structural differences in nests in forests vs. savannahs<sup>25</sup>. But the most admirable sun-induced nest shape differences can be seen in Australian “magnetic termites” *Amitermes meridionalis*<sup>26</sup>. The nests are wedge-shaped with apparent north-south orientation which prevents overheating at noon and enables maintaining the warmth of nest in the evening.

Effective ventilation takes place as part of nest thermoregulation in many ant species, being regulated by the opening and closing of nest entrances (see below). A ventilation system in nests of the leaf-cutting ant genus *Atta* was described by Kleineidam *et al.*<sup>27</sup>. There is not a thermal gradient big enough to generate thermal convection flow; rather the ventilation in *Attini* nests is driven by the wind. There are many openings on the nest surface, which are functionally divided into entry and exit tunnels. Wind flowing over the nest from any direction causes air to exit from the central tunnel and to enter tunnels at the nest periphery<sup>27</sup>. This ensures exchange of respiratory gasses and optimal thermal conditions for symbiotic fungi which are damaged by temperatures higher than 30°C<sup>28</sup>.

### Behavioural reactions of ant workers

Behavioural reactions of ants are based on sensing temperature and temperature preferences<sup>5</sup>. To react to these gradients, ants have evolved inherent temperature preferences, which are the key element in thermoregulatory behaviour<sup>4,29</sup>. Nurse workers are able to choose the optimal temperature for pupae production and sexual brood incubation and to move the brood along temperature and humidity gradients to achieve the best conditions for its development<sup>5,29,30</sup>.

The optimal temperature range is variable for different groups of social insects, for example the brood of the honey bee *Apis mellifera* develops fastest at 35°C<sup>31</sup>. In *Formica polycetena* a temperature 29°C is preferred for pupal development<sup>14</sup>, whilst colonies of *Solenopsis invicta* can grow only between 24 and 36°C<sup>1</sup>. In contrast the genus *Myrmica* is adapted to cold climates, *M. rubra*<sup>4</sup> and *M. punctiventris*<sup>32</sup> prefer temperatures between 19 and 21°C, about 8°C lower than the temperature preferred by other ants.

Temperature preferences can be affected by many factors including age and sex<sup>33</sup>, working caste or feeding condition<sup>1</sup>, or prior acclimation<sup>34</sup>. Ant queens in *Formica polycetena*<sup>35</sup> and *Solenopsis invicta*<sup>1</sup> prefer slightly higher temperatures than workers, especially during the egg-laying phase; inactive queens may prefer cooler temperatures. Workers generally prefer lower temperatures, which decrease their metabolic rate and increase their lifespan<sup>1,36</sup>. A decrease of 2°C can lengthen the worker lifespan in *S. invicta* by 14%<sup>37</sup>. Preferences of nurse workers tend to be shifted towards the higher temperatures that favour brood development<sup>1,4,21,29</sup>. Similar patterns have also been found in *Apis mellifera*<sup>5,31</sup>.



Most ant species rely on brood translocation along temperature gradients as the main thermoregulatory strategy<sup>6,9,23,29,30,38</sup>. The brood translocation usually has characteristic time rhythms, for example *Camponotus mus* follow a photoperiodic circadian rhythm. In the presence of a temperature gradient, nurse workers move the brood twice each day<sup>29</sup>. The first displacement starts at 2 pm, when the brood is transported from the colder night location to a warmer day location. This movement occurs 6 h after sunrise, i.e., in the middle of photophase. At 10 pm (8 h after the first displacement and 2 h after nightfall), the brood is transported back to the night location. Under artificial light/dark day cycles the brood translocation rhythm changes according to the new photophase length<sup>29</sup>. In *Solenopsis invicta* moving the brood up and down along temperature gradients does not seem to depend on the time of day or photoperiod<sup>49</sup>.

In response to temperature gradients, leaf-cutting ants from the genus *Acromyrmex* move not only the brood but also the symbiotic fungi which provide their food. The fungus requires high humidity and temperatures between 25 and 30°C<sup>28</sup>. *Acromyrmex ambiguus* workers move the fungus garden according to humidity conditions, but they are also capable of nest humidity regulation by changing nest architecture. The flow of dry air into the colony is a signal for workers to plug ventilation tunnels to prevent nest from drying out<sup>38</sup>. Similar behaviour has been proposed for termites<sup>39</sup>.

When the nest interior becomes too hot, workers can reduce the inner temperature in several ways. In ants and termites nest cooling is usually achieved by changes in building behaviour. Workers of leaf-cutting ants in the genera *Atta* and *Acromyrmex* open tunnels to allow air circulation<sup>27,30,38</sup>; this behaviour could be limited by a trade off for humidity control<sup>40</sup>. Ants of the genus *Formica* can also partly remove the nest material, which reduces the wall thickness and increases heat dissipation<sup>16</sup>. In the genus *Eciton*, loosening of bivouacs' structure (temporary nests similar to a honeybee swarm) is an effective way of cooling<sup>41</sup>.

Even more efficient ventilation systems providing both temperature regulation and respiratory gas exchange can be found in nests of the termite *Matorermes bellicose*. These nests can have either externally or internally driven ventilation, depending on the habitat, nest shape (cathedral vs. dome shaped nest) or the time of day<sup>42</sup>. Cathedral shaped nests in open habitats are warmed by the sun, which creates a steep thermal gradient leading to convection currents in peripheral air tunnels. Dome shaped nests located in the forest rely more on internally driven ventilation. The same is true for cathedral nests at night<sup>42</sup>.

In contrast, bees, wasps and bumblebees cool their nests by wing-fanning and regurgitating water droplets. Water is spread over the brood comb surface enabling cooling through evaporation<sup>5</sup>. Cooling by water evaporation is very effective. Lindauer<sup>43</sup> placed a bee hive onto a lava plain where the surface temperature reached 70°C. Taking water ad libitum, the bees were able to maintain the hive temperature at the favoured 35°C.

Some social insect species have evolved highly elaborated systems of thermoregulation that enable to keep stable temperatures inside their nests. Bees, bumblebees and wasps are capable of direct incubation of selected pupae. Specialized workers sit on the surface of the brood cell and maintain their thoracic temperature over 35°C. Bees sitting inside empty brood cells can heat six brood cells at one time<sup>44</sup>. Metabolic heat can also be used for protection, as shown in the interaction between the predatory hornet *Vespa mandarina japonica* and Japanese honeybees *Apis cerana japonica*<sup>45</sup>. If the hornet attacks a honeybee nest it is surrounded by bee workers who increase their body temperature to a level which is lethal for the hornet but not for the honeybees<sup>45</sup>.

Although ants cannot actively produce heat they are able to use indirect metabolic heat (i.e. heat produced as a by-product of metabolism) for ensuring brood development. This ability has so far been postulated for the *Formica rufa* group<sup>3,15,46</sup> and the army ant genus *Eciton*<sup>41,47,48</sup>.

The Neotropical army ants *Eciton hamatum* and *Eciton burchelli* form temporary swarms called bivouacs, which can regulate temperature very precisely to ensure optimal conditions for developing brood<sup>41</sup>. According to Franks<sup>48</sup> bivouacs have a similar construction to a bee swarm; they can be divided into an outer mantel and inner core, which together maintain a stable temperature between 27.5 and 29.5°C regardless of the ambient temperature. On cold days the bivouacs change shape: they become more hemispherical to reduce the surface to volume ratio<sup>48</sup>. Franks<sup>48</sup> postulates that all the heat required by the bivouac can be produced by ant metabolism.

Red wood ants of the Palearctic genus *Formica* (*Formica rufa* group) are supposed to use metabolic heat to maintain a heat core, an area with high and stable temperatures, in their nests. High temperatures are required for sexual brood development; nests producing sexual offspring always have higher temperatures than those producing only workers<sup>46</sup>. The heat core's position moves according to nest shape and size<sup>3,15</sup>. The temperature inside nests of red wood ants begins to increase very early in the spring, even when the nest surface is covered by ice and snow<sup>46</sup>. At this time some nests can contain larvae, pupae, and even some winged individuals, indicating that the inner heating must have started much earlier, because larval development cannot start in a cold nest and requires some weeks of constant warm temperature<sup>21</sup>. It is supposed that in large nests of *F. rufa* containing over 1 million workers, spring nest heating can start as an autocatalytic process<sup>46</sup> that relies on utilizing lipid reserves in young workers<sup>50</sup>.

Another factor contributing to quick spring increase of nest temperature in red wood ants is a temperature intake by ant bodies. The *Formica* ants are dark colored so they heat up quickly when exposed to the sun during their outside-nest activities. In the spring ants are observed to create clusters on the mound surface as they bask in the sun<sup>51</sup>. Their bodies contain a substantial amount of water which has high thermal capacity making ant bodies an ideal

medium for heat transfer. After getting hot enough the ants move inside the nest where the accumulated heat is released. This principle works throughout the year but in spring it is most obvious and supported by ant clustering on the nest surface<sup>15,46</sup>.

Daily temperature fluctuations in the red wood ants nest seem to be correlated with temperature-dependent changes in ant density and ant aggregations in the nest. The highest nest temperatures usually occur in the afternoon or in the evening which corresponds with the return of foragers<sup>15,46</sup>. This apparently results from the heat brought into the nest by returning workers (heat coming from absorbed solar energy) as well as the heat generated by worker metabolic heat production within the nest. In some nests the temperature drops slightly in the morning when ants leave the nest<sup>15,16</sup>. Heat coming from the metabolism of foragers clustered in the nest center on cool days, when ambient temperature limits outdoor activities, could also explain a negative correlation between the inner nest temperature and the ambient temperature found occasionally in spring<sup>46</sup>.

The seasonal fluctuations in the thermoregulation behaviour of *Formica polyctena* along a geographic gradient were studied by Frouz & Finer<sup>49</sup>. Both in Finland and the Czech Republic the ant colonies maintained a high nest temperature (over 20°C) in spring and summer, for about 65–129 days. A rapid increase in the inner nest temperature in early spring was observed, mostly at the beginning of April. Annual nest temperature peaked in June in both locations and decreased gradually from August to November. Nest temperatures fluctuated more in the Czech Republic than in Finland, possibly because of greater differences between day and night ambient temperatures<sup>49</sup>.

An interesting question is why *F. polyctena* maintain stable nest temperatures for the same period in Finland and the Czech Republic even though the length of the vegetation season and the ambient temperatures in Finland and Czech Republic are different. This might be explained by the reproduction cycle of the queen. Regular shifts between reproduction and diapause has been documented in *F. polyctena* queens. The queen enters diapause after 100 days of reproduction even at a constant temperature and photoperiod<sup>35,52</sup>. It was postulated that ants maintain high temperatures only during the queen's reproduction phase<sup>49</sup>. After that the nest temperature drops, despite the fact that the outside temperature usually does not limit foraging and the ants are still active.

#### Use of metabolic heat for nest thermoregulation in ants

Maintenance of a high inner nest temperature has been observed in ants, especially in species which build above-ground nests or inhabit tree hollows<sup>15,46,53</sup>. Heating of these structures is much easier than heating underground nests, because the surrounding soil has a large heat capacity and conductivity.

In moderate climates most ants build nests in the soil where the temperature is quite stable (Table 1) or on the soil surface under a layer of leaf litter where the temperature can be buffered by the insulating properties of the nest material. Many species in the Northern Hemisphere also nest under rocks or stones which serve as heat

collectors (Table 1). In the tropics only a few species nest in soil and the majority of species inhabit small pieces of rotting wood<sup>5</sup>. More precise microclimate regulation is achieved in the mound-building species of the genera *Atta*, *Acromyrmex*, *Myrmicaria*, *Pogonomyrmex*, *Solenopsis*, *Iridomyrmex*, *Formica*, and *Lasius* (Table 1).

The maintenance of a stable temperature in red wood ant genus *Formica* nests during spring and summer is widely known and has been the subject of many studies<sup>12,16,46,49,53</sup>. These ants are able to maintain thermal homeostasis in the nest because of the insulation and heat storage provided by the nest material<sup>15,20</sup>. Mound size is generally correlated with the number of inhabitants<sup>54,55</sup>. In small nests located in sunny areas the solar radiation and the insulation properties of the nest material are thought to be the key elements in nest thermoregulation<sup>11,12</sup>. In larger nests there are internal sources of heat production, such as ant and microbial metabolic heat, that enable the maintenance of high inner temperatures even in a permanently cold environment<sup>46,49</sup>.

Many other ant species (see Table 1) build hill-shaped nests from soil. These nests show large spatiotemporal variations in temperature and ants select the optimal temperature for brood development by brood displacement<sup>1</sup>. These nests, however, do not have a stable heat core. The heat core where the temperature is stable and higher than ambient temperature for an extended period of time (several months) can be found only in a minority of ant species. Why is this the case?

The heat core exists in the nests/hives of winged insects that are capable of active heating, i.e. bees, wasps, bumblebees (thermogenesis in flying muscles), and some ants, especially the genus *Formica*<sup>3,15,46</sup>, the army ant genus *Eciton*<sup>41,47,48</sup> and probably in fungus-growing termites<sup>42</sup>. But there is no evidence of a stable heat core in *Solenopsis invicta* or in *Acromyrmex heyeri*, which also build upper-ground hills from materials with suitable insulation properties such as soil or dead vegetation. As discussed earlier, thermoregulation can also be the result of nest architecture, and only those species that build nests with a low thermal heat capacity and a low thermal conductivity are likely to maintain a heat core. In summary, the use of metabolic heat production for maintenance of a heat core depends on the insulation properties of the nest and the size of the individual workers and of the entire colony.

The latest review about nest thermoregulation in social insects<sup>6</sup> distinguished three types of ant thermoregulation strategies: "First, like many social bees, some ant species rely on protection from a cavity, such as a tree stump or underground burrows<sup>56</sup>. Second some migrate their nest frequently, varying the amount of cover they select, depending on the temperature and season<sup>57,58</sup>. Third some others move their brood to areas of optimal temperature within the same nest"<sup>29</sup>. We suggest dividing the last category in the following way: a) ants that move the brood in daily cycles to places with optimal temperatures within the whole nest structure, for example *Solenopsis invicta*<sup>9</sup> or *Camponotus mus*<sup>29</sup> b) ants that keep a stable heat core inside their nest and do not move the brood from the nest interior, including the ants from *Formica rufa* group<sup>3,15</sup>.

## Conclusion

Despite a wide variety of thermoregulatory strategies observed among ant societies some general trends can be found. Two opposite thermoregulatory strategies in mound building ants could be distinguished. Firstly nests with low insulative properties which work as solar collectors and thus increase the available thermal gradient for brood development. Secondly nests which steadily maintain higher inner temperature thanks to low thermal conductivity of the nest material, good insulative properties and metabolic heat produced by ants or associated micro organisms. An example of this strategy is seen in the *Formica rufa* ant group.

## Author contributions

Both authors contributed equally and agreed the final manuscript for publication.

## Competing interests

No competing interests were disclosed.

## Grant information

The author(s) declared that no grants were involved in supporting this work.

## References

- Porter SD, Tschinkel WR: **Fire ant thermal preferences: behavioral control of growth and metabolism.** *Behav Ecol Sociobiol.* 1993; **32**(5): 321–329.  
[Publisher Full Text](#)
- Challet M, Jost C, Grimal A, *et al.*: **How temperature influences displacements and corpse aggregation behaviors in the ant *Messor sancta*.** *Insect Soc.* 2005; **52**(4): 309–315.  
[Publisher Full Text](#)
- Coenen-Stass D, Schaarschmidt B, Lamprecht I: **Temperature distribution and calorimetric determination of heat production in the nest of the wood ants *Formica polyctena* (Hymenoptera Formicidae).** *Ecology.* 1980; **61**: 238–244.  
[Publisher Full Text](#)
- Brian MV: **Temperature choice and its relevance to brood survival and caste determination in the ant *Myrmica rubra* L.** *Physiol Zool.* 1973; **46**(4): 245–252.  
[Reference Source](#)
- Wilson EO: **The insect societies.** Belknap Press of Harvard University Press, Massachusetts. 1971; 548.  
[Reference Source](#)
- Jones JC, Oldroyd BP: **Nest Thermoregulation in Social Insects.** *Adv in Insect Phys.* 2006; **33**: 153–191.  
[Publisher Full Text](#)
- Porter SD: **Impact of temperature on colony growth and developmental rates of the ant *Solenopsis invicta*.** *J Insect Phys.* 1988; **34**(12): 1127–1133.  
[Publisher Full Text](#)
- Carlson SR, Whitford WD: **Ant mound influence on vegetation and soils in semiarid mountain ecosystem.** *American Midland Naturalist.* 1991; **126**(1): 125–139.  
[Reference Source](#)
- Penick CA, Tschinkel WR: **Thermoregulatory brood transport in the fire ant *Solenopsis invicta*.** *Insect Soc.* 2008; **55**(2): 176–182.  
[Publisher Full Text](#)
- Hölldobler B: **Territorial Behaviour in the Green Tree Ant (*Oecophylla smaragdina*).** *Biotropica.* 1983; **15**(4): 241–250.  
[Publisher Full Text](#)
- Brandt CJ: **The thermal diffusivity of the organic material of a mound of *Formica polyctena* Foerst in relation to the thermoregulation of the brood (Hymenoptera, Formicidae).** *Neth J Zool.* 1980; **30**(2): 326–344.  
[Publisher Full Text](#)
- Kilpeläinen J, Punttila P, Finér L, *et al.*: **Distribution of ant species and mounds (Formica) in different-aged managed spruce stands in eastern Finland.** *J Appl Entomol.* 2008; **132**(4): 315–325.  
[Publisher Full Text](#)
- Frouz J, Kalčík J, Cudlín P: **Accumulation of phosphorus in nests of red wood ants *Formica s. str.*** *Ann Zool Fennici.* 2005; **42**(3): 269–275.  
[Reference Source](#)
- Coenen-Stass D: **Zum Verhalten der roten Waldameise, *Formica polyctena* (Hymenoptera, Formicidae) im Klimagradient während der Brutpflege.** *Verhandlungen der Deutschen Zoologischen Gesellschaft.* 1985; **78**: 204–112.  
[Reference Source](#)
- Frouz J: **The effect of nest moisture on daily temperature regime in the nests of *Formica polyctena* wood ants.** *Insect Soc.* 2000; **47**(3): 229–235.  
[Publisher Full Text](#)
- Horstmann K, Schmid H: **Temperature regulation in nests of the wood ant, *Formica polyctena* (Hymenoptera: Formicidae).** *Entomologia Generalis.* 1986; **11**(3–4): 229–236.  
[Publisher Full Text](#)
- Castella G, Chapuisat M, Christe P: **Prophylaxis with resin in wood ants.** *Anim Behav.* 2008; **75**(4): 1591–1596.  
[Publisher Full Text](#)
- Mciver JD, Torgersen TR, Cimon NJ: **A supercolony of the thatch ant *Formica obscuripes* Forel (Hymenoptera: Formicidae) from the Blue Mountains of Oregon.** *Northwest Sci.* 1997; **71**(1): 18–29.  
[Reference Source](#)
- Bollazzi M, Roces F: **The thermoregulatory function of thatched nests in the South American grass-cutting ant, *Acromyrmex heyeri*.** *J Insect Sci.* 2010; **10**(137): 1–17.  
[PubMed Abstract](#) | [Publisher Full Text](#) | [Free Full Text](#)
- Seeley TD, Heinrich B: **Regulation of temperature in the nest of social insects.** In: *Insect Thermoregulation* (HEINRICH, B. Ed.). John Wiley and Sons, Inc., 1981; pp. 160–234.
- Kneitz G: **Versuche zur Wärmeorientierung von Arbeiterinnen der Waldameisenart *Formica polyctena* Foerst. (Hymenoptera, Formicidae).** *Insect Soc.* 1966; **13**: 285–296.  
[Publisher Full Text](#)
- Vogt JT: **Quantifying imported Fire ant (Hymenoptera: Formicidae) mounds with airborne digital imagery.** *Environ Entomol.* 2004; **33**(4): 1045–1051.  
[Publisher Full Text](#)
- Hölldobler B, Wilson EO: **The Ants.** The Belknap Press of Harvard University Press, Cambridge, 1990; 732 pp.  
[Reference Source](#)
- Vogt JT, Walleit B, Freeland TB Jr: **Imported fire ant (Hymenoptera: Formicidae) mound shape characteristics along a north-south gradient.** *Environ Entomol.* 2008; **37**(1): 198–205.  
[PubMed Abstract](#) | [Publisher Full Text](#)
- Korb J, Linsenmair KE: **The effects of temperature on the architecture and distribution of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds in different habitats of a West African Guinea savanna.** *Insect Soc.* 1998; **45**(1): 51–65.  
[Publisher Full Text](#)
- Grigg GC: **Some consequences of the shape and orientation of 'magnetic' termite mounds.** *Aust J Zool.* 1973; **21**(2): 231–237.  
[Publisher Full Text](#)
- Kleineidam C, Ernst R, Roces F: **Wind induced ventilation of the giant nests of the leaf-cutting ant *Atta vollenweideri*.** *Naturwissenschaften.* 2001; **88**(7): 301–305.  
[PubMed Abstract](#) | [Publisher Full Text](#)
- Powell RJ, Stradling DJ: **Factors influencing the growth of the *Attamyces bromaticus*, a symbiont of Attine ants.** *Trans Br Mycol Soc.* 1986; **87**(2): 205–213.  
[Publisher Full Text](#)
- Roces F, Núñez JA: **Brood translocation and circadian variation of temperature preference in the ant *Campotonus mus*.** *Oecologia.* 1989; **81**(1): 33–37.  
[Publisher Full Text](#)



30. Bollazzi M, Roces F: **To build or not to build: circulating dry air organizes collective building for climate control in the leaf-cutting ant *Acromyrmex ambiguus*.** *Anim Behav.* 2007; **74**(5): 1349–1355.  
[Publisher Full Text](#)
31. Jones JC, Myerscough MR, Graham S, *et al.*: **Honey bee nest thermoregulation: diversity promotes stability.** *Science.* 2004; **305**(5682): 402–404.  
[PubMed Abstract](#) | [Publisher Full Text](#)
32. Banschbach VS, Levit N, Herbers JM: **Nest temperatures and thermal preferences of a forest ant species: is seasonal polydomy a thermoregulatory mechanism?** *Insect Soc.* 1997; **44**(2): 109–122.  
[Publisher Full Text](#)
33. Cokendolpher JC, Francke OF: **Temperature preferences of four species of the fire ants (*Hymenoptera: Formicidae: Solenopsis*).** *Psyche.* 1985; **92**(1): 91–101.  
[Publisher Full Text](#)
34. Coenen-Stass D: **Untersuchungen fiber die jahreszeitlichen Klimapriferenz der roten Waldameise *Formica polyctena* (Hymeno-ptera, Formicidae).** Mitteilungen der Deutschen Gesellschaft für Allgemeine und Angewandte Entomologie. 1987; **5**: 44–48.
35. Kipyatkov VE, Schederova SS: **Seasonal changes in behavior patterns of the ant *Formica polyctena* in an artificial nest with temperature gradient.** *Zool Zhurnal.* 1985; **65**(12): 1847–1857.  
[Reference Source](#)
36. Ceusters R: **Social homeostasis in colonies of *Formica polyctena* Foerst.** (Hymenoptera, Formicidae): nest form and temperature preferences. Proc. 8th Int. Cong. International Union for the Study of Social Insects. Wageningen, 1977; pp. 111–112.  
[Reference Source](#)
37. Calabi P, Porter SD: **Worker longevity in the fire ant *Solenopsis invicta*: Ergonomic considerations of correlations between temperature, size and metabolic rates.** *J Insect Physiol.* 1989; **35**(8): 643–649.  
[Publisher Full Text](#)
38. Bollazzi M, Roces F: **Thermal preference for fungus culturing and brood location by workers of the thatching grass-cutting ant *Acromyrmex heyeri*.** *Insect Soc.* 2002; **49**(2):153–157.  
[Publisher Full Text](#)
39. Weir J: **Air flow, evaporation and mineral accumulation in mounds of *Macrotermes subhyalinus* (rambur).** *J Anim Ecol.* 1973; **42**(3): 509–520.  
[Publisher Full Text](#)
40. Bollazzi M, Roces F: **Leaf-cutting ant workers (*Acromyrmex heyeri*) trade off nest thermoregulation for humidity control.** *J Ethol.* 2010; **28**(2): 399–403. Japan Ethological Society and Springer.  
[Publisher Full Text](#)
41. Schneirla TC: **Army Ants: a Study in Social Organization (TOPOFF, H. Ed.).** Freeman, San Francisco. 1971.  
[Reference Source](#)
42. Korb J, Linsenmair KE: **Thermoregulation of termite mounds: What role does ambient temperature and metabolism of the colony play?** *Insect Soc.* 2000; **47**(4): 357–363.  
[Publisher Full Text](#)
43. Lindauer M: **Temperaturregulierung und Wasserhaushalt im Bienenstaat.** *Z Vergl Physiol.* 1954; **36**(4): 391–432.  
[Publisher Full Text](#)
44. Kleinhenz M, Bujok B, Fuchs S, *et al.*: **Hot bees in empty broodnest cells: heating from within.** *J Exp Biol.* 2003; **206**(Pt 23): 4217–4231.  
[PubMed Abstract](#) | [Publisher Full Text](#)
45. Ono M, Igarashi T, Ohno E, *et al.*: **Unusual thermal defense by a honeybee against mass attack by hornets.** *Nature.* 1995; **337**(6547): 334–336.  
[Publisher Full Text](#)
46. Rosengren R, Fortelius W, Lindström K, *et al.*: **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.** *Ann Zool Fennici.* 1987; **24**: 147–155.  
[Reference Source](#)
47. Hölldobler B, Wilson EO: **The Ants.** The Belknap Press of Harvard University Press, Cambridge, 1990; 732 pp.  
[Publisher Full Text](#)
48. Franks NR: **Thermoregulation in army ant bivouacs.** *Physiol Entomol.* 1989; **14**(4): 397–404.  
[Publisher Full Text](#)
49. Frouz J, Finer L: **Diurnal and seasonal fluctuations in wood ant (*Formica polyctena*) nest temperature in two geographically distant populations along a south-north gradient.** *Insect Soc.* 2007; **54**(3): 251–259.  
[Publisher Full Text](#)
50. Martin SJ: **Thermoregulation in *Vespa simillima xanthoptera*. (Hymenoptera, Vespidae).** *Kontyu.* 1988; **56**(3): 674–677.  
[Reference Source](#)
51. Zahn M: **Temperatursinn, Wärmehaushat und Bauweise der rote Waldameisen (*Formica rufa* L.).** *Zoologische Beitrage.* 1958; **3**: 127–194.
52. Kipyatkov VE, Schederova SS: **The endogenous rhythm of queens' reproductive activity in red wood ants (*Formica* group).** *Zool Zhurnal.* 1990; **69**(5): 40–52.  
[Reference Source](#)
53. Raignier A: **L'économie thermique d'une colonie polycalique de la fourmi des bois (*Formica rufa polyctena* Foerst).** *La Cellule.* 1948; **51**: 289–368.  
[Reference Source](#)
54. Tschinkel WR: **Seasonal life history and nest architecture of a winter-active ant, *Prenolepis imparis*.** *Insect Soc.* 1987; **34**(3): 143–164.  
[Publisher Full Text](#)
55. Chen YH, Robinson EJJ: **A comparison of mark-release-recapture methods for estimating colony size in the wood ants *Formica lugubris*.** *Insect Soc.* 2013; **60**(3): 351–359.  
[Publisher Full Text](#)
56. Chen Y, Hansen LD, Brown JJ: **Nesting sites of the carpenter ant, *Camponotus vicinus* (Mayr) (Hymenoptera: Formicidae) in northern Idaho.** *Environ Entomol.* 2002; **31**(6): 1037–1042.  
[Publisher Full Text](#)
57. Ofer J: ***Polyrhachis simplex*, the weaver ant of Israel.** *Insect Soc.* 1970; **17**(1): 49–81.  
[Publisher Full Text](#)
58. Miyata H, Shimamura T, Hirotsawa H, *et al.*: **Morphology and phenology of the primitive ponerine army ant *Onychomyrmex hedleyi* (Hymenoptera: Formicidae: Ponerinae) in a highland rainforest of Australia.** *J Nat Hist.* 2003; **37**(1): 115–125.  
[Publisher Full Text](#)
59. Sanada-Morimura S, Satoh T, Obara Y: **Territorial behavior and temperature preference for nesting sites in a pavement ant *Tetramorium tsushimae*.** *Insect Soc.* 2006; **53**(2): 141–148.  
[Publisher Full Text](#)
60. Cole BJ: **Nest architecture in the Western harvester ant, *Pogonomyrmex occidentalis* (Cresson).** *Insect Soc.* 1994; **41**(4): 401–410.  
[Publisher Full Text](#)
61. Fletcher DJC, Crewe RM: **Nest structure and thermoregulation in the stingless bee *Trigona (Plebeina) denoiti vachal* (Hymenoptera: Apidae).** *J Entomol Soc South Afr.* 1981; **44**(2): 183–196.  
[Reference Source](#)
62. Lüscher M: **Air-conditioned termite nests.** *Sci Am.* 1961; **205**: 138–145.  
[Publisher Full Text](#)
63. Ishay J: **Thermoregulation by social wasps: behavior and pheromones.** *Trans N Y Acad Sci.* 1973; **35**(6): 447–462.  
[PubMed Abstract](#) | [Publisher Full Text](#)
64. Ishay JS, Barenholz-Paniry V: **Thermoelectric effect in hornet (*Vespa orientalis*) silk and thermoregulation in a hornet's nest.** *J Insect Physiol.* 1995; **41**(9): 753–759.  
[Publisher Full Text](#)
65. Greaves T: **Temperature studies of termite colonies in living trees.** *Aust J Zool.* 1964; **12**(2): 250–262.  
[Publisher Full Text](#)
66. Morse RA, Laigo FM: ***Apis dorsata* in the Philippines.** *Monogr. Philipp Assoc Entomol.* 1969; **1**: 1–96.  
[Reference Source](#)
67. Nielsen MG: **An attempt to estimate energy flow through a population of workers of *Lasius alienus*. (Forst), (Hymenoptera: Formicidae).** *Natura Jutlandica.* 1972; **16**: 99–107.  
[Reference Source](#)
68. O'Donnell S, Foster RL: **Thresholds of response in nest thermoregulation by worker bumble bees, *Bombus bifarius nearcticus* (Hymenoptera: Apidae).** *Ethology.* 2001; **107**(5): 387–399.  
[Publisher Full Text](#)
69. Cassill DL, Tschinkel WR, Vinson SB: **Nest complexity, group size and brood rearing in the fire ant, *Solenopsis invicta*.** *Insect Soc.* 2002; **49**(2): 158–163.  
[Publisher Full Text](#)

# Open Peer Review

Current Referee Status:



---

## Version 2

Referee Report 28 March 2014

doi:10.5256/f1000research.4093.r4237



**Clint Penick**

Department of Biology, North Carolina State University, Raleigh, NC, USA

The authors have addressed the major points I raised in the previous version.

**I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.**

**Competing Interests:** No competing interests were disclosed.

---

## Version 1

Referee Report 03 March 2014

doi:10.5256/f1000research.3163.r3521



**Clint Penick**

Department of Biology, North Carolina State University, Raleigh, NC, USA

The authors have provided a clear update to the literature on thermoregulation of ant nests and also include interesting anecdotes from the literature, such as Lindauer's experiment with bees on lava plains. The arrangement of the article focuses on species that regulate temperature by moving brood across a temperature gradient (e.g. *Solenopsis*) vs. species that modify the thermal environment to maintain a core nest temperature (e.g. *Formica polyctena*). This distinction is perhaps the most interesting part of the paper, but in its current form the organization is not clear.

I have the following comments:

1. The authors make their strongest argument for distinguishing between these two strategies in the second to last paragraph. This paragraph should instead be the last paragraph of the Introduction, which would help establish their argument earlier. In addition, several other sections throughout the manuscript could make this distinction more apparent (especially in "*Behavioural reactions of ant workers*").
2. It may help to identify which species fit your definitions. *Pogonomyrmex*, *Solenopsis invicta*, *Camponotus*, and *Acromyrmex* fit into brood/fungus movers; *Formica*, *Atta*, *Eciton*, termites, and

bees seem to fit more into core nest temperature maintainers.

3. Likewise, the table does not clearly fit within the papers main theme. It may help to add a column that specifies whether each type of nest is associated with brood translocation, maintaining a stable core temperature, or possibly neither.
4. One question that is not addressed in this paper is why these two strategies exist? There is some discussion about wet vs. dry thatch nests in open and forested areas, but I think it would make sense to describe the ecological conditions where each thermoregulation strategy is commonly used in more detail.
5. The discussion about nest ventilation in *Atta* species is not quite accurate. Currently, there is little evidence that nest ventilation strongly impacts temperature; rather, nest ventilation facilitates CO<sub>2</sub> exchange. This has also been argued with respect to termite nests, where termite nest chimneys do not seem to affect nest temperature.

**I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.**

**Competing Interests:** No competing interests were disclosed.

Author Response 19 Mar 2014

**Štěpánka Kadochová**, Charles University, Prague, Czech Republic

We thank Clint Penick very much for his review and approval of our review paper. Suggested comments and changes have been included in the latest version of the paper. For cases of authors disagreement with the referee please see comments below.

*Point 4 – why those strategies exist?*

Reply: More discussion concerning this topic could be found in part „Use of metabolic heat for nest thermoregulation in ants“

*Point 5 – ventilation in Atta species*

Reply: Authors used information quoted in references, which suppose the ventilation to affect nest temperature. (Kleineidam et. al 2001; Powell and Stradling 1986, Bollazzi and Roces 2010). However to make situation clear the sentences about ventilation have been changed to „This ensures exchange of respiratory gasses and optimal thermal conditions for symbiotic fungi which are damaged by temperatures higher than 30°C“ and „Even more efficient ventilation systems, providing both temperature regulation and respiratory gasses exchange, can be found in nests of the termite *Matorermes bellicose*.“

**Competing Interests:** No competing interests were disclosed.

Referee Report 04 February 2014

doi:10.5256/f1000research.3163.r2859



**Haitao Wu**

Northeast Institute of Geography and Agroecology, Chinese Academy of Sciences, Changchun, China

This review manuscript represents an interesting study into the various thermoregulation strategies used in ant nests and mounds. A particular strength of the manuscript is the conclusion that there are two main types of thermoregulation strategies used: 'thermal gradient' in nests or a 'stable temperature' with a heat core. The review concentrates mainly on three aspects to reveal these strategies: nest/mound material and architecture properties, ant behavioral reaction and ant metabolic heat. The manuscript is well written and the discussion seems to be sound. I believe it is a good paper on ant nest ecology, but there are several issues that should be considered.

1. Upon reading this paper it is clear that the two different thermoregulatory strategies are its core point, which is explained from three aspects. However these two thermoregulatory strategies are an existing phenomena which are simply being discussed and explored in more detail and should therefore not be the 'conclusion' of this article. Instead I think it would be better to state the existence of these two strategies in the Introduction section and then discuss the mechanisms of the phenomena in the rest of the article.
2. Some of the content is rather long and would benefit from being condensed a little to make the overall message clearer. For example: the termites in Table 1 and the details of strategies used by bees, bumblebees and wasps. As this paper focuses on ant thermoregulation characteristics, the content on other insects should be deleted as they are not really necessary.
3. The explanations of "*ant metabolic heat*" for ant nest thermoregulation in "*Use of metabolic heat for nest thermoregulation in ants*" are not clear. From the explanations given I still cannot understand how ant metabolic heat impacts on ant mound temperatures or how the ants adopt an ant mound temperature. This content needs to be further explained.
4. The conclusion could do with a rewrite. It should not only reiterate the two opposite thermoregulatory strategies but also condense the messages from other sections, namely: nest/mound material and architecture properties, ant behavioral reaction and ant metabolic heat.

**I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard.**

**Competing Interests:** No competing interests were disclosed.

Author Response 19 Mar 2014

**Štěpánka Kadochová**, Charles University, Prague, Czech Republic

We thank Haitao Wu very much for his review and approval of our review paper. Suggested comments and changes have been included in the latest version of the paper. For cases of authors disagreement with the referee please see comments below.

*Point 2 – details of thermoregulatory strategies in other insects*

Reply: The strategies of other social insects species are used as comparism, especially the bees thermoregulation which is very well studied. Authrs would like to point out certain paralel between the thermoregulation in *Formica polyctena* mound to that in bee hive, even though achieved by different mechanisms

**Point 3 – ant metabolic heating**

Reply: The concept of „metabolic heating“ has been described using all known information so far. The metabolic heat production of *Formica rufa* ants has not been studied since the Coenen-Strass study in 1980 so the exact physiological mechanism of metabolic heating has not been clarified yet.

**Competing Interests:** No competing interests were disclosed.

Referee Report 22 January 2014

doi:10.5256/f1000research.3163.r2858



**Jouni Sorvari**

Department of Environmental Science, University of Eastern Finland, Kuopion, Finland

This is an interesting review on nest thermoregulation strategies in social insects. I think the work is sound and I agree with most parts of the text. However, I think that the authors give too much weight to an assumption that the “dry nest strategy” is a typical strategy for red wood ants. At least in Finland, the large and populous nests are usually located in shaded forests and seem to perform better than the dry nests located in open areas. This is however, overall a good work and deserves to be approved after some fine-tuning.

**Title and Abstract:**

The title expects focus on *Formica rufa*, but in fact the species focused on is *Formica polyctena*, a member of the *Formica rufa* species group. I recommend changing the title so that the focus is on *Formica rufa* group (or “red wood ants”). The Abstract is ok.

**Article content:**

The temperature-humidity regulation of red wood ant nest mounds is a very complex process. Because young small nests of *Formica polyctena* need direct solar radiation to increase the inner temperature of nest, the new nests need to be built in open spots in or close to forests<sup>123</sup>. Later, during natural succession those spots will turn into forests, i.e., more shaded habitat but richer in food. The nests will become more shaded but due to the “wet nest strategy” they are no longer dependent on direct sun light. Therefore, both of the two types of thermoregulation strategies are applied in natural populations, but in different stages of nest the development.

The situation would be different if the forest succession did not advance and the nest grows in a spot which stays open for a longer period. This is a typical situation in habitats with anthropogenic influence, where the natural succession and penetration of forest towards agricultural or urban field is prevented. Then the same strategy that is used in shaded forest is not optimal for more permanently open areas. Therefore, the statement that “*The dry nest thermoregulatory strategy is more common than the wet nest strategy in F. polyctena*” may be true due to anthropogenic pressure, but would possibly not be so in natural habitats. In addition, the statement seems to be based on data studied in two locations in Czech Republic without mention of the naturalness of the habitats. The more fragmented the forests are the higher the proportion of nests that are located in, or close to forest edges and other open areas, possibly causing an impression that the ant prefers open areas.



I recommend using term “moist nest” instead of “wet nest”, because “wet” sounds too wet.

The nest architecture and building method of *Oecophylla* weaver ants is mentioned in the text, but their function in thermoregulation is not mentioned. The authors should either describe how the architecture (or building method) affects thermoregulation of such a nest, or remove the sentence.

Although *Acromyrmex heyeri* builds thatched nests this species does not belong to the ‘thatch ants’ which is in fact an American term reserved for red wood ants of the *Formica rufa* group.

#### The table:

Large and most populous nests of the red wood ants, especially the polygynous ones, e.g., *Formica aquilonia* and *F. polyctena*, are often located in shaded forests where direct sun light does not cause high oscillations in outer layers of the nest. It is possible that the description does not fit mature nests in natural forest environment, but young and smaller nests, or nests in anthropogenic fragmented forests.

#### References list:

The reference list should be proofread because of some mistakes e.g., in reference #13 *Formicas. Str.* -> *Formica s. str.*; in some references the species name is not in italics where it probably should be; and the journal abbreviation for Insectes Sociaux should always be Insect Soc.

#### References

1. Punttila P: Succession, forest fragmentation, and the distribution of wood ants. *Oikos*. 1996; **75**: 291-298 [Reference Source](#)
2. Sorvari J, Hakkarainen H: Deforestation reduces nest mound size and decreases the production of sexual offspring in the wood ant *Formica aquilonia*. *Ann Zool Fennici*. 2005; **48**: 259-267 [Reference Source](#)
3. Kilpeläinen J, Punttila P, Finér L, Niemelä P, Domisch T, Jurgensen MF, Neuvonen S, Ohashi M, Risch AC, Sundström L: Distribution of ant species and mounds (*Formica*) in different-aged managed spruce stands in eastern Finland. *J Appl Entomol*. 2008; **132**: 315-325 [Publisher Full Text](#)

**I have read this submission. I believe that I have an appropriate level of expertise to confirm that it is of an acceptable scientific standard, however I have significant reservations, as outlined above.**

**Competing Interests:** I am currently writing a book chapter together with J. Frouz, but the chapter is about different subject. Frouz J, Jilkova V & Sorvari J: Chapter 10: Nutrient cycling and ecosystem function. In: Stockan JA & Robinson EJH (eds.) *Wood ant ecology and conservation*. Cambridge University Press, Cambridge, UK

Author Response 19 Mar 2014

**Štěpánka Kadochová**, Charles University, Prague, Czech Republic

We thank Dr. Jouni Sovari very much for his review and valuable comments concerning our review paper. All typos and mistakes have been corrected; suggested comments and changes have been included in the latest version of the paper including the change of title. For comments which need more explanation please see authors replies below.

We hope that their explanation and changes made are sufficient enough for the paper version 2 to be accepted.

*JS: I recommend using term “moist nest” instead of “wet nest”, because “wet” sounds too wet.*

Reply: The major reason for using wet nests was to be consistent with previous literature. Term „wet nests“ was adopted because it is how the thermoregulation strategy was described in the previous literature namely Frouz 1996, 2000, Frouz and Finner 2007 . Moreover the moisture of nest material (measured gravimetrically) should reach up to 72%. We believe such level of moisture justify using term wet (15. Frouz J: The effect of nest moisture on daily temperature regime in the nests of *Formica polyctena*. wood ants. Insec Soc. 2000; 47(3): 229–235.)

*JS: “... Oecophylla weaver ants is mentioned in the text, but their function in thermoregulation is not mentioned ...”*

Reply: This is very good note, however the thermoregulatory function of *Oecophylla* nests is not described in any paper so far. We double check that text do not imply any thermoregulation function in these nest. The nest of *Oecophylla* ants were mentioned only to emphasis the great variability of nesting strategies occurring in ants.

*JS – Table 1 „. It is possible that the description does not fit mature nests in natural forest environment, but young and smaller nests, or nests in anthropogenic fragmented forests.“*

Reply: Authors agree with the referee, the thermoregulatory strategy description is based mainly on limited number of studies performed in Czech republic and in Finland (49. Frouz J, Finner L: Diurnal and seasonal fluctuations in wood ant (*Formica polyctena*) nest temperature in two geographically distant populations along a south-north gradient. Insect Soc. 2007; 54(3): 251–259). These studies include large variety of nest sizes from nest with volume several litres to volume many thousand of liters. We agree that role of solar radiation is bigger in smaller nests and inner heating is more important in bigger nest and we note this in Table 1  
Moreover to make it clear authors mention the possible of different temperature fluctuation in the text as follow: „The seasonal temperature fluctuations ... studied by Frouz & Finner<sup>49</sup>... both in Finland and the Czech Republic the ant colonies maintained a high nest temperature. Nest temperatures fluctuated more in the Czech Republic than in Finland, possibly because of greater differences between day and night ambient temperatures.“

**Competing Interests:** No competing interests were disclosed.