

Nest Thermoregulation in Social Insects

Julia C. Jones and Benjamin P. Oldroyd

Behaviour and Genetics of Social Insects Laboratory, School of Biological Sciences, The University of Sydney, Australia

- 1 Introduction 154
- 2 Passive mechanisms 156
 - 2.1 Nest site selection and colony emigration 156
 - 2.2 Nest orientation 161
 - 2.3 Nest Architecture 164
- 3 Active nest thermoregulation 172
 - 3.1 Active colony responses to low temperatures 172
 - 3.2 Direct Incubation 175
 - 3.3 Active colony responses to high temperatures 177
- 4 Coordination of thermoregulation 180
 - 4.1 The task threshold model 181
 - 4.2 Coordination with communication 182
 - 4.3 The importance of inter-individual variability 182
- 5 Conclusions 184
- References 185

Abstract

Most social insect species are able to regulate the temperature within their nests. In this review, we examine the variety of mechanisms that social insect species have evolved to regulate temperature. We divide these mechanisms into two broad categories: active and passive. 'Passive' temperature regulation includes such mechanisms as nest site selection to optimize internal nest temperature, nest structures that permit passive heating or cooling, or simple behaviour such as brood translocation to regions within a nest where temperatures are most favourable. 'Active' temperature regulation refers to behaviour where individuals modify nest temperature by physical activity like wing fanning or evaporative cooling.

Although there is enormous variation in the thermoregulatory mechanisms, there are also many similarities. All thermoregulatory mechanisms are self-organized and arise from simple rules followed by each individual worker.

1 Introduction

Part of the ecological success of social insects (all termites and ants, and some wasps and bees) is that they have at least some ability to regulate temperatures within their nests (Wilson, 1971). This often allows them to be physically active even when non-social insects of similar size would either be moribund with cold or seeking refuge from heat. Many social insect species regulate their nest temperatures within specific, sometimes very narrow, boundaries, despite extremes in ambient temperature. Honey bee colonies, for example, are able to maintain brood nest temperatures within the range of 33–36 °C, even when the ambient temperature ranges from well below freezing to above 45 °C (e.g. Himmer, 1932; Lindauer, 1955; Fahrenholz *et al.*, 1989).

If nest temperatures are not kept within the species-specific boundaries, there are often undesirable consequences. In some termites and ants, for example, the growth of the fungi that they cultivate for food may be affected (Powell and Stradling, 1986; Korb and Linsenmair, 2000a; Bollazzi and Roces, 2002). In many species, abnormalities can develop in the brood, or adults may not emerge at all (Himmer, 1927, 1932; Brian, 1963, 1973; Jay, 1963; Ishay, 1973; Kronenberg and Heller, 1982; Roces and Nunez, 1989; Tautz *et al.*, 2003; Jones *et al.*, 2005; McMullan and Brown, 2005). In honey bees, even slightly atypical brood rearing temperatures can affect the behaviour of the bees as adults (Tautz *et al.*, 2003; Jones *et al.*, 2005).

In this review we examine the wide variety of mechanisms that social insect species have evolved to regulate the temperature of their nests and brood (Table 1). We divide these mechanisms into two broad categories: active and passive. ‘Passive’ temperature regulation includes such mechanisms as nest site selection to optimize internal nest temperature, nest structures that permit passive heating or cooling, or simple behaviour such as brood translocation to regions within a nest where temperatures are most favourable. ‘Active’ temperature regulation refers to behaviour where individuals modify nest temperature by physical activity like wing fanning (Fig. 1) or evaporative cooling.

Both active and passive thermoregulation requires mechanisms that coordinate the activities of individual workers so that the outcome is a stable or more stable brood nest temperature. For active mechanisms of thermoregulation, this is obvious: the number of workers engaged in cooling or heating behaviour must rise and fall according to the current temperature within the nest. Less obviously, the same holds true for passive mechanisms. For example, a termite mound is constructed by tens of thousands of workers, none of which has any perception of the overall shape of the mound, or its intricately engineered ventilation tunnels and appropriate solar orientation. Thus, systems of passive nest thermoregulation

TABLE 1 Active and passive thermoregulatory systems used in different social insect groups (see text for details)

Social Insect Group	Passive Thermoregulation			
	Nest orientation	Nest architecture	Nest site selection/ colony emigration	
Ants	S	S	M	
Bees: Honey bees	S	S	A	
Stingless bees	?	M	A	
Bumble bees	S	A	A	
Wasps: Polistinae	?	S	A	
Vespinae	?	A?	A	
Termites	S	S	S	

Social Insect Group	Active Thermoregulation			
	Clustering/ generating metabolic heat	Direct incubation	Fanning	Water evaporation
Ants	S	N	N	N
Bees: Honey bees	A	A*	A	A
Stingless bees	S?	?	S	N
Bumble bees	A	A	A	N
Wasps: Polistinae	?	N?	A	A
Vespinae	M	M	A	S
Termites	S	N	N	N

S = Some species

M = Most species

A = All species

N = No species

*This behaviour has not been examined in all species, but we suggest that most, if not all, honey bee species incubate their brood directly.

require the coordination of the activities of workers that build the nest, so that the colony-level outcome of stable brood nest temperatures is achieved.

The mechanisms that coordinate the activities of individual workers are best understood from the principles of self-organization, which describe how a system can acquire order and structure “through interactions internal to the system without intervention by external directing influences” (Camazine *et al.*, 2001). Below we will review our current understanding of how the behaviour of individuals acting independently can nonetheless result in the emergent property of a stable nest temperature, and the apparent importance of inter-individual variance in generating stability. We begin, however, with a survey of the mechanisms of nest thermoregulation, both passive and active, that have evolved across social insect taxa.



FIG. 1 A honey bee (*Apis mellifera*) worker fanning at the entrance of her nest (Photo by M. Ricketts).

2 Passive mechanisms

Nest site selection, nest orientation and nest architecture are the primary mechanisms used by social insects to regulate their nest's microclimate. These passive mechanisms provide a buffer between brood nest temperature and ambient temperature, and therefore greatly affect the ease with which workers can regulate the temperature inside their nest by more energetically expensive active mechanisms. For example, [Korb and Linsenmair \(2000a\)](#) found that the coefficients of variation were not significantly different in internal nest temperature of the African termite species *Macrotermes bellicosus*, is not different between occupied and unoccupied mounds (occupied: 0.54°C , unoccupied: 0.48°C). However, mean mound temperatures are lower ($\sim 27^{\circ}\text{C}$) in nests heated only by the sun compared with nests with active termites and fungi ($\sim 30^{\circ}\text{C}$). In this section, we provide examples of the variety of passive mechanisms used by social insects for nest thermoregulation.

2.1 NEST SITE SELECTION AND COLONY EMIGRATION

Nest site selection plays a major role in the ability of social insect colonies to maintain stable nest temperatures. Nest site choice falls into two broad categories. For many species, the main criterion when selecting a nest site is physical protection against environmental perturbations; others select sites where the microclimate provides a relatively stable temperature.

2.1.1 *Bees*

Some honey-bee and all bumble-bee and stingless-bee species nest in cavities; predominantly tree hollows, but also in disused rodent burrows, cavities in old termite nests and under the leaf litter. These cavities provide insulation, thereby helping colonies to retain metabolic heat and providing protection from variations in ambient temperature (Wille and Michener, 1973; Heinrich, 1979; Engels *et al.*, 1995). However, the open-nesting honey bees, which occur in tropical environments, build a nest in the open, choosing sites with appropriate levels of solar radiation. As the open-nesting honey bee species form the basal clades of the honey bee tribe (Engel and Schultz, 1997; Arias and Sheppard, 2005), the colonization of temperate areas may have been facilitated by the move into protective cavities (Ruttner, 1988; Oldroyd and Wongsiri, 2006).

In cavity-nesting western honey bees (*A. mellifera*), cavity selection by swarms is based on a variety of attributes. In general, favoured cavities have a volume of at least 15 l, an entrance with a sunny aspect, a small entrance size (smaller than 75 cm²), an entrance on the floor of the cavity and an elevation of several metres (> 3 m) above the ground (Seeley, 1976, 1977; Avitabile *et al.*, 1978; Seeley and Morse, 1978; Jaycox and Parise, 1980, 1981; Rinderer *et al.*, 1981, 1982; Schmidt and Hurley, 1995; Camazine *et al.*, 1999). All of these properties enhance nest thermoregulation. Inside the cavity, the workers build a number of vertical combs out of wax, the upper and peripheral areas of which are used for storing pollen and honey while the centre contains the brood (Seeley, 1976; Camazine, 1991). The central location of the brood area means that the brood is insulated by the surrounding honey store.

The giant mountain honey bee (*A. laboriosa*) prefers nest sites with a southerly aspect to build its single exposed comb (Underwood, 1986, 1990). Similarly Doedikar *et al.* (1977) and Reddy (1993) found a strong tendency for established nests of the common giant honey bee *Apis dorsata* to be orientated in a north-south direction (Fig. 2). Presumably, this maximizes solar radiation and minimizes exposure to cold winds (Oldroyd and Wongsiri, 2006). The dwarf honey bees *A. florea* and *A. andreniformis* select shaded sites (Wongsiri *et al.*, 1997) and will migrate their nest if it subsequently becomes exposed to the sun (Seeley *et al.*, 1982).

For many stingless bee species, selecting an appropriate cavity appears to be the primary mechanism for keeping nest temperatures optimal, despite high ambient temperatures. For example, in southern Africa, all *Trigona* species nest inside a cavity, either deep underground (60–100 cm in *T. denoiti*) or inside a tree hollow. The nest depth of *T. denoiti* and insulating properties of the tree cavity in the case of *T. griboidoi* imply that the nests are rarely thermally stressed (Moritz and Crewe, 1988).



FIG. 2 The giant honey bee *Apis dorsata* selects sheltered nest sites like this one on an apartment building in Bangalore India (Photo by B. Oldroyd).

2.1.2 Wasps

Social wasps nest in a variety of locations, including underground and tree cavities, and in enclosed and open nests suspended from tree branches (Ishay, 1973). Microclimate has been found to influence nest site selection and reproductive strategies in *Polistes* wasps. Females of the temperate species *Polistes fuscatus* are more likely to initiate nests in warm sites. Such sites lead to earlier production of workers and larger founding groups, than cool sites (Jeanne and Morgan, 1992). These authors suggest that larger founding groups occur because warm sites are more attractive to female joiners and usurpers. In addition, philopatry may have evolved due to selection acting on founding females to nest in climatically favourable sites.

2.1.3 Ants

Ants are one of the most diverse insect suborders comprising 70% of all social insect species. This diversity is reflected in the range of environments they occupy, from deep in soil to forest canopies (Holldobler and Wilson, 1990). We identify three main strategies by which ant species regulate nest temperatures. First, like many social bees, some ant species rely on protection from a cavity, such as a tree stump or underground burrow (Chen *et al.*, 2002). Second, some species migrate their nests frequently, varying the amount of cover they select, depending on the temperature and season (Ofer, 1970; Kuriachan and Vinson, 2000; Miyata *et al.*, 2003). Third, still others move their brood to areas of optimal temperature within the same nest (Roces and Nunez, 1989, 1995; Bollazzi and Roces, 2002; Pranschke and Hooper-Bui, 2003).

In some ant species, nest location is important for regulating nest temperature and also affects additional forms of temperature control. In

northern Idaho, the carpenter ant *Camponotus vicinus*, for example, nests mostly in fallen logs and tree stumps (Chen *et al.*, 2002). These ants select open dry sites, where the temperature is significantly higher, over closed canopy areas (Chen *et al.*, 2002). Similarly, for the wood ant *Formica polyctena*, a temperate species of northern Europe and Scandinavia, nest site choice is an important aspect of nest temperature regulation and also affects the nest heating strategy used by the ants. At dry sites, the ants utilize solar radiation to heat their nests. In addition to orientating the mound to maximize incident solar radiation, the workers maximize this effect by basking on the outside of the mound. The dry nest material has a low thermal capacity and so the thermal energy in the workers' bodies can increase the nest temperature, especially in the evening when many heated workers return to the interior of the nest (Frouz, 2000). The surface of the dry nest also provides insulation as there is a low loss of thermal energy during the night. In contrast, nests at wet and shaded sites utilize the decomposing plant matter in their mounds as a source of heat (Frouz, 2000).

Nest migration is perhaps the most common method of temperature control used by ants. Migratory species adjust the amount of cover they select for their nest, depending on the temperature and season. The primitive ponerine ant *Onychomyrmex hedleyi*, for example, occurring in the highland rainforests of North Queensland, Australia, migrates frequently (Miyata *et al.*, 2003). Similarly, the weaver ant *Polyrhachis simplex* of Israel, migrates seasonally, in the winter and early spring (Ofer, 1970), and colonies of the polygynous form of the red imported fire ant (*Solenopsis invicta*) often migrate their nests in response to changing ambient temperatures (Kuriachan and Vinson, 2000). Both *O. hedleyi* and *P. simplex* increase the amount of protection selected for their nests in the cooler seasons. *O. hedleyi* colonies bivouac in the upper leaf litter layer in the warm and rainy seasons, from November to March. In the cool and dry season, from April to October, most colonies bivouac in the lower litter layer or up to 12 cm below the ground in natural cavities and cracks or holes dug by other insects or earthworms (Miyata *et al.*, 2003). During the summer, *P. simplex* ants build their nests in the litter of dried leaves, under stones or in the hollow of a tree stump. In winter, the majority of nests are located within cavities (Ofer, 1970). The transient nature of the nests, in both these species, implies that selecting appropriate cover is a critical thermoregulatory mechanism.

Although an appropriate brood incubation temperature is primarily achieved by selecting an appropriate site for the nest, brood incubation temperature is precisely controlled by workers moving the brood from one part of that nest to another, depending on the brood's stage of development and temperatures in different parts of the nest (Roces and Nunez, 1989, 1995; Bollazzi and Roces, 2002; Pranschke and Hooper-Bui, 2003) (Fig. 3). This occurs both in species with large, permanent nests or mounds, and in species with more transient nests.



FIG. 3 A *Solenopsis invicta* mound, opened on the side closest to the sun, showing the placement of brood during mid-morning (Photo courtesy of W. Tschinkel. Reprinted by permission of the publisher from THE FIRE ANTS by Walter S. Tschinkel, Plate 10, Cambridge Mass.: The Belknap Press of Harvard University Press, Copyright © 2006 by the President and Fellows of Harvard College). (A) Intact mound, (B) sunny-side with the mound surface removed, (C) mound cut in vertical section, after surface removal. During mid-morning, the temperature just under the mound surface was $\sim 30^{\circ}\text{C}$ while in the mound core it was 23°C (Tschinkel, 2006).

Camponotus mus nests under stones or in rotting wood on the ground, where colonies experience large temperature fluctuations. Rather than constantly moving the brood around within the nest as the temperature changes, *C. mus* nurse workers regulate the temperature of their brood by moving it to the preferred temperature at two fixed times – the hottest and coolest times of the day (Roces and Nunez, 1995). The brood is therefore kept well within the daily maximum and minimum, but experience considerable fluctuations in temperature throughout the day. Using artificial nests housed in a 12 h/12 h light/dark cycle, with two temperature options (27.5°C and 30.8°C) known to be selected by the ants in relation to the light:dark cycle, Roces and Nunez (1989) found that a total of four to five workers translocated the brood twice a day. One translocation occurred in the middle of the light period (at 30.8°C), when the highest environmental temperatures occur, and again 8 h later, during the night (at 27.5°C) (Roces and Nunez, 1989, 1995). Thus, the threshold of thermal tolerance in *C. mus* workers is related to the time of day. Highest thermal sensitivity occurs during the two daily translocation times: the middle of the photophase and two hours after the onset of the dark period. At these times, workers are more likely to transport brood in response to minor temperature changes. For example, shortly after 2 p.m., nurses began moving the brood as soon as the temperature was increased experimentally by $0.1\text{--}0.2^{\circ}\text{C}$ above the selected temperature of 30.8°C ; whereas, later in the day (anticipating a fall in temperature?), nurse workers will tolerate temperatures up to 3.7°C , above 30.8°C . Nurse workers of *C. rufipes*, a dominant species in subtropical and tropical regions of South America where temperature fluctuations are less marked, also show some circadian rhythmicity in sensitivity to temperature changes, but retain a constant preference. Nurse workers have a higher tolerance for high temperatures in the middle

of the light period, when differences of 6.7–7.8 °C above the mean preferred temperature (25 °C) are tolerated (Roces and Nunez, 1995). In the dark period, on the other hand, workers are more sensitive to temperature increases and begin to move the brood as soon as the temperature averages 1.9 °C above 25 °C. However, *C. rufipes* show no rhythm in their translocation of brood along an artificial thermal gradient in their nest (Roces and Nunez, 1995).

Similar brood and fungal garden translocations, in response to temperature variation, are carried out by workers in species with more permanent nests (Weber, 1957; Navarro and Jaffe, 1985; Lapointe *et al.*, 1998; Roces and Kleineidam, 2000; Bollazzi and Roces, 2002; Pranschke and Hooper-Bui, 2003). Workers of the thatching grass cutting ant *Acromyrmex heyeri*, for example, construct a thatch mound with dry grass and soil that protects a central fungus garden. The thatch mound provides insulation, but as with *C. mus* and *C. rufipes*, workers also translocate the brood and fungal food that they culture, in response to low and high temperatures (Bollazzi and Roces, 2002). Similarly, in red imported fire ant (*S. invicta*) populations of Louisiana, the presence of brood in the above-ground section of the nest (the mound) is strongly associated with mound temperature (Pranschke and Hooper-Bui, 2003) (Fig. 3). *S. invicta* brood are only found in mounds when mound temperatures are between 25 °C and 30 °C. The brood is moved by workers to subterranean parts of the nest when the temperature in the above-ground section exceeds 32 °C (Pranschke and Hooper-Bui, 2003). By using a controlled temperature gradient, Bollazzi and Roces (2002) showed that *A. heyeri* uses a similar strategy: workers quickly translocate all items of brood and fungus when the temperature exceeds 36 °C, and prefer temperatures between 24 °C and 25 °C. For *A. heyeri*, the probability of brood and fungus removal was less at the lower end of the temperature gradient (10 °C) and the temperatures selected by the workers were also slightly lower, 22 °C and 21 °C. Brief exposure to low temperatures may not compromise the growth and development of the fungus (Bollazzi and Roces, 2002).

Migration within the nest is also used by some termites to track the best brood rearing temperatures (Cabrera and Rust, 1996; Cabrera and Kamble, 2001).

2.2 NEST ORIENTATION

In some termite and ant species, nest temperatures are moderated by nest orientation. Nest orientation often influences the amount of solar radiation absorbed by a nest and the time of day that the highest radiation is received. Many species orientate their nests so that it is warmed by solar radiation in the cool of the morning. Other species orientate the nest so that it offers the smallest possible profile to incident solar radiation during the middle of the day (Table 1).

2.2.1 *Termites*

Two termite species (*Amitermes meridionalis* and *A. laurensis*) occurring in northern Australia rely on the structure and orientation of their mounds for regulating nest temperature. These termites build wedge-shaped 'magnetic' mounds where the long axis of the mounds is oriented north-south (Grigg and Underwood, 1977; Jacklyn, 1992) (Fig. 4). Mean mound orientation differs significantly between populations, depending on their longitude. Jacklyn (1992) changed the orientation of some mounds by giving them 'a nudge with a four-wheel drive vehicle'. He showed that the temperature gradient between the east and west faces was significantly altered by the change in orientation. Similarly, the rate of cooling on the eastern face during the afternoon was consistently affected by mound orientation. During the cooler dry season, mounds of natural orientation experience rapid morning heating on their eastern face, followed by a temperature plateau until the sun sets. Thus, the geographic variation in mean mound orientation is an adaptive response to environmental variation across northern Australia (Jacklyn, 1992). During the dry season, when daily minimum temperatures decline, large numbers of termites, including workers, larvae and reproductive nymphs, move to the eastern face in the morning and stay there during the day, probably to reduce the variation in temperature they experience.

2.2.2 *Ants*

The orientation and shape of ant nests influence the amount of solar radiation that reaches the surface of the nests (Hubbard and Cunningham, 1977). Imported fire ant (*S. invicta*) mounds are oval in shape, with the majority of the long axes oriented north-south. This shape and orientation means that the sides of the mound with the greatest surface area face the sun early in the morning and late in the afternoon. Nest mounds of *Formica ulkei* near Chicago are also asymmetrically shaped, with the long slope aligned so that it receives maximum solar radiation (Scherba, 1958). If a nest is experimentally shaded to alter the aspect receiving greatest radiation intensity, the ants adjust the alignment of the longest slope of the nest. A further example is found in the nests of *Formica truncorum* in northern Norway, where workers only place nesting material against the southern face of tree stumps (Elton, 1932).

Mounds of the North American harvester ant *Pogonomyrmex occidentalis* are constructed to maximize exposure to solar radiation on one slope of the dome and minimize it on another (Cole, 1994). The nest cones slope more towards the south and east because the peak of the mound is displaced from centre to the north and west. The mainly south-eastern direction of the nest cone increases the collection of solar radiation in the



FIG. 4 Magnetic termite, *Amitermes meridionalis*, mounds in Litchfield National Park, North West Australia. The long axis is oriented (A) north-south, and (B) east-facing parts are heated by the morning sun. (C) Several of these mounds can be found in the same area (Photos courtesy of Nathan Lo).

morning (Cole, 1994). In addition, the nest entrance is oriented towards the south-east, allowing workers at the nest entrance to make maximum use of solar radiation falling on the south-eastern slope. Interestingly, these adaptations result in a range of temperatures (although not as extreme as ambient temperature variation) within the mound. The temperature of the nest 5 cm below the ground varies from 12.9 °C to 41.8 °C while the range

of temperature fluctuation at a depth of 5 cm below the peak of the cone varies between 10.7 °C and 43.3 °C. Workers appear to take advantage of the range of temperatures available by moving their brood to appropriate areas of the nest cone (Cole, 1994), similar to the brood movements of the ant species discussed above.

2.3 NEST ARCHITECTURE

Social insects' nests vary enormously in both structure and materials, but the different designs all have a common end point – maintenance of a more stable brood nest temperature than ambient. Some structural features are important for retaining heat, while others are effective in dissipating it.

2.3.1 *Bees*

In many bee species, the nest is insulated by the cavity chosen as the nest site. More precise temperature regulation is achieved through the construction of protective layers around the nest, comb shape and brood position in the comb.

Bumble bees, add materials such as grass and plant parts to the nest in order to improve insulation. In addition, the workers build a canopy of wax over the nest to trap metabolic heat. If the temperature in the nest increases, the workers may partially remove the wax canopy.

Similarly, many stingless bee species build nests insulated by three main layers (Fig. 5). First, the cavity is lined with batumen (a Portugese word meaning “wall”) made of propolis (plant gums, saps or resins collected outside the hive) or a mixture of wax and propolis, and sometimes vegetable matter and mud (Wille and Michener, 1973). The batumen seals the nest cavity, except for the entrance and, in some species, ventilating holes. The batumen layer, is also used to seal off sections of the cavity that are too large for the nest (Wille and Michener, 1973). Second, immediately within the batumen lining there is often a layer of storage pots for pollen and honey made of cerumen (a mixture of wax and propolis). Third, inside the layer of storage pots there is an involucrem made of thin vertical leaves of cerumen joined to each other and to the pots. Usually, the involucrem encloses the brood comb completely (Wille and Michener, 1973).

The involucrem section of the nest is very important for heat conservation in many stingless bee species (Fletcher and Crewe, 1981; Roubik and Peralta, 1983; Engels *et al.*, 1995). *Melipona* build more involucrem in cooler climates than in equatorial forests (Engels *et al.*, 1995; Roubik, 2006). In *T. denoiti* nests, the layers of the involucrem act as baffles, which inhibit air movement and reduce loss of heat by convection (Fletcher and Crewe, 1981). Similarly, in *S. postica* the leaves of the involucrem provide

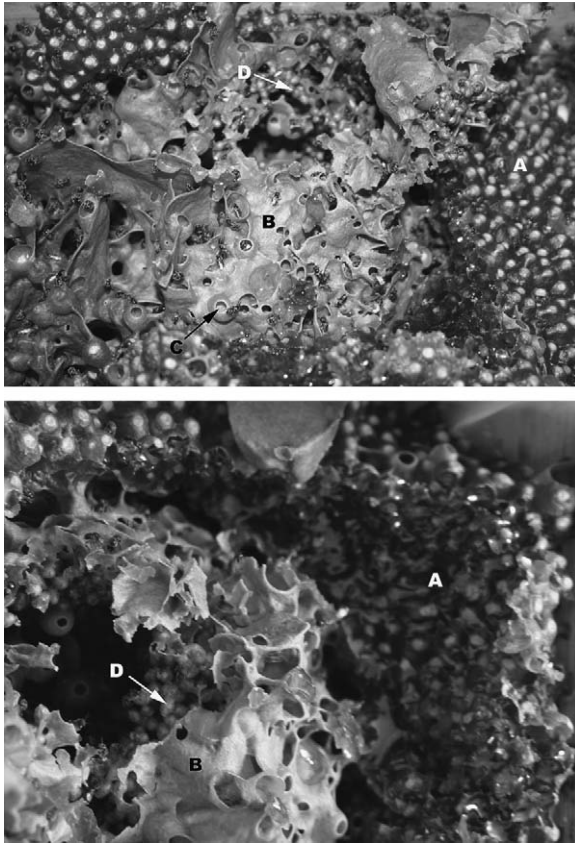


FIG. 5 Nest structure of *Austroplebeia australis*. The main nest layers for this species are the storage pots and involucrum enclosing the brood cells. (A) Honey pots, (B) involucrum, (C) storage pots (honey or pollen), and (D) brood cells (Photos courtesy of Peter Oxley).

effective insulation – during cool nights the temperature difference between the outer and inner layers of the involucrum (a distance of 1 cm) can be as much as 5 °C (Engels *et al.*, 1995). Also, in *Melipona rufiventris* and *M. seminigra* nests, in Brazil, the temperature inside the involucrum near the brood fluctuates less than ambient (ranging from 31 °C to 32.3 °C, where ambient ranged from ~23 °C to 30 °C) (Roubik and Peralta, 1983). The ability of *Melipona* species to maintain stable nest temperatures is mostly achieved by the involucrum, which traps much of the heat produced by the metabolism of the brood (Roubik and Peralta, 1983). Other stingless bee species, such as *Leurotrigona muelleri* and *Frieseomelitta varia*, do not build closely packed brood combs, but construct brood cells in a loosely-joined matrix. It seems likely that a spiral brood comb efficiently conserves heat

generated by the brood, whereas the matrix-style of brood cell construction facilitates heat dissipation (Fletcher and Crewe, 1981; Engels *et al.*, 1995). Interestingly, three sibling species of Australian stingless bees, temperate to tropical *Trigona carbonaria*, sub-tropical *T. davenporti* and tropical *T. hockingsi* (Franck *et al.*, 2004) differ strikingly in the construction of their brood comb, with *T. hockingsi* and *T. davenporti* constructing an open matrix of brood cells, whereas temperate *T. carbonaria* builds a densely packed spiral brood comb (Fig. 6). It remains to be seen if these two hugely variant forms of nest construction arise from environmental (temperature) cues or if these are truly species-specific traits.

In those stingless bee species that construct nests in the open, the nest is covered by insulating layers of batumen. Open-nesting species such as *Trigona corvina* and *T. spinipes* may also construct openings in the batumen, which are probably used for ventilation and temperature regulation (Wille and Michener, 1973).



FIG. 6 Nest structure of two stingless bee species (*Trigona hockingsi* and *T. carbonaria*). (A) *T. hockingsi* builds an open matrix of brood comb and (B) *T. carbonaria* builds densely packed spiral brood comb (Photos by B. Oldroyd).

Other aspects of nest architecture also help regulate the temperature in stingless bee nests. Species that construct a compact spiral brood comb (Fig. 6) utilize small cavities for nesting and can thus reduce the amount of heat lost via convection relative to species that utilize larger cavities. In addition, the absence of wax pillars used for access to the combs allows for a reduction in the space between the combs (Fletcher and Crewe, 1981). In many species, the entrance tube, which projects from the substrate or the nest surface in exposed nests, is closed over at night with soft cerumen from around the entrance. Closing the nest is mostly useful for defence but may also aid temperature regulation (Wille and Michener, 1973; Chinh *et al.*, 2005; Roubik, 2006). Species occurring in subtropical regions sometimes leave the opening closed for several days in cold weather (Wille and Michener, 1973). The long narrow entrance tube in species such as *T. denoiti* encumbers cooling by fanning, but the depth of the nests (60–100 cm) in the ground is sufficient to achieve a stable nest temperature even when ambient temperatures are high (Moritz and Crewe, 1988). When Moritz and Crewe (1988) recorded the temperature in nests of *T. denoiti* in Transvaal, South Africa, at an outside air temperature of 60.9 °C the internal temperature of a *T. denoiti* nest remained at 32 °C (Moritz and Crewe, 1988).

2.3.2 Wasps

Some social wasp species also build specific structures, sometimes within existing cavities, which help maintain stable nest temperatures. These mechanisms vary from constructing combs inside a cavity to building an exposed comb of heat-conserving shape and size, and even producing heat-generating thermoelectric pupal caps.

Species in the wasp subfamilies Vespinae and Polistinae utilize different thermoregulatory mechanisms and differ in their abilities to regulate nest temperature. These differences are mainly due to the contrasting nest architecture between the two groups. Polistinae nests consist of exposed comb, so effective thermoregulation of the brood relies predominantly on the environment at the site chosen for the nest (Jeanne and Morgan, 1992). Vespinae nests are enclosed by a thick paper jacket, which for many species is constructed inside a naturally-occurring cavity. Therefore, heat generated inside the nest can be stored and the nest temperature regulated (Gibo *et al.*, 1974a, 1974b; Seeley and Heinrich, 1981; Martin, 1988, 1992).

Foundresses or *Polistes riparius* of northern Japan, build what has been called a ‘functional envelope’ (Yamane and Kawamichi, 1975). The foundress constructs a number of empty cells at the side and lower periphery of the vertical nests and elongates the cells beyond the length of the pupal cocoons (Fig. 7). Other species, also occurring in cooler regions, construct their nests in this way (Yamane, 1988; Hozumi and Yamane, 2001). Hozumi and Yamane (2001) used paper models under field conditions to

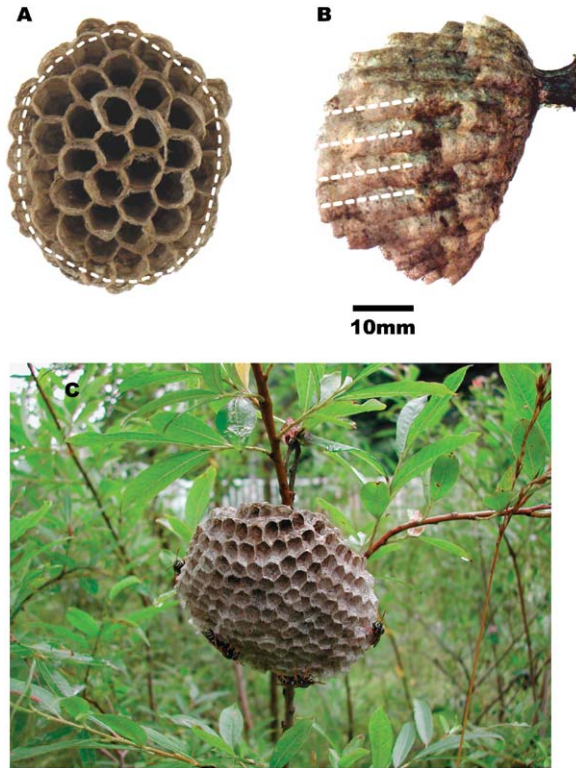


FIG. 7 The 'functional envelope' of the nest comb of *Polistes riparius* (Photos courtesy of Satoshi Hozumi). (A) View from the cell entrance of a *P. riparius* nest, the white circle indicates the brood area of the nest bordered by empty cells. (B) Lateral view of *P. riparius* nest, white lines show elongation of the cells beyond cocoon lengths. The nest shown in (A) and (B) was collected during the founding stage, just before the emergence of workers. (C) A mature nest of *P. riparius* in the field.

identify the role of the functional envelope in thermoregulation. Models with more or longer cells maintained temperatures above ambient for most of the night (Hozumi and Yamane, 2001). The extra cells presumably increase the ability of the colony to retain warmth, and provide some protection from wind and dew.

Comb shape also influences the thermal characteristics of exposed wasp nests. Yamane (1988) compared brood cell temperatures between two nest architectures in the tropical region of Padang, Sumatera Barat – the slender vertical comb of *Ropolidia variegata jacobsoni* and the oblong vertical comb of *R. fasciata*. When exposed to solar radiation, the slender combs of *R. variegata* were significantly cooler than those of *R. fasciata*. This difference probably arises because at least one side of the wall of all

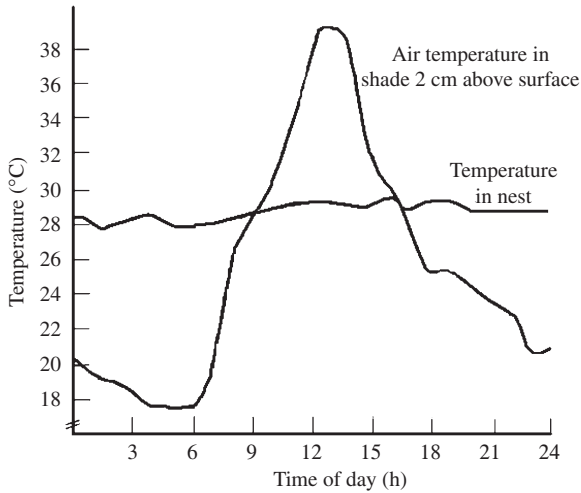


FIG. 8 The effect of exposure of the nest of the hornet *Vespa orientalis* to solar radiation during a 24 h period (courtesy Professor Jacob S. Ishay, reproduced with permission of Elsevier (Ishay and Barenholz-Paniry, 1995) and Rentokil Pest Control). The silk pupal caps help keep the temperature of the pupa stable.

cells of *R. variegata* are exposed, which facilitates radiation of heat (Yamane, 1988). This difference may explain the preferred nest sites of these two species. *R. variegata* often nests at sites constantly exposed to direct sunlight, whereas *R. fasciata* nests in shady sites, like the underside of broad evergreen leaves (Yamane, 1988).

The silk caps of pupal cells of *Vespa orientalis* assist in thermoregulating the brood (Ishay and Barenholz-Paniry, 1995). There are two main characteristics of the silk coating and the layer between the silk and pupa that help in thermoregulation. First, the silk layer insulates the pupae. Second, it acts as an energy accumulator which stores electrical charge during periods when there is heat available and releases the energy as heat during cooler temperatures (Ishay and Barenholz-Paniry, 1995). Figure 8 shows that the silk surrounding the pupae, particularly the silk caps, help regulate pupal temperature. The regulating effect of the silk is also localized and cells containing no brood (and having no cap) have a lower temperature (Joseph and Ishay, 2004).

2.3.3 Termites

Termite nests are often significant structures, which include intricate features for controlling the temperature of the chambers within. In mound-building species, variation in wall thickness, mound surface design or projecting structures, and as we have already seen, mound orientation,

are some of the nest characteristics that help provide a stable nest temperature. In addition, termite mound architecture is important for gas exchange.

The nest architecture of the termite *Macrotermes bellicosus* is an important contributor to effective nest thermoregulation. This species inhabits the Comoé National Park of the north-eastern Ivory Coast in West Africa, where there are two main habitat types: shrub savannah and gallery forest (Korb and Linsenmair, 1998b). Temperatures in the shrub savannah are generally higher and more variable than in the gallery forest. *M. bellicosus* appropriately adjusts the architecture of its nest to optimize nest thermoregulation in these different habitats. Mounds in the warmer savannah are relatively thin-walled and 'decorated' with numerous ridges and turrets. By contrast, mounds in open stands of the cooler gallery forest are dome-shaped and have thick walls with few projecting structures (Fig. 9). Thus, relative to the heat-dissipating architecture of the savannah mounds, mounds in the forest have reduced surface area and retain more heat (Korb and Linsenmair, 1998a,b, 1999).

Korb and Linsenmair (1998b) demonstrated the importance of nest architecture in thermoregulation by reducing the level of shading of forest-dwelling mounds, so that they experienced temperatures more like those in the savannah. In response to this manipulation, workers increased the surface complexity of their mounds until they resembled mounds in the savannah. Mounds in the gallery forest were found to have higher heat capacities than mounds of similar height in the shrub savannah, due to their thick walls. The temperature at the centre of the nest, where the brood chambers, fungus garden and the royal cell are, are kept at about 30 °C in the shrub savannah habitat. The cooler forest habitat, and ventilation requirements (see below), means that the interior of the mounds of the gallery forest are about 2 °C lower than those in the shrub savannah, despite the structural modifications to the nest's exterior. This means that the gallery forest is a suboptimal thermal habitat because 30 °C is the optimal temperature for the growth and development of termites, and for fungus cultivation (Korb and Linsenmair, 1998b).

The architecture of termite mounds is also important for effective ventilation of the nest and a large variety of nest structures are used to control ventilation; from enormous chimney projections, to air passages close to the surface in enclosed mounds with no chimney (Luscher, 1961; Weir, 1973; Darlington, 1984; Turner, 1994, 2001; Korb and Linsenmair, 2000b). The structure of the nest must satisfy the dual needs of effective ventilation and temperature regulation. For example, Korb and Linsenmair (2000b) showed that there is a trade-off between temperature regulation and gas exchange in the mounds of *M. bellicosus* in the cooler habitat of the gallery forest. In the forest habitat, the termites construct dome-shaped mounds with thick walls and reduced surface areas to reduce heat loss, but the

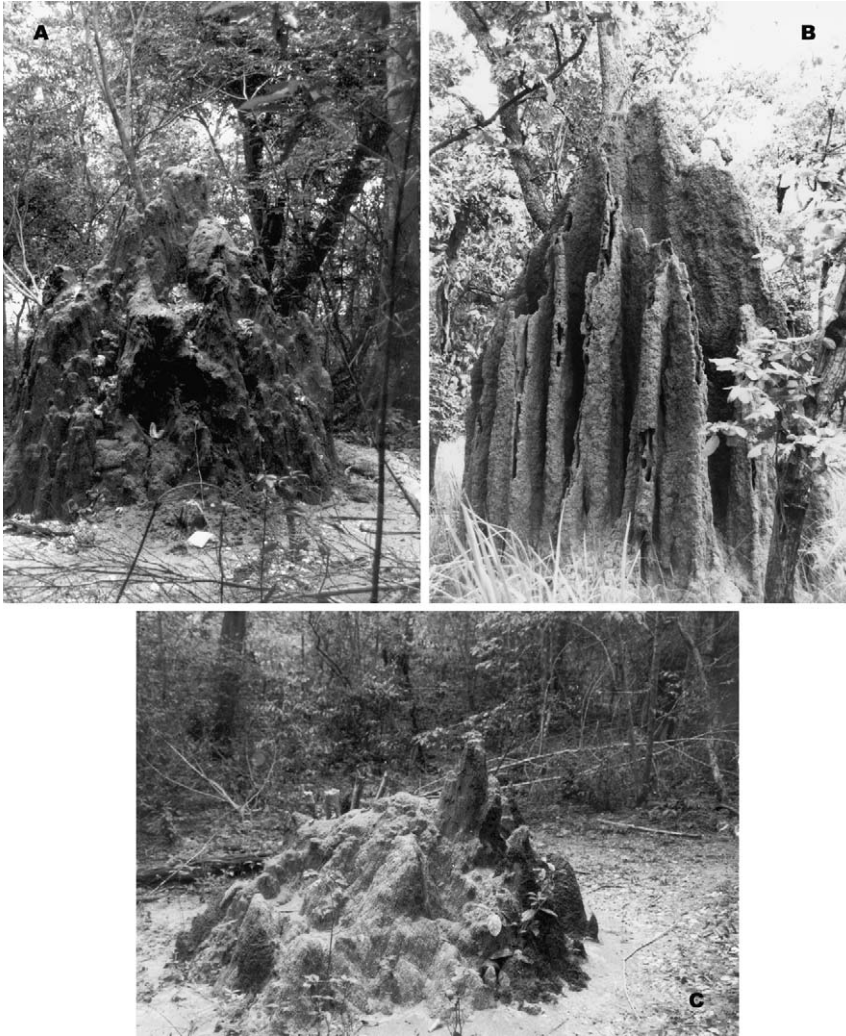


FIG. 9 *Macrotermes bellicosus* mounds in the Comoé National Park, West Africa (Photos courtesy of Judith Korb, reproduced with permission of Springer Science and Business Media; Korb, 2003). (A) Large gallery forest mound, (B) large savannah mound, and (C) small gallery forest mound.

reduction in surface area is constrained by the need to exchange respiratory gases; termites and their fungi have a high metabolic rate. In these mounds, gas exchange is limited almost entirely to the surface at the crest of the mound. By contrast, in savannah mounds, temperature does not restrict the amount of surface area available for gas exchange and respiratory gases are exchanged by holes across the entire surface of the mound.

Consequently, the interior of forest mounds have higher CO₂ concentrations than savannah mounds (Korb and Linsenmair, 2000b).

3 Active nest thermoregulation

In addition to passive thermoregulatory mechanisms, at least some species from most major social insect taxa actively heat or cool their nests. Some behaviour, such as clustering and generating metabolic heat to keep the colony warm at cool ambient temperatures (ants, termites, bees and wasps) and fanning of the wings to drive warm air out of the colony at warm ambient temperatures (bees and wasps), are common to different species, and even orders.

3.1 ACTIVE COLONY RESPONSES TO LOW TEMPERATURES

3.1.1 *Bees*

One of the behavioural responses of most, if not all, social bee species to low temperatures is clustering. Workers are able to maintain stable brood nest temperatures at low ambient temperatures by forming tight clusters on or around the brood area and generating metabolic heat. Workers adjust the cluster shape and density by moving closer together or further apart, allowing them to fine-tune their response to temperature change.

Clustered bees generate metabolic heat (Free and Simpson, 1963; Fahrenheit *et al.*, 1989), primarily by rapidly contracting and releasing their thoracic flight muscles (Kronenberg and Heller, 1982), while the muscles are disengaged from the wings. Below an ambient temperature of about 15 °C, honey bee (*A. mellifera*) workers, for example, gather together in a compact spherical cluster covering the brood (Kronenberg and Heller, 1982). Clustering reduces colony heat loss because the surface area available for heat exchange is minimized (Seeley, 1985). Both cavity- and open-nesting Asian honey bees have similar clustering behaviour to the European honey bee (Dyer and Seeley, 1991). For example, in the open-nesting species *A. florea* and *A. dorsata*, the workers who form a curtain over the comb move closer together at low ambient temperatures (Fig. 10). In *A. mellifera*, the threshold for clustering may be lower in the absence of brood than when it is present (Kronenberg and Heller, 1982). During winter, when there is no brood, variations in the colony temperature is larger than when the brood is present, despite the fact that workers still form clusters and generate metabolic heat using their flight muscles (Fahrenheit *et al.*, 1989; Stabentheiner *et al.*, 2003).

Stingless bees use strategies similar to that of honey bees for warming their nests. When exposed to cool ambient temperatures *Trigona denoiti* and



FIG. 10 *Apis florea* colony (Photo courtesy of Nadine Chapman). Workers that form the protective curtain covering the comb move closer together at low ambient temperatures, and further apart at high ambient temperatures.

Scaptotrigona postica workers are able to generate heat within the nest, presumably by clustering on the brood and quivering their flight muscles (Fletcher and Crewe, 1981; Engels *et al.*, 1995). However, *S. postica* also uses other mechanisms to retain thermal energy; workers gather small pieces

of cerumen in their mandibles and plaster the coldest area of the brood nest with a thick layer. Also, foraging is curtailed and the comb surface is covered with 1–2 layers of slowly moving bees (Engels *et al.*, 1995).

3.1.2 Wasps

Like honey-bee colonies, mature colonies of Vespine wasps can maintain constant nest temperatures (Gibo *et al.*, 1974a,b; Makino and Yamane, 1980; Martin, 1988, 1992). As their nests are enclosed, heat generated inside can be retained to keep the nest warm. Adult wasps congregate on top of the brood to increase nest temperature (Ishay, 1973) and probably produce heat in a similar fashion to honey-bee workers. In addition, adults also warm the nest by blowing warm air from the tracheal openings towards the pupae in their cocoons or even on pupae that have been extracted from their cocoons (Ishay and Barenholz-Paniry, 1995). The larvae of hornet brood are also thought to play a role in nest warming by activating their muscles (Ishay and Barenholz-Paniry, 1995). However, in some species, the ability of a colony to produce heat and maintain an elevated nest temperature depends on the season and reproductive stage of the colony. After the production of reproductives, and when the nest population declines, the thermoregulatory ability of the colony may also decline (Gibo *et al.*, 1974a,b). Martin (1988) suggests that the key to maintaining a constant nest temperature ($\sim 29^\circ\text{C}$ in *Vespa simillima xanthoptera*) is the maintenance of the colony biomass/worker activity above a level where heat production is greater than heat loss, even in the absence of the founding queen.

3.1.3 Termites

Some termites generate metabolic heat and cluster together to achieve stable nest temperatures. In the Australian termites *Coptotermes acinaciformis* and *C. frenchi*, the bark and wood of the living tree, and the walls of the nursery provide effective insulation, retaining heat within the nursery (Greaves, 1964). In colonies of both species, a difference of up to 20°C is recorded between the metabolically-generated temperature at the centre of the nursery and the centre of an uncolonized tree (Greaves, 1964). The area of elevated temperature in the nursery is smaller in winter than in summer, suggesting that the termites aggregate in winter (Greaves, 1964).

3.1.4 Ants

Ants also gather together and generate heat. Similar to bees, both open- and mound-nesting species use comparable mechanisms for maintaining stable nest temperatures.

On cold days in early spring, workers of the red wood ant *Formica* species often engage in 'sunning behaviour' in which clusters of workers aggregate on the nest surface to absorb solar radiation (see above). However, in a behaviour remarkably similar to that of clustering honey bees and Vespine wasps, *Formica* workers in large nests are able to aggregate at the centre of their nest where they can generate an internal nest temperature of 25–30 °C, even when the ambient temperature is around 0 °C (Rosengren *et al.*, 1987). Thus, large nests are mostly independent of the need for solar radiation to achieve nest temperatures at which workers can be metabolically active. In contrast, workers in smaller colonies must engage in basking to allow nests to achieve a temperature where workers can be active. In large colonies, the heat-dependent activation of ant metabolism after the winter dormancy period may rely on positive feedback, where once some of the ants become warm enough for their metabolism to be activated, their activity warms other workers, and this can take place within the nest rather than relying on basking (Rosengren *et al.*, 1987).

Army ants form nests or bivouacs in which the bodies of workers make up the shelter by interlocking their tarsal claws. The thermoregulatory properties of bivouacs have been studied in *Eciton hamatum* and *E. burchelli*, two neotropical species that nest above the ground in open cavities, such as under the trunks of fallen trees (Schneirla *et al.*, 1954; Jackson, 1957; Franks, 1989). The workers of both species maintain a uniform temperature in the centre of the bivouac where the brood is located. For example, *E. burchelli* workers maintain the central nest temperature at about 28 °C with a variation of only 2 °C, although the ambient temperature of their rainforest habitat only varies by about 6–7 °C (peaking at 27 °C and falling to a minimum of 22 °C). In *E. burchelli* colonies, the heat required to maintain optimal temperatures for the brood is attained by the metabolic activity of the workers within the bivouac. Workers regulate the temperature by forming or closing ventilation channels within the nest structure (Franks, 1989). Bivouacs also change shape diurnally, becoming smaller and reducing their surface area to volume ratio when it is cold (Franks, 1989). Thermoregulation in honey-bee swarms (see Section 4.1) has remarkable parallels with army ant bivouacs.

3.2 DIRECT INCUBATION

3.2.1 *Bees and wasps*

In embryo nests of *Vespa simillima*, queens warm their brood by 2.5–4 °C above ambient by 'curling' behaviour, in which the queen curls her body around the pedicel of the nest (Makino and Yamane, 1980). When the first larvae appear, they too contribute to heat production in the colony (Gibo

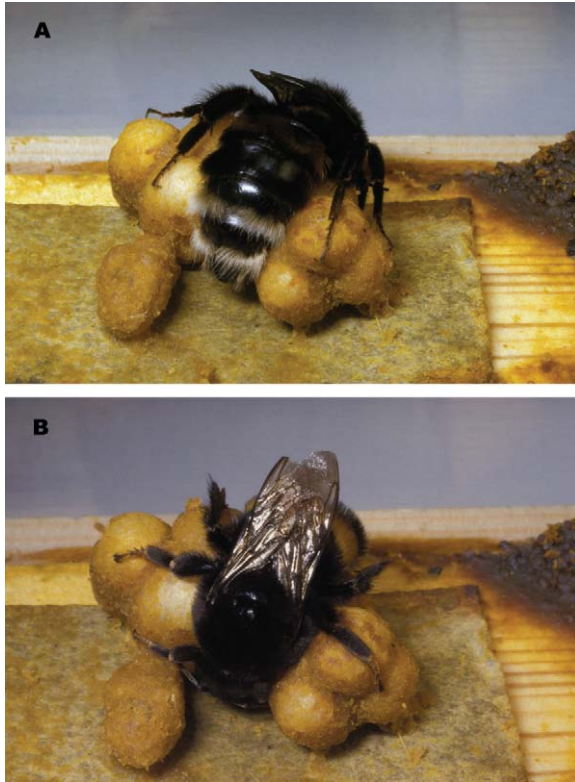


FIG. 11 A bumble bee (*Bombus terrestris*) queen incubating her brood clump (A) and (B) (Photos courtesy of Madeleine Beekman).

et al., 1977). Hornet workers directly incubate the brood by entering empty cells adjacent to pupae and placing their abdomen against the cocoon and pumping their abdomen to generate heat (Ishay, 1973).

During colony founding in bumble bees, the queen wraps herself around the brood clump and faces towards the honey pot whenever she is not foraging (Fig. 11). The queen presses her abdomen on to the brood clump to both insulate and incubate the brood (Heinrich, 1974a). While incubating, the queen produces heat in her thorax and distributes it to her abdomen (Heinrich and Kammer, 1973) by abdominal contractions (Heinrich, 1979). She also deposits a pheromone when she lays eggs, which allows her to restrict her incubation efforts to the area of the nest that contains the brood (Heinrich, 1974b). As the colony size increases, adult bees (both workers and drones) incubate the nymphs. By modulating metabolic activity, adults are able to regulate their abdominal temperature and therefore maintain the brood temperature within a narrow range (Heinrich, 1972). Incubating bees maintain their thorax (which provides

heat flow to the abdomen) between 34.5°C and 37.5°C even when the ambient temperature varies from 3°C to 33°C.

Incubation behaviour in response to low temperatures has also been reported for individual honey-bee workers (Bujok *et al.*, 2002). Incubating workers assume a crouched posture, in which they press their warm thoraces onto the brood cell caps. Bujok *et al.* (2002) used thermographic infrared images of brood comb to reveal 'hot spots' on the capped brood area, where individual workers had been pressing their thoraces. Similar to social wasps, workers also heat the brood by entering empty cells directly adjacent to brood cells and maintaining a warm thoracic temperature (Kleinhenz *et al.*, 2003).

3.3 ACTIVE COLONY RESPONSES TO HIGH TEMPERATURES

3.3.1 *Bees and wasps*

Social insects, predominantly bees and wasps, also use behavioural responses to cool moderately high nest temperatures (Table 1). The most common cooling behaviours, possible only in species where workers are alate, are wing fanning (where workers fan their wings, while standing in a stationary position, to drive warm air away from the nest, as shown in Fig. 1) and evaporative cooling (where workers collect water and place droplets on the surface of the brood comb).

At high ambient temperatures, both cavity- and open-nesting honey-bee workers fan the nest with their wings (Hazelhoff, 1954; Dyer and Seeley, 1991). Cavity-nesting bees fan on the combs inside their nest and also at the nest entrance, while open-nesting bees fan on the surface of workers that form the protective curtain over the nest (Oldroyd *et al.*, 1994). Fanning direction appears to be important in temperature regulation. For example, *Apis mellifera* workers face towards the nest when fanning, whereas *A. cerana* and *A. koschevnikovi*, which are also cavity-nesting species, workers face away from the nest (Sakagami, 1960). In the open-nesting dwarf species *A. florea*, workers fan facing up the comb, whereas *A. andreniformis*, another open-nesting dwarf species, workers fan facing down the comb (Thapa and Wongsiri, 1994). It would be interesting to model what effect fanning direction has on nest thermoregulation.

Bumble bees, stingless bees, and *Polistes* and *Vespula* wasps also fan their nests to regulate nest temperature (Hasselrot, 1960; Moritz and Crewe, 1988; Jeanne and Morgan, 1992; Hunt *et al.*, 1995; Riabinin *et al.*, 2004; Roubik, 2006).

Honey bees, paper wasps and hornets use water evaporation to cool their nests. In this behaviour, workers distribute water throughout the nest, placing it in the small hollows that form on the margins of capped brood cells (Lindauer, 1954; Ishay and Barenholz-Paniry, 1995). Honey bees



FIG. 12 An *Apis dorsata* colony. Workers are spread out on the comb to reduce brood nest temperature (Photo by Ben Oldroyd).

(both cavity and open nesting) also spread water across the rim of open cells. Tongue lashing is also employed, in which workers draw a water droplet into a thin layer with their tongue (Lindauer, 1954; Dyer and Seeley, 1991; Jacklyn, 1992). Effective evaporative cooling requires appropriate coordination between water foragers and workers using water in the nest (Lindauer, 1954; Moritz and Southwick, 1992). The unloading time experienced by returning water foragers provides them with information on the water demands of the colony. In a heat-stressed colony, returning foragers are rapidly unloaded by hive bees and this informs the other foragers that they should continue foraging (Lindauer, 1954).

Also, cavity-nesting honey-bee workers partially evacuate their nest (Dunham, 1931) at high ambient temperatures. Similarly, in open-nesting species, temperature is regulated by changes in the density of the curtain of workers that surround the nest – at high temperatures the curtain becomes very loose (Dyer and Seeley, 1991) (Fig. 12). Evacuation, and presumably large spaces between bees on an exposed comb, reduces brood nest temperature because workers avoid releasing the waste heat of metabolism within the nest. Thus, leaving the nest is more efficient than actively regulating the temperature (Dunham, 1931). The giant honey bees (*A. dorsata* and *A. laboriosa*) have an additional mechanism that may also help reduce the temperature of the nest (Seeley *et al.*, 1985; Mardan, 1989; Batra, 1996; Kastberger *et al.*, 1996; Woyke *et al.*, 2000). A large number of the bees (approx. 20% of the colony) depart from the nest for 3–5 min before returning to the nest (Kastberger *et al.*, 1996; Woyke *et al.*, 2003). On some

occasions, the departing bees synchronously defecate – possibly helping to rapidly reduce the temperature of heat-stressed insects (Mardan and Kevan, 1989). In cavity-nesting bees (*A. mellifera*), workers may shield the brood comb from high ambient temperatures by positioning themselves on hot interior regions of the nest walls (Starks and Gilley, 1999).

During the warmest part of the day, workers of the nocturnal neotropical wasp *Apoica pallens* retreat from the margins of their nest, exposing numerous cell rows. At the same time, wasps at the margins of the cluster rest with their heads inside comb cells (Hunt *et al.*, 1995). Similar to the giant honey bees, hundreds of wasps may briefly depart their nest in the early evening (Hunt *et al.*, 1995). This behaviour may also be related to regulating nest temperature.

Stingless bees also actively ventilate their nests; workers fan their wings within the nest while facing outwards, towards the entrance (Moritz and Crewe, 1988; Roubik, 2006). Fanning allows the nest to ‘breathe’, whereby air is exchanged frequently in a ‘tidal’ fashion. In two African species, *T. denoiti* (ground-nesting) and *T. gribodoi* (tree cavity-nesting), all air in the nest is exchanged every 1–7 h (Moritz and Crewe, 1988). Despite small entrance tubes being the only opening in some nests, fanning probably also helps regulate nest temperature (Fletcher and Crewe, 1981; Moritz and Crewe, 1988). As with some termite nests, there appears to be a trade-off between ventilation and temperature regulation in *T. denoiti*, where gas exchange is reduced during the day to prevent the nest becoming overheated. During the day, the volume of air moving in and out of a *T. denoiti* colony is considerably less than at night. Reduced air circulation during the day apparently prevents overheating, as only a small amount of fresh but hot air is drawn into the nest. However, lack of ventilation is associated with an increase in CO₂ levels. During the night, when the outside air is cooler, the volume of air moving through the nest is significantly greater than during the day. Therefore, CO₂ levels are reduced by active ventilation only at night. In contrast, in *T. gribodoi* the ‘breathing’ frequency is higher than in *T. denoiti*, probably because the temperatures experienced by nests are not as severe (a maximum of 36 °C outside in the shade of the tree, compared with as high as 60 °C during the day at the soil surface outside a *T. denoiti* nest entrance). Moritz and Crew interpreted this ‘breathing’ in both nest types as evidence for worker fanning within the nest cavity. Both species were able to maintain constant nest temperatures despite variations in ambient temperature (Moritz and Crewe, 1988). It would be interesting to test the mode of gas exchange in individuals of each species. We suggest that gas exchange mechanisms at the individual level may be in line with ventilation (by fanning) mechanisms at the colony level. Under the chthonic hypothesis for the evolution of the discontinuous gas exchange cycle (DGC) in insects, where the DGC is thought to optimize gas exchange in hypoxic and or hypercapnic environments (Lighton, 1998;

Chown *et al.*, 2006), we might expect *T. denoiti* to use the DGC and *T. gribodoi* to use a more continuous gas exchange system. In addition, it may be possible that *T. denoiti* uses the DGC during the day and a more continuous mode of gas exchange at night, similar to the colony-level variation in ventilation.

Fanning by stingless bee workers has also been reported in *S. postica* (Roubik and Peralta, 1983; Engels *et al.*, 1995), where workers fan towards and inside the entrance tube, and we have personally observed workers fanning in nests of *Asutroplebia australis*. However, like bumble bees, stingless bees apparently do not use evaporative cooling for thermoregulation; spreading of water across the cells or tongue lashing has never been reported (Engels *et al.*, 1995). For species occurring in warm climates, the nest cavity is the colony's primary means of protection from high ambient temperatures. Thus, for species like *S. postica*, which nest inside tree trunks above the understorey vegetation, exposure to extremely high temperatures is unlikely and cooling is probably unnecessary. In contrast, temperatures significantly lower than the brood nest range (32 ± 3 °C) occur nearly every night, and therefore warming is a daily requirement for effective nest thermoregulation (Engels *et al.*, 1995).

4 Coordination of thermoregulation

In the previous sections, we surveyed the many active and passive mechanisms that social insect colonies use to regulate the temperature of their brood. We have described the activities of individual workers that engage in behaviour such as wing fanning or brood transportation to help regulate temperature. However, the efforts of individual workers (Table 1) would be in vain if there were no overarching mechanisms that result in a colony-level outcome of a stable brood nest temperature that is close to that required for normal development of the brood. Understanding these overarching systems is currently an area of active research (see Camazine *et al.* (2001) for a recent comprehensive review).

When we humans install an air-conditioning system, we install a control unit that monitors the temperature of the rooms and directs the refrigeration unit to turn on or off in response to the current temperature. Such a control system is completely centralized. A social insect nest, in contrast, has no such centralized control. Control is distributed among all the workers of the nest. Each worker monitors the condition of her own environment and will engage or not engage in a task, depending on her perception of the appropriate response. Key to understanding these systems of distributed control is to perceive how the simple rules followed by individual workers in response to very localized information can nonetheless result in well-regulated colony-level outcomes.

4.1 THE TASK THRESHOLD MODEL

Social insect nests can be regarded as ‘complex systems’; those in which patterns at the global level emerge solely from many interactions among the lower-level components (Camazine *et al.*, 2001). The emergent behaviour of the group of interacting agents cannot be predicted from the behaviour of any one agent, yet the group behaviour is often highly predictable from the behaviour of an average agent. In the case of social insect nests, the agents are individual workers, and the emergent ‘self-organized’ behaviour is the colony-level phenotype – some phenomenon like a stable brood nest temperature.

Modelling studies have shown how a colony-level outcome, such as the temperature at the centre of a swarm of honey bees or a bivouac of army ants can be precisely regulated solely by individual bees responding to their own body temperature, and without the need for communication among workers. A honey-bee swarm is a combless cluster of about 10,000 workers, a queen and a few drones. The swarm issues from a parent colony and hangs in a rugby football-shaped clump some metres from its parent colony. The swarm needs to regulate its core temperature in such a way as to conserve food reserves (contained in the stomachs of the workers), while maintaining a large number of active workers who are sufficiently warm so that they can scout for new nest sites (see Winston, 1987 for review).

Empirically, we know that workers in the centre of a honey-bee swarm maintain a temperature very close to 35°C. These warm bees are surrounded by a mantle of cooler bees, whose temperature is about three degrees above ambient (Nagy and Stallone, 1976). Workers regulate the temperature of the swarm cluster by producing metabolic heat and by adjusting the compactness of the swarm cluster – denser when it is cold, and looser when it is warm.

Two mathematical models based on partial differential equations describing heat flux through a swarm cluster that changes density in response to temperature show that a qualitatively similar outcome to real-world swarms (stable core temperature and changing density of the cluster) can be achieved solely by workers responding to their own core temperature by adjusting their metabolic rate and closeness to their neighbours (Myerscough, 1993; Watmough and Camazine, 1995). These models demonstrate that communication among workers within the swarm is not required in order to achieve the colony-level phenotype – the outcome is entirely self-organized. Of course, these modelling results do not mean that workers in a swarm do not communicate (for example, by pheromones or sounds) to help them regulate the temperature of the swarm, only that communication and coordination is not necessary to achieve a precise core temperature. As we have no evidence that there is communication about thermoregulation within a swarm of honey bees, it seems likely that mechanisms such as those postulated by Watmough and Camazine are a good approximation of reality.

4.2 COORDINATION WITH COMMUNICATION

Although the models discussed above are *prima facie* evidence that communication among individual workers is not necessary to regulate the temperature in the core of a swarm of honey bees, in other systems workers *do* communicate with each other. Communication is necessary when individual workers are required to assess the needs of their colony as a whole and cannot directly make such an assessment individually. These mechanisms requiring communication are still entirely self-organized, and operate in the absence of a centralized control.

A good example of a self-organized system in which inter-individual communication is important is the means by which a honey-bee swarm selects a new nest site (Seeley and Buhrman, 1999, 2001; Britton *et al.*, 2002; Seeley and Visscher, 2003, 2004; Janson *et al.*, 2005). Other examples include the regulation of water collection by honey-bee colonies (see Seeley, 1995 for review).

A further example in which communication using pheromones and environmental cues is important, is the construction of termite mounds. Modelling studies, based on behavioural studies using varying levels of 'real' life parameters, have shown how following simple communication rules, such as 'I will build here because others have', can result in intricate nest mounds of large proportions. 'Architectural' differences in mound structures can emerge, not necessarily because of a change in individual behaviour, but due to changes in local environmental cues. Diversity in the landscape, often caused by previous building activities of the termites themselves or variation in pheromone levels, and differences in environmental conditions, such as wind, enable the construction of different architectural components of the nest, such as pillars or walls (Bonabeau *et al.*, 1998; Ladley and Bullock, 2005). For example, evenly spaced pillars are constructed by termite builders which are attracted to 'cement pheromone' given off by recently deposited building material. A positive feedback loop is established where initially, building material is picked up, moved and deposited at random, but a tendency to deposit material where there is a high level of cement pheromone causes a concentration of deposition in certain spots, thus generating the pillars. More complex structures can arise from variations in this theme, caused by environmental cues. For example, a more open structure may be built at high temperatures when pheromones disperse rapidly.

4.3 THE IMPORTANCE OF INTER-INDIVIDUAL VARIABILITY

As we have seen, an effective thermoregulation system such as that which probably occurs in honey-bee swarms and army ant bivouacs can emerge from a set of simple rules followed by each individual worker (e.g.

Bonabeau *et al.* (1996)). In theory, the number of individuals involved in nest ventilation could be regulated by the simple rule: 'if air temperature is above 35 °C then fan wings'. If the temperature is high, the stimulus to act is high, whereas if the temperature is low, no worker will ventilate. Such a rule would result in a brood nest temperature that is closer to 35 °C than ambient. However, nest thermoregulation is so precise that in all probability more sophisticated systems are used to regulate the number of fanning workers.

Returning now to our air-conditioner analogy, consider a single old-fashioned wall unit with its single thermostat situated within itself. As the thermostat detects that incoming air is lower than a certain user-set temperature, it switches off the refrigerator unit. As the temperature of the incoming air rises, the thermostat then switches the refrigerator back on. Since this kind of a system can only be either on or off, and because the regulatory unit and the cooling unit are co-located, there is a strong tendency for the room temperature to oscillate around the desired temperature while rarely being at the desired temperature. A system that is more likely to achieve a stable temperature will deploy multiple thermostats distributed around the room and several refrigeration units whose output can be modulated. Such a system is capable of a graded response to temperature change: when only one thermostat achieves its threshold temperature, only one cooling unit is switched on.

We argue that intrinsic variability of workers comprising a social insect colony can be an important component of an efficient thermoregulatory system. Agent-based modelling by Myerscough and Oldroyd (2004) has shown that if all members of a social insect colony have precisely the same threshold for engaging in a task like nest heating, the emergent property of the system can be unstable. Rather, like the old-fashioned air-conditioner, the workers are either all on or all off, leading to wild oscillations in temperature around the threshold temperature (Myerscough and Oldroyd, 2004; Graham *et al.*, 2006). In contrast, modelling shows that if workers in a nest have a range of thresholds for engaging in nest thermoregulation, and these thresholds average out at the target temperature, then the colony-level outcome is much more stable than if all workers have the same threshold. This somewhat counter-intuitive outcome is analogous to the room monitored by several thermostats regulating independent cooling units.

In bumble-bee colonies, workers do indeed differ in their response thresholds for the behaviour of fanning (O'Donnell and Foster, 2001; Weidenmuller, 2004) and in other response parameters important for nest climate control. Some individuals fan every time they are exposed to a stimulus intensity exceeding their threshold, while others fan only rarely (Weidenmuller, 2004). Workers also vary in how persistently they respond to a given stimulus intensity. Weidenmuller's (2004) study provides

evidence that reinforcement is important for task specialization. The temperature threshold that would induce individual workers to commence fanning decreased across trials; thus workers with low thresholds are more likely to become specialists because their threshold will be reached more often. For bumble bees, where the queen usually mates with a single male, it is unclear what causes these differences in individual responsiveness.

In some species, especially honey bees, variance in task threshold seems to be genetically determined (reviewed in Oldroyd and Thompson, 2007) while in others, e.g. some termites whose colonies arise from a single king and queen, variance can arise from environmental factors such as larval feeding (reviewed in Oster and Wilson, 1978; Fraser *et al.*, 2000). Jones *et al.* (2004) provided empirical support for the intuitions derived from modelling: a direct link between genotypic diversity, genetically-based task specialization and an improved colony-level phenotype. First, Jones *et al.* (2004) demonstrated that genetically diverse colonies are, on average, better able to regulate the temperature of their brood nest during a short (1 h) period of extremely high temperature (40 °C) and at fluctuating ambient temperatures over a period of one week. Second, they showed that the distribution of patriline in fanning and non-fanning workers is non-random. Third, they illustrated that the distribution of patriline in fanning and non-fanning workers changes with ambient temperature.

5 Conclusions

In this review we have shown that temperature regulation in social insect nests can be remarkably precise and may involve a variety of heating and cooling mechanisms coordinated without the benefit of an individual thermo-director. We have highlighted two main issues. First, a variety of often very similar strategies for temperature regulation have evolved in different social insect groups. Some mechanisms, such as clustering and building nest structures that aid in temperature control, span many taxa. Others, such as the bizarre electro-heating pupal caps of *Vespa orientalis* appear to be unique. Second, we have explored how the simple actions of many individuals combine to form a colony-level outcome that can maintain optimal brood nest temperatures. We have given examples of the rules and mechanisms behind coordinated colony responses to temperature change in honey bees. Examples of collective thermoregulatory behaviour from other species are less well explored.

Nest thermoregulation is a useful model system for studying the mechanisms of self-organization in social insect nests, because temperature, both ambient and inside the nest, can be easily quantified and compared across species.

References

- Arias, M. C. and Sheppard, W. S. (2005). Phylogenetic relationships of honey bees (Hymenoptera: Apinae: Apini) inferred from nuclear and mitochondrial DNA sequence data. *Mol. Phyl. Evol.* **37**, 415–422.
- Avitabile, D. P., Donovan, K. J. and Stafstrom, D. P. (1978). Natural nest sites of honeybee colonies in trees in Connecticut, USA. *J. Apic. Res.* **17**, 222–226.
- Batra, S. W. (1996). Biology of *Apis laboriosa*, a pollinator of apples at high altitude in the Himalaya range of Garhwal, India (Hymenoptera: Apidae). *J. Kans. Entomol. Soc.* **69**, 177–181.
- Bollazzi, M. and Roces, F. (2002). Thermal preference for fungus culturing and brood location by workers of the thatching grass-cutting ant *Acromyrmex heyeri*. *Ins. Soc.* **49**, 153–157.
- Bonabeau, E., Deneubourg, J. and Theraulaz, G. (1996). Quantitative study of the fixed threshold model for the regulation of division of labour in insect societies. *Proc. R. Soc. Lond. B.* **263**, 1565–1569.
- Bonabeau, E., Theraulaz, G., Deneubourg, J., Franks, N. R., Rafelsberger, O., Joly, J. and Blanco, S. (1998). A model for the emergence of pillars walls and the royal chamber in termite nests. *Philos. Trans. R. Soc. Lond. B.* **353**, 1561–1576.
- Brian, M. V. (1963). Studies of caste differentiation in *Myrmica rubra* L. *Ins. Soc.* **2**, 91–102.
- Brian, M. V. (1973). Temperature choice and its relevance to brood survival and caste determination in the ant *Myrmica rubra* L. *Physiol. Zool.* **46**, 245–252.
- Britton, N. F., Franks, N. R., Pratt, S. C. and Seeley, T. D. (2002). Deciding on a new home: how do honeybees agree? *Proc. R. Soc. Lond. B.* **269**, 1383–1388.
- Bujok, B., Kleinhenz, M., Fuchs, S. and Tautz, J. (2002). Hot spots in the bee hive. *Naturwissenschaften* **89**, 299–301.
- Cabrera, B. J. and Kamble, S. T. (2001). Effects of decreasing thermophotoperiod on the Eastern subterranean termite (Isoptera: Rhinotermitidae). *Environ. Entomol.* **30**, 166–171.
- Cabrera, B. J. and Rust, M. K. (1996). Behavioral responses to light and thermal gradients by the Western drywood termite (Isoptera: Kalotermitidae). *Environ. Entomol.* **25**, 436–445.
- Camazine, S. (1991). Self-organizing pattern formation on the combs of honey bee colonies. *Behav. Ecol. Sociobiol.* **28**, 61–76.
- Camazine, S., Visscher, P. K., Finley, J. and Vetter, R. S. (1999). House-hunting by honey bee swarms: collective decisions and individual behaviors. *Ins. Soc.* **46**, 348–360.
- Camazine, S., Deneubourg, J., Franks, N. R., Sneyd, J., Theraulaz, G., Bonabeau, E. (2001). What is self-organization? *Self-Organization in Biological Systems*. Princeton, NJ: Princeton University Press.
- Chen, Y., Hansen, L. D. and Brown, J. J. (2002). Nesting sites of the carpenter ant, *Camponotus vicinus* (Mayr) (Hymenoptera: Formicidae) in northern Idaho. *Environ. Entomol.* **31**, 1037–1042.
- Chinh, T. X., Sommeijer, M. J., Boot, W. J. and Michener, C. D. (2005). Nest and colony characteristics of three stingless bee species in Vietnam with the first description of the nest of *Listotrigona carpenteri* (Hymenoptera: Apidae: Meliponini). *J. Kans. Entomol. Soc.* **78**, 363–372.
- Chown, S. L., Gibbs, A. G., Hetz, S. K., Klok, C. J., Lighton, J. R. B. and Marias, E. (2006). Discontinuous gas exchange in insects: a clarification of hypotheses and approaches. *Physiol. Biochem. Zool.* **79**, 333–343.

- Cole, B. J. (1994). Nest architecture in the Western harvester ant, *Pogonomyrmex occidentalis* (Cresson). *Ins. Soc.* **41**, 401–410.
- Darlington, J. P. E. C. (1984). Two types of mound built by the termite *Macrotermes subhyalinus* in Kenya. *Insect Sci. Appl.* **5**, 481–492.
- Doedikar, G. B., Ghatge, A. I., Phadke, R. P., Mahindre, D. B., Kshirsager, K. K., Muvel, K. S. and Thaker, C. V. (1977). Nesting behaviour of Indian honeybees III. Nesting behaviour of *Apis dorsata* Fab. *Indian Bee Journal* **39**, 1–12.
- Dunham, W. E. (1931). A colony of bees exposed to high external temperatures. *J. Econ. Entomol.* **24**, 606–611.
- Dyer, F. C. and Seeley, T. D. (1991). Nesting behavior and the evolution of worker tempo in four honey bee species. *Ecology* **72**, 156–170.
- Elton, C. (1932). Orientation of the nests of the *Formica truncorum* F. in north Norway. *J. Anim. Ecol.* **1**, 192–193.
- Engel, M. S. and Schultz, T. R. (1997). Phylogeny and behavior in honey bees (Hymenoptera: Apidae). *Ann. Entomol. Soc. Am.* **90**, 43–53.
- Engels, W., Rosenkranz, P. and Engels, E. (1995). Thermoregulation in the nest of the neotropical stingless bee *Scaptotrigona postica* and a hypothesis on the evolution of the temperature homeostasis in highly eusocial bees. *Stud. Neotropical Fauna and Environ.* **30**, 193–205.
- Fahrenholz, L., Lamprecht, I. and Schrickler, B. (1989). Thermal investigation of a honey bee colony: thermoregulation of the hive during summer and winter and heat production of members of different bee castes. *J. Comp. Physiol. B*, **159**, 551–560.
- Fletcher, D. J. C. and Crewe, R. M. (1981). Nest structure and thermoregulation in the stingless bee *Trigona (Plebeina) denoiti* Vachal (Hymenoptera: Apidae). *J. Entomol. Soc. South Africa* **44**, 183–196.
- Franck, P., Cameron, E., Good, G., Rasplus, J. Y. and Oldroyd, B. P. (2004). Nest architecture and genetic differentiation in a species complex of Australian stingless bees. *Mol. Ecol.* **13**, 2317–2331.
- Franks, N. R. (1989). Thermoregulation in army ant bivouacs. *Physiol. Entomol.* **14**, 397–404.
- Fraser, V. S., Kaufman, B., Oldroyd, B. P. and Crozier, R. H. (2000). Genetic influence on caste allocation in the ant *Camponotus consobrinus*. *Behav. Ecol. Sociobiol.* **47**, 188–194.
- Free, J. B. and Simpson, J. (1963). The respiratory metabolism of honey-bee colonies at low temperatures. *Entomol. Exp. App.* **6**, 234–238.
- Frouz, J. (2000). The effect of nest moisture on daily temperature regime in the nests of *Formica polyctena* wood ants. *Ins. Soc.* **47**, 229–235.
- Gibo, D. L., Dew, H. E. and Hajduk, A. S. (1974b). Thermoregulation in colonies of *Vespula arenaria* and *Vespula maculata* (Hymenoptera: Vespidae) II. The relation between colony biomass and calorie production. *Can. Entomol.* **106**, 873–879.
- Gibo, D. L., Temporale, A., Lamarre, T. P., Soutar, B. M. and Dew, H. E. (1977). Thermoregulation in colonies of *Vespula arenaria* and *Vespula maculata* (Hymenoptera: Vespidae) III. Heat production in queen nests. *Can. Entomol.* **109**, 615–620.
- Gibo, D. L., Yarascavitch, R. M. and Dew, H. E. (1974a). Thermoregulation in colonies of *Vespula arenaria* and *Vespula maculata* (Hymenoptera: Vespidae) under normal conditions and under cold stress. *Can. Entomol.* **106**, 503–507.
- Graham, S., Myerscough, M. R., Jones, J. C. and Oldroyd, B. P. (2006). Modelling the role of intracolony genetic diversity on regulation of brood temperature in honey bee (*Apis mellifera* L.) colonies. *Ins. Soc.* **53**, 226–232.

- Greaves, T. (1964). Temperature studies of termite colonies in living trees. *Aust. J. Zool.* **12**, 250–262.
- Grigg, G. C. and Underwood, A. J. (1977). An analysis of the orientation of 'magnetic' termite mounds. *Aust. J. Zool.* **25**, 87–94.
- Hasselrot, T. B. (1960). Studies on Swedish bumblebees (Genus *Bombus* Latr.): their domestication and biology. *Opusc. Entomol. Supplementum*, **17**, 1–192.
- Hazellhoff, E. H. (1954). Ventilation in a bee-hive during summer. *Physiol. Comp. Oecol.* **3**, 343–364.
- Heinrich, B. (1972). Patterns of endothermy in bumble bee queens, drones and workers. *J. Comp. Physiol.* **77**, 65–79.
- Heinrich, B. (1974a). Thermoregulation in bumblebees. I. Brood incubation by *Bombus vosnesenskii* queens. *J. Comp. Physiol.* **88**, 129–140.
- Heinrich, B. (1974b). Pheromone induced brooding behavior in *Bombus vosnesenskii* and *B. edwardsii* (Hymenoptera: Bombidae). *J. Kans. Entomol. Soc.* **47**, 396–404.
- Heinrich, B. (1979). *Bumblebee Economics*. Cambridge, MA: Harvard University Press.
- Heinrich, B. and Kammer, A. (1973). Activation of the fibrillar muscles of the bumblebee during warm-up stabilization of thoracic temperature, and flight. *J. Exp. Biol.* **58**, 677–688.
- Himmer, A. (1927). Ein Beitrag zur Kenntnis des Warmehaushalts im Nestbau sozialer Hautfluger. *J. Comp. Physiol. A* **5**, 375–389.
- Himmer, A. (1932). Die Temperaturverhältnisse bei den sozialen. *Biol. Rev.* **7**, 224–253.
- Hölldobler, B. and Wilson, E. O. (1990). *The Ants*. Cambridge, MA: Harvard University Press.
- Hozumi, S. and Yamane, S. (2001). Incubation ability of the functional envelope in paper wasp nest (Hymenoptera, Vespidae, *Polistes*): I. Field measurements of nest temperature using paper models. *J. Ethol.* **19**, 39–46.
- Hubbard, M. D. and Cunningham, W. G. (1977). Orientation of mounds of the ant *Solenopsis invicta* (Hymenoptera, Formicidae, Myrmicinae). *Ins. Soc.* **24**, 3–7.
- Hunt, J. H., Jeanne, R. L. and Keeping, M. (1995). Observation on *Apoica pallens*, a nocturnal Neotropical social wasp (Hymenoptera: Vespidae, Polistinae, Epiponini). *Ins. Soc.* **42**, 223–236.
- Ishay, J. S. (1973). Thermoregulation by social wasps: behavior and pheromones. *Trans. N. Y. Acad. Sci.* **35**, 447–462.
- Ishay, J. S. and Barenholz-Paniry, V. (1995). Thermoelectric effect in hornet (*Vespa orientalis*) silk and thermoregulation in a hornet's nest. *J. Insect Physiol.* **41**, 753–759.
- Jacklyn, P. M. (1992). "Magnetic" termite mound surfaces are oriented to suit wind and shade conditions. *Oecologia* **91**, 385–395.
- Jackson, W. B. (1957). Microclimate patterns in the army ant bivouac. *Ecology* **38**, 276–285.
- Janson, S., Middendorf, M. and Beekman, M. (2005). Honeybee swarms: how do scouts guide a swarm of uninformed bees? *Anim. Behav.* **70**, 349–358.
- Jay, S. C. (1963). The development of honeybees in their cells. *J. Apic. Res.* **2**, 117–134.
- Jaycox, E. R. and Parise, S. G. (1980). Homesite selection by Italian honey bee swarms, *Apis mellifera ligustica* (Hymenoptera: Apidae). *J. Kans. Entomol. Soc.* **53**, 171–178.
- Jaycox, E. R. and Parise, S. G. (1981). Homesite selection by swarms of black-bodied honey bees, *Apis mellifera caucasica* and *A. m. carnica* (Hymenoptera: Apidae). *J. Kans. Entomol. Soc.* **54**, 697–703.
- Jeanne, R. L. and Morgan, R. C. (1992). The influence of temperature on nest site choice and reproductive strategy in a temperate zone *Polistes* wasp. *Ecol. Entomol.* **17**, 135–141.

- Jones, J. C., Helliwell, P., Beekman, M., Maleszka, R. and Oldroyd, B. P. (2005). The effects of rearing temperature on developmental stability and learning and memory in the honey bee, *Apis mellifera*. *J. Comp. Physiol. A* **191**, 1121–1129.
- Jones, J. C., Myerscough, M. R., Graham, S. and Oldroyd, B. P. (2004). Honey bee nest thermoregulation: diversity promotes stability. *Science* **305**, 402–404.
- Joseph, Z. and Ishay, J. S. (2004). Silk structure in the hornet cocoon. *J. Electron Microsc.* **53**, 293–304.
- Kastberger, G., Winder, O., Hoetzel, T. and Rasputnig, G. (1996). Behavioral features of a periodic form of massed flight activity in the giant honey bee *Apis dorsata*. *Apidologie* **27**, 381–395.
- Kleinhenz, M., Bujok, B., Fuchs, S. and Tautz, J. (2003). Hot bees in empty broodnest cells: heating from within. *J. Exp. Biol.* **206**, 4217–4231.
- Korb, J. (2003). Thermoregulation and ventilation of termite mounds. *Naturwissenschaften* **90**, 212–219.
- Korb, J. and Linsenmair, K. (1998a). Experimental heating of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds: what role does microclimate play in influencing mound architecture? *Ins. Soc.* **45**, 335–342.
- Korb, J. and Linsenmair, K. (1998b). The effects of temperature on the architecture and distribution of *Macrotermes bellicosus* (Isoptera, Macrotermitinae) mounds in different habitats of a West African Guinea savanna. *Ins. Soc.* **45**, 51–65.
- Korb, J. and Linsenmair, K. (1999). The architecture of termite mounds: a result of a trade-off between thermoregulation and gas exchange? *Behav. Ecol.* **10**, 312–316.
- Korb, J. and Linsenmair, K. (2000a). Thermoregulation of termite mounds: what role does ambient temperature and metabolism of the colony play? *Ins. Soc.* **47**, 357–363.
- Korb, J. and Linsenmair, K. (2000b). Ventilation of termite mounds: new results require a new model. *Behav. Ecol.* **11**, 486–494.
- Kronenberg, F. and Heller, H. C. (1982). Colonial thermoregulation in honey bees (*Apis mellifera*). *J. Comp. Physiol. B.* **148**, 65–76.
- Kuriachan, I. and Vinson, S. B. (2000). A queen's worker attractiveness influences her movement in polygynous colonies of the red imported fire ant (Hymenoptera: Formicidae) in response to adverse temperature. *Environ. Entomol.* **29**, 943–949.
- Ladley, D. and Bullock, S. (2005). The role of logistic constraints in termite construction of chambers and tunnels. *J. Theor. Biol.* **234**, 551–564.
- Lapointe, S. L., Serrano, M. S. and Jones, P. G. (1998). Microgeographic and vertical distribution of *Acromyrmex landolti* (Hymenoptera: Formicidae) nests in a neotropical savanna. *Environ. Entomol.* **27**, 636–641.
- Lighton, J. R. B. (1998). Notes from underground: towards ultimate hypotheses of cyclic discontinuous gas-exchange in Tracheate Arthropods. *Am. Zool.* **38**, 483–491.
- Lindauer, M. (1954). Temperaturregulierung und Wasserhaushalt im Bienenstaat. *J. Comp. Physiol. A.* **36**, 391–432.
- Lindauer, M. (1955). Schwarmbienen auf Wohnungssuche. *J. Comp. Physiol. A.* **37**, 263–324.
- Luscher, M. (1961). Air-conditioned termite nests. *Sci. Am.* **205**, 138–145.
- Makino, S. and Yamane, S. (1980). Heat production by the foundress of *Vespa simillima*, with description of its embryo nest (Hymenoptera: Vespidae). *Insecta Matsumurana* **19**, 89–101.
- Mardan, M. B. (1989). Thermoregulation in the Asiatic giant honeybee *Apis dorsata* (Hymenoptera: Apidae). Ph.D. dissertation, University of Guelph, Ontario.
- Mardan, M. B. and Kevan, P. G. (1989). Honeybees and yellow rain. *Nature* **341**, 191.
- Martin, S. J. (1988). Thermoregulation in *Vespa simillima xanthoptera* (Hymenoptera, Vespidae). *Kontyu* **56**, 674–677.

- Martin, S. J. (1992). Nest thermoregulation in *Vespa affinis* (Hymenoptera, vespidae). *Jpn. J. Entomol.* **60**, 483–486.
- McMullan, J. B. and Brown, M. J. F. (2005). Brood pupation temperature affects the susceptibility of honeybees (*Apis mellifera*) to infestation by tracheal mites (*Acarapis woodi*). *Apidologie* **36**, 97–105.
- Miyata, H., Shimamura, T., Hirosawa, H. and Higashi, S. (2003). Morphology and phenology of the primitive ponerine army ant *Onychomyrmex hedleyi* (Hymenoptera: Formicidae: Ponerinae) in a highland rainforest of Australia. *J. Nat. Hist.* **37**, 115–125.
- Moritz, R. F. A. and Crewe, R. M. (1988). Air ventilation in nests of two African stingless bees *Trigona denoiti* and *Trigona gribodoi*. *Experientia* **44**, 1024–1027.
- Moritz, R. F. A. and Southwick, E. E. (1992). *Bees as Superorganisms*. Berlin: Springer.
- Myerscough, M. R. (1993). A simple model for temperature regulation in honeybee swarms. *J. Theor. Biol.* **162**, 381–393.
- Myerscough, M. R. and Oldroyd, B. P. (2004). Simulation models of the role of genetic variability in social insect task allocation. *Ins. Soc.* **51**, 146–152.
- Nagy, K. A. and Stallone, J. N. (1976). Temperature maintenance and CO₂ concentration in a swarm cluster of honey bees, *Apis mellifera*. *Comp. Biol. Physiol. A*, **55**, 169–171.
- Navarro, J. G. and Jaffe, K. (1985). On the adaptive value of nest features in the grass-cutting ant *Acromyrmex landolti*. *Biotropica* **17**, 347–348.
- O'Donnell, S. and Foster, R. L. (2001). Thresholds of response in nest thermoregulation by worker bumble bees, *Bombus bifarius nearcticus* (Hymenoptera: Apidae). *Ethology* **107**, 387–399.
- Ofer, J. (1970). *Polyrhachis simplex* the weaver ant of Israel. *Ins. Soc.* **17**, 49–82.
- Oldroyd, B. P., Sylvester, H. A., Wongsiri, S. and Rinderer, T. E. (1994). Task specialization in a wild bee, *Apis florea* (Hymenoptera: Apidae), revealed by RFLP banding. *Behav. Ecol. Sociobiol.* **34**, 25–30.
- Oldroyd, B. P. and Wongsiri, S. (2006). *Asian Honey Bees Biology, Conservation and Human Interactions*. Cambridge, MA: Harvard University Press.
- Oldroyd, B. P. and Thompson, G. J. (2007). Behavioural genetics of the honey bee, *Apis*. *Adv. Ins. Physiol.* **33**, 1–49.
- Oster, G. F. and Wilson, E. O. (1978). *Caste and Ecology in the Social Insects*. Princeton, NJ: Princeton University Press.
- Powell, R. J. and Stradling, D. J. (1986). Factors influencing the growth of *Attamyces bromatificus*, a symbiont of attine ants. *Trans. Br. Mycol. Soc.* **87**, 205–213.
- Pranschke, A. M. and Hooper-Bui, L. M. (2003). Influence of abiotic factors on red imported fire ant (Hymenoptera: Formicidae) mound population ratings in Louisiana. *Environ. Entomol.* **32**, 204–207.
- Reddy, S. M. and Reddy, C. C. (1993). Studies on the distribution of nests of giant honey bee (*Apis dorsata* F.). *Indian Bee Journal* **55**, 36–39.
- Riabinin, K., Kozhevnikov, M. and Ishay, J. S. (2004). Ventilating activity at the hornet nest entrance. *J. Ethol.* **22**, 49–53.
- Rinderer, T. E., Collins, A. M., Bolten, A. B. and Harbo, J. R. (1981). Size of nest cavities selected by swarms of Africanized honeybees in Venezuela. *J. Apic. Res.* **20**, 160–164.
- Rinderer, T. E., Tucker, K. W. and Collins, A. M. (1982). Nest cavity selection by swarms of European and Africanized honey bees. *J. Apic. Res.* **21**, 98–103.
- Roces, F. and Kleineidam, C. (2000). Humidity preference for fungus culturing by workers of the leaf-cutting ant *Atta sexdens rubropilosa*. *Ins. Soc.* **47**, 348–350.

- Roces, F. and Nunez, J. A. (1989). Brood translocation and circadian variation of temperature preference in the ant *Camponotus mus*. *Oecologia* **81**, 33–37.
- Roces, F. and Nunez, J. A. (1995). Thermal sensitivity during brood care in workers of two *Camponotus* ant species: circadian variation and its ecological correlates. *J. Insect Physiol.* **41**, 659–669.
- Rosengren, R., Fortelius, W., Lindstrom, K. and Luther, A. (1987). 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. Fenn.* **24**, 147–155.
- Roubik, D. W. (2006). Stingless bee nesting biology. *Apidologie* **37**, 1–20.
- Roubik, D. W. and Peralta, F. J. A. (1983). Thermodynamics in nests of two *Melipona* species in Brasil. *Acta Amazon.* **13**, 453–466.
- Ruttner, F. (1988). *Biogeography and Taxonomy of Honeybees*. Berlin: Springer.
- Sakagami, S. F. (1960). Preliminary report of the specific difference of behavior and other ecological characters between European and Japanese honeybees. *Acta Hymenopterol.* **1**, 171–198.
- Scherba, G. (1958). Reproduction, nest orientation and population structure of an aggregation of mound nests of *Formica ulkei* Emery (Formicidae). *Ins. Soc.* **5**, 201–213.
- Schmidt, J. O. and Hurley, R. (1995). Selection of nest cavities by Africanized and European honey bees. *Apidologie* **26**, 467–475.
- Schneirla, T. C., Brown, R. Z. and Brown, F. C. (1954). The bivouac or temporary nest as an adaptive factor in certain terrestrial species of army ants. *Ecol. Monogr.* **24**, 269–296.
- Seeley, T. D. (1976). The nest of the honey bee (*Apis mellifera* L.). *Ins. Soc.* **23**, 495–512.
- Seeley, T. D. (1977). Measurement of nest cavity volume by the honey bee (*Apis mellifera*). *Behav. Ecol. Sociobiol.* **2**, 202–227.
- Seeley, T. D. (1985). *Honeybee Ecology*. Princeton, NJ: Princeton University Press.
- Seeley, T. D. (1995). *The Wisdom of the Hive*. Cambridge, MA: Harvard University Press.
- Seeley, T. D. and Morse, R. A. (1978). Nest site selection by the honey bee, *Apis mellifera*. *Ins. Soc.* **25**, 323–337.
- Seeley, T. D. and Heinrich, B. (1981). Regulation of temperature in the nests of social insects. In: *Insect Thermoregulation* (ed. Heinrich, B.), pp. 159–234. New York: Wiley.
- Seeley, T. D., Seeley, R. H. and Akratanakul, P. (1982). Colony defence strategies of the honeybees in Thailand. *Ecol. Monogr.* **52**, 43–63.
- Seeley, T. D., Nowicke, J. W., Meleson, M., Guillemin, J. and Akratanakul, P. (1985). Yellow rain. *Sci. Am.* **253**, 128–137.
- Seeley, T. D. and Buhrman, S. C. (1999). Group decision making in swarms of honey bees. *Behav. Ecol. Sociobiol.* **45**, 19–31.
- Seeley, T. D. and Buhrman, S. C. (2001). Nest-site selection in honey bees: how well do swarms implement the ‘best-of-N’ decision rule. *Behav. Ecol. Sociobiol.* **49**, 416–427.
- Seeley, T. D. and Visscher, P. K. (2003). Choosing a home: how the scouts in a honey bee swarm perceive the completion of their group decision making. *Behav. Ecol. Sociobiol.* **54**, 511–520.
- Seeley, T. D. and Visscher, P. K. (2004). Group decision making in nest-site selection by honey bees. *Apidologie* **35**, 101–116.
- Stabentheiner, A., Pressl, H., Papst, T., Hrassnigg, N. and Crailsheim, K. (2003). Endothermic heat production in honeybee winter clusters. *J. Exp. Biol.* **206**, 353–358.

- Starks, P. T. and Gilley, D. C. (1999). Heat shielding: a novel method of colonial thermoregulation in honey bees. *Naturwissenschaften* **86**, 438–440.
- Tautz, J., Maier, S., Groh, C., Rossler, W. and Brockmann, A. (2003). Behavioural performance in adult honey bees is influenced by the temperature experienced during their pupal development. *Proc. Natl. Acad. Sci. USA* **100**, 7343–7347.
- Thapa, R. and Wongsiri, S. (1994). Distinct fanning behaviour of two dwarf honeybees *Apis andreniformis* (Smith) and *Apis florea* (Fab.). In: *Second International Conference of the Asian Apicultural Association* (ed. Sakai, T.), pp. 344–345. Yogyakarta.
- Tschinkel, W. R. (2006). *The Fire Ants*. Cambridge, MA: Belknap Press.
- Turner, J. S. (1994). Ventilation and thermal constancy of a colony of a southern African termite (*Odontotermes transvaalensis*: Macrotermitinae). *J. Arid Environ.* **28**, 231–248.
- Turner, S. J. (2001). On the mound of *Macrotermes michaelsoni* as an organ of respiratory gas exchange. *Physiol. Biochem. Zool.* **74**, 798–822.
- Underwood, B. A. (1986). The natural history of *Apis laboriosa* in Nepal. MSc thesis, Cornell University.
- Underwood, B. A. (1990). Seasonal nesting cycle and migration patterns of the Himalayan honey bee *Apis laboriosa*. *Natl. Geogr. Res.* **6**, 276–290.
- Watmough, J. and Camazine, S. (1995). Self-organized thermoregulation of honeybee clusters. *J. Theor. Biol.* **176**, 391–402.
- Weber, N. A. (1957). Dry season adaptations of fungus growing ants and their fungi. *Anat. Rec.* **128**, 638.
- Weidenmuller, A. (2004). The control of nest climate in bumblebee (*Bombus terrestris*) colonies: interindividual variability and self reinforcement in fanning response. *Behav. Ecol.* **15**, 120–128.
- Weir, J. S. (1973). Air flow, evaporation and mineral accumulation in mounds of *Macrotermes subhyalinus* (Rambur). *J. Anim. Ecol.* **42**, 509–520.
- Wille, A. and Michener, C. D. (1973). The nest architecture of stingless bees with special reference to those of Costa Rica (Hymenoptera: Apidae). *Rev. Biol. Trop.* **21**, 1–278.
- Wilson, E. O. (1971). *The Insect Societies*. Cambridge, MA: Harvard University Press.
- Winston, M. L. (1987). *The Biology of the Honey Bee*. Cambridge, MA: Harvard University Press.
- Wongsiri, S., Lekprayoon, R., Thapa, A., Thirakupt, K., Rinderer, T. E., Sylvester, H. A., Oldroyd, B. P. and Boocham, U. (1997). Comparative biology of *Apis andreniformis* and *Apis florea* in Thailand. *Bee World* **78**, 23–35.
- Woyke, J., Wilde, J. and Wilde, M. (2000). Swarming, migrating and absconding of *Apis dorsata* colonies. In: *Seventh International Conference on tropical bees: Management and Diversity and Fifth Asian Apicultural Association Conference* (ed. Wongsiri, S.), pp. 183–188. Cardiff: International Bee Research Association.
- Woyke, J., Wilde, J. and Wilde, M. (2003). Periodic mass flight of *Apis laboriosa* in Nepal. *Apidologie* **34**, 121–127.
- Yamane, S. (1988). A preliminary note of the thermal property in two different types of *Ropalidia* combs (Hymenoptera, Vespidae). *Kontyu* **56**, 896–900.
- Yamane, S. and Kawamichi, T. (1975). Bionomic comparisons of *Polistes biglumis* (Hymenoptera, Vespidae) at two different localities in Hokkaido, northern Japan, with reference to its probable adaptation to cold climate. *Kontyu* **43**, 214–232.