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REVIEW

# Thermogenesis in stingless bees: an approach with emphasis on brood's thermal contribution

Maiko Roberto Tavares Dantas

**MRT Dantas** (Corresponding author)
Department of Animal Sciences, Universidade Federal Rural do Semi-Árido (UFERSA), Mossoró, RN, Brazil.

email: mk_ufersa@hotmail.com

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**Abstract** The animals behave as a thermodynamic system complex, which remains all the time exchanging energy with the environment. In this context, the body temperature of bees considerably accompanies variations in ambient temperature, and the performance of most of its activity is largely affected by air temperature. When these individuals are exposed to temperatures above or below the optimum range for the species during its pupal stage, these, when they survive, have morphological deficiencies, physiological or behavioral as adults. These insects use physiological activities such as internal temperature control mechanisms of the nest. Social insects like honey bees demonstrate certain thermoregulatory ability to nest in which they live, known as the colonial endotherm. This strategy has an interesting feature, which the animals are endothermic when performing motor and ectothermic during inactivity. The meliponines (stingless bees) are highly social bees, working together to maintain the colony, keeping almost constant the temperature throughout the year. The mechanisms of thermoregulation these animals are called passive thermoregulation, it is due solely to the construction of involucre and nesting (brood comb structures) and not the motor activities of individuals. Therefore, in most species of stingless bees, with rare exceptions, are the only mechanisms that they have to termorregulate. Maintaining a constant temperature is critical for normal growth and development of the larval and pupal stages. It is known that the brood combs also contribute to colonial thermoregulation through its thermogenesis, and larvae and pupae more mature have higher heat input to the brood comb along its development.

**Keywords**: colonial thermoregulation, social bees, thermoregulatory ability

## Introduction

Temperature is one of the abiotic factors of enormous importance that affects the morphophysiology of living beings on the entire planet. Its variations cause changes in the metabolism of organisms, causing changes in body development, productivity and reproduction in its various segments (Heinrich 1981; Heinrich 1993; Heinrich 1994; Mardan and Kevan 2002; Roldão 2011). The body temperature of an animal refers to the quantity of stored thermal energy per unit of body mass. This energy can be increased or decreased by thermolysis and thermogenesis processes, respectively (Silva 2000). In these processes are involved behavioral, autonomous and adaptive mechanisms (Silva 2000).

The animals act as a thermodynamic complex system, which remains all the time exchanging energy with the environment (Silva 2000). Due to this process, the ambient tends to induce physiological changes in such organisms in the short and long term, influencing the amount of energy exchanged between them, there is however, the need of physiological adjustments to the occurrence of heat balance and consequent adaptation and survival of an animal (Baêta and Souza 1997).

The homeotherms animals (mammals and birds, mostly) have physiological mechanisms that maintain relatively constant their body temperature due to a high metabolic rate generated by intense metabolic energy production in your cells. Due to this heat generation in the tissue, these animals are also called endotherms. Those who belong to the category of poikilotherms animals, do not have a constant body temperature, varying according to the ambient temperature. These bodies designated as animal "cold-blooded" are ectothermic, meaning they do not have an internal mechanism to regulate the temperature of your body, being strongly influenced by the environment (Silva 2000).

The bees belong to the Insecta class, where most representatives are poikilotherms. The body temperature of bees considerably follows the variations in ambient temperature, and the performance of the vast majority of its activities is largely affected by air temperature (Nããs 1989; Silva 2000; Vollet Neto 2011). In this way, or your body stays with variable temperature to that which exists in the environment where it is inserted, or has behavioral habits which allow them to keep the temperature at acceptable levels for your body (Nããs 1989).

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Usually the performance of any activity in ectotherms animals increases with the rise in temperature until stabilize at an optimum temperature performance, then going to decrease until the lethal temperature, defining the thermal sensitivity of the organism in question (Huey and Kingsolver 1989; Angilletta 2002; Angilletta Jr et al 2006; Vollet Neto 2011). When individuals are exposed to temperatures above or below of the optimum range for the species during its pupal stage, these, when they survive, have morphological, physiological or behavioral disabilities as adults (Heinrich 1993; Mardan and Kevan 2002; Tautz et al 2003; Jones et al 2005).

Because the temperature directly affects the metabolism of insects, it influences the development of young and adults in bees (Schmolz and Schulz 1995; Tautz et al 2003; Halcroft et al 2013ab). Therefore, any change about the climate significantly interferes in actions in the short and long term of the bees (migration, swarming, food and water intake, morphological and behavioral alterations, use of heat exchange mechanisms) (Silva 2000).

## Thermoregulation in bees

The thermoregulation is the ability of an organism has to control and maintain its internal conditions by temperature, with behavioral or physiological response regarding to their natural environment (May 1979). Heinrich (1993) says that insects can present various thermoregulatory mechanisms, which include behavioral (such as postural adjustments in flight and positioning on the ground), anatomical (abundance and distribution by) and physiological mechanisms (such as heat loss control and metabolic heat production).

The fact that some insects thermoregulate has attracted the curiosity of scientists since the beginning of last century. Some authors found that the bees have strategies to produce metabolic heat (which enables the flight at low ambient temperatures), cool the body during flight to prevent overheating due to high metabolic rates of this activity (Heinrich 1981), as well as control the heat flow within the colonies (Heinrich 1980a; Heinrich 1993; Heinrich and Esch 1994; Roberts and Harrison 1998).

Among the factors that may influence the duration of the development in brood of a sort of bee, are the environmental conditions, especially the amount of food and the temperature (Heinrich 1981). Thus, the growth rate or size achieved by insects in the stage of larvae and pupae are not fixed (Tautz et al 2005).

To achieve successful development of the brood and for the survival of young bees and larvae (which are probably ectotherms), there must be a good maintenance and control of the temperature inside the colony, depending directly on the temperature and the amount of oxygen in the environment (Heinrich 1993; Petz et al 2004; Moyes and Schulte 2010). Bees use physiological activities such as internal temperature control mechanism of the nest, thereby maintaining a satisfactory control for the development of the brood and/or adult bees. For Seeley (2006), the mechanisms responsible for it impressive thermoregulatory ability include a seamlessly integrated set of behaviors and physiological devices by which colonies thermoregulate.

### *Colonial heterothermy and endothermy in social bees*

Social bees demonstrate certain thermoregulatory capacity in the nest to which inhabit, known as colonial endothermy (Roubik and Peralta 1983; Loli 2008; Roldão 2011). These animals have an interesting feature, are endothermic when performing motor activities and ectothermic during inactivity (Heinrich 1979ab; Heinrich 1980ab; Heinrich 1993; Roberts And Harrison 1998; Crailsheim et al 1999; Grodziki and Caputa 2005; Loli 2008; Carvalho 2009). This temporary endothermy strategy is known as heterothermy (Heinrich 1974; Heinrich 1981; Heinrich 1993; Moyes and Schulte 2010).

It is very important that social bees keep heterotherms features. Their brood, unlike adults, have a close development relationship to the nest temperature. The ability of colonial thermoregulation is due in part to the structural characteristics of the nest in its thermal insulation and the fact of the endotherms characteristics of individuals (Heinrich 1993; Carvalho 2009; Roldão 2011).

According to several authors, social bees work together to maintain the colony keeping almost constant the temperature throughout the year (Heinrich 1980ab; Kronenberg and Heller 1982; Southwich 1982; Southwich 1983; Grodziki and Caputa 2005; Ferreira 2014). The colonial endothermy has a high energy cost to bees, where the adoption of this thermoregulatory strategy provides heating to the nest during periods of cold stress and allows it to cool down when it is overheated to maintain thermal homeostasis (Josephson 1981).

### *Colonial thermoregulation in honey bees*

One of the best-studied groups of insects of today is that of the social insects, mainly due to their ecological role. Among the social insects, are highlighted honeybees for having one of the most complex social organizations, and the bee *Apis mellifera* (Apidae, Apini) the best known and studied in recent centuries (Kronenberg and Heller 1982; Carvalho 2009).

*A. mellifera* bees are known to strictly control the internal temperature of their nests within a close temperature range between 33-36 °C (Tautz et al 2003; Jones and Oldroyd 2007). This control is especially so due to the joint effort of the bees themselves, called active thermoregulation (Jones and Oldroyd 2007). A. mellifera, by having an effective thermoregulatory system fits well with the large climatic variations during the year, being able to dissipate exceeded heat by evaporation, radiation and convection mechanisms (Church 1959ab).

In situations of cold stress, the *A. mellifera* workers heat the nest by metabolic heat production, contracting quickly and continuously the muscles responsible for the movement of flight wings (Heinrich 1980a; Heinrich 1993; Heinrich and Esch 1994; Roberts and Harrison 1998; Jones and Oldroyd 2007; Roldão 2011). For temperatures above 36 °C (heat stress), they are strategically positioned on the nest entrance and vibrate their wings, cooling it by ventilation caused by the beating of wings (Heinrich 1974; Heinrich 1996).

Free and Simpson (1963) studied the respiratory metabolism of *A. mellifera* colonies and found that when exposed to low temperatures, the worker were engaged in warming the nest through corporal heat production due to the grouping of bees in the brood area. Stabentheiner et al (2003) also observed that the agglomeration of workers heat the area creates. The strong dependence of the temperature forces the bees to maintain thermal homeostasis in the brood area to avoid delays in the development of larvae and pupae during low temperature periods (Petz et al 2004).

The excess heat inside of the nest causes the worker to collect a lot of water, thereby increasing the humidity within the colony considerably, in order to decrease the temperature of the colony (Almeida 2008). When the ambient temperature is high the workers spread the water transported in the maw over the entire surface of the colony's brood cells and the consequent evaporation there is a decrease in the internal temperature of the colony (Lindauer 1955; Esch 1960; Heinrich 1974). The active ventilation in this process causes evaporation and results in an active cooling (Lindauer 1955).

## *Colonial thermoregulation in stingless bees*

Unlike honeybees, the stingless bees (Apidae, Meliponini) have a lower ability to actively regulate the microclimate of their colonies (Jones and Oldroyd 2007; Roldão 2011). Thus, this puts the stingless bees as important models that may allow a better comprehension of the evolution of the diversity of successful strategies in social insects to deal with the thermal heterogeneity (Vollet Neto 2011). When studied the thermoregulatory capacity in stingless bees, found out that it varies according to the species studied (Michener 1974).

Camargo (1972) and Kerr et al (1984) observed a large increase in the activities of these bees when the ambient temperature is in the temperature range between 34 and 40 °C. This range is very common to regions located in the tropics, where stingless bees almost exclusively inhabit. Apparently, not require a strict control of the nest temperature. In these regions, the temperature undergoes small fluctuations in its annual variation (Jones and Oldroyd 2007).

The colonial thermoregulation of meliponines varies according to the kind and the ambient temperature. In colonies of *Melipona rufiventris* and *Melipona seminigra*, the brood area was maintained in the 31-32 °C range in an environment with average of 30 °C (Roubik and Peralta 1983). The *Melipona beecheii* and *Melipona fuliginosa* maintained the nest at temperatures in the 23-30 °C range, in regions where the ambient temperature varied between 18.2 to 36 °C (Moo-Valle et al 2000). In the studies by Ferreira (2014), the brood area of *Melipona subnitida* remained in the 27-33 °C range, while the ambient temperature varied between 22.9 to 34.6 °C. Sakagami (1982) reported that at ambient temperature of approximately 15 °C, Trigona spinipes could maintain the brood area at 35 °C

Few species of stingless bees inhabit non-tropical regions, and therefore, are exposed to climates with well-differentiated seasonality. There is for example, *Melipona colimana*, which displays both cooling active mechanisms and heat generation in response to sudden changes in temperature (Macías-Macías et al 2011), *Plebeia remote*, which stops the posture before the season more cold (Van Benthem et al 1995) and *Austroplebeia australis*, which can survive and develop well their brood even in a region where there are seasons with extreme temperatures (-0.4 °C to 37.6 °C) (Halcroft et al 2013b).

It stipulates that the stingless bees are able to maintain a more or less stable temperature in the brood area, so that it becomes possible the emergence of brood that needs to be within the ideal temperature range for the full development (Kerr et al 1984; Roldão 2011). The mechanisms of thermoregulation in these bees are named of passive thermoregulation (Jones and Oldroyd 2007; Vollet Neto 2011; Macías-Macías et al 2011). It attributed this function to these strategies in many species of stingless bees as the construction of involucre and nesting.

## Passive thermoregulation in stingless bees: Nesting

The Meliponini nest in various types of substrates such as underground cavities associated or not with nests of other social insects, termites assets, hollow trees and vines, cracks in walls and rocks, in nests of arboreal ants, in abandoned bird nests and even free nests fixed in branches and tree trunks (Schwarz 1948; Kerr et al 1967; Camargo 1970; Wille; Michener 1974; Michener 1974; Roubik 1989; Posey and Camargo 1985; Camargo and Wittmann 1989; Kerr et al 1996).

Except for *M. colimana* (Macías-Macías et al 2011), usually the stingless bees have no active mechanism of temperature control. They depend mainly on the thermal insulation of their rearing grounds for maintaining temperature stability for proper development of the brood throughout the year (Couto and Camillo 2007). Importantly, this passive mechanism involves an important selection of colony nesting site, being cited by Engels et al (1995) and Jones and Oldroyd (2007) as a primary mechanism for controlling the temperature.

## Passive thermoregulation in stingless bees: Involucre

The capacity of the species of stingless bees in maintaining homogeneous temperature in the nest and mainly due to the involucre presence, which intercepts and stores large amounts of thermal energy produced by metabolism (thermogenesis) of the brood (Roubik and

Peralta 1983; Roldão 2011). The involucre is a mixture of resin and wax (cerumen) surrounding the area creates and can be described as structural adaptation of colony that helps to retain the heat for eggs and pupae present in brood combs (Zucchi and Sakagami 1972; Jones and Oldroyd 2007).

In general, the meliponines build larger quantities of involucre in colder climates than in equatorial regions forests (Engels et al 1995; Roubik 2006). For example, in nest of *Trigona denoiti* in South Africa, the layers of involucre act as thermal energy conservative, since they involve the brood area and inhibits air circulation within the nest, reducing heat loss by convection (Fletcher and Crewe 1981). Engels et al (1995) studied *Scaptotrigona postiça* in São Paulo-Brazil, and similarly, this thermoregulatory strategy provided an efficient insulation to brood with a mean of 32 °C in this area. During the cold nights, the temperature difference between the outer and inner layers of the involucre (with a distance of 1cm) may reach 51 °C.

In the nests of *M. rufiventris* and *M. seminigra* evaluated by Roubik and Peralta (1983) in the state of Amazonas - Brazil, the temperature inside the involucre near the brood cells varied much less (1.3 °C) than that of the environment (7 °C). On species meliponines that do not produce involucre, for example *Frieseomelitta varia* and *Leurotrigona muelleri* (Engels et al 1995), these are not efficient in increasing the temperature of the brood area and could raise it only 2 to 8 °C above the temperature environment (Sakagami 1982).

## Thermoregulation in the brood area of social bees

According to Seeley (2006), precise control of temperature in the brood area can be seen as one of the greatest innovations of the biology of bees that it became possible by the evolution of an individual level for a well-structured society. To maintain a constant temperature is critical for normal growth and development of the larval and pupal stages (Himmer 1927; Degrandi-Hoffman et al 1993).

On the studies by Hess (1926), Himmer (1927) and Dunham (1929) with honeybees, between the end of winter and the beginning of autumn, which is the annual period of development brood, the temperature in the center of the nest area (region of the brood combs) was kept between 33 and 36 °C, with an approximate average of 34.5 °C and oscillating typically less than 1 °C per day, showing the excellent ability thermoregulatory in *Apis mellifera*. Also studying the same species, Tautz et al (2003) submitted the brood to different constant temperatures (32 °C, 34.5 °C and 36 °C) to check its development. They concluded that brood subjected to 36 °C during pupation obtained a performance significantly better in growth than to those undergoing 32 °C and 34.5 °C. However, Jones et al (2005) found that brood of *A. mellifera* subjected to temperatures above or below 35 °C, resulted in workers with a reduction in their memorization capacity and implementing tasks, which reduces the colony's survival rate. Thus concluding, that 35 ºC was the optimal temperature for the best development of this species.

Some species of stingless bees have been studied and found their ability to thermoregulate their brood areas above the ambient temperature (Sakagami 1982; Roubik and Peralta 1983; Engels et al 1995; Moo-Valle et al 2000; Sung et al 2008; Roldão 2011). The temperature is very stable in the brood area (Roubik and Peralta 1983), and the ideal range for the best development brood in most meliponini is between 28 to 36 °C (Nieh and Sánchez 2005). In these bees, the presence of involucre in the nest is very important for heat conservation in many species of stingless bees (Fletcher and Crewe 1981; Roubik and Peralta 1983; Engels et al 1995; Jones and Oldroyd 2007). Another strategy that seems to have an effective capacity to store heat generated by workers in nest is to build brood combs in a spiral form (Fletcher and Crewe 1981; Engels et al 1995). Thus suggesting that the spatial geometry of the combs can influence the exchange of heat.

## Contribution of the brood of social bees in colonial thermoregulation

In studying the meliponines, some authors have reported that the presence of larval mass (with food, eggs, larvae and pupae) it seems that in addition to increasing the internal temperature of the colony through the generation of metabolic heat (thermogenesis) in brood area, can also stock this heat. In part, this is due to pupae and larvae in development contain a lot of water, which has a high capacity to retain heat (Roubik and Peralta 1983; Sung et al 2008; Roldão 2011; Ferreira 2014). Thus, it is suggested that adult bees act as heat generators, larval mass acts to keep the temperature constant in the nest (Sung et al 2008; Stabentheiner et al 2010; Dantas 2014). Therefore, larvae and pupae contribute to their own thermal homeostasis through their metabolic heat, even with its small mass (Petz et al 2004).

Similarly, to bees, the brood of other insect species, such as the larvae of Lepidoptera Eriogaster lanestris, can store thermal energy for a considerable period during development (Ruf and Fiedler 2000). Kukal et al (1988) studied larvae of *Gynaephora groenlandica* tolerant to cold arctic environment and found that in 60% of their time they sought be warming in the sun and 20% were feeding. Both activities are jointly used for the metabolic heat production (body temperature may exceed 20 °C in relation to the environment). In the study by Charabidze et al (2011), was analyzed the heat emission caused by clusters larvae of *Lucilia sericata* (Diptera: Calliphoridae) during feeding. They concluded that the large generated metabolic heat was proportional to the size and number of larvae feeding. They could observe values of up to 50 °C of this larval mass and differences that reached 20 °C between the mass and the ambient temperature.

Petz et al (2004) studied *Apis mellifera carnica*, it was found that O2 consumption and CO2 production were lifted up as the larvae were subjected to higher temperatures. As larvae and pupae have smaller and greater mass, respectively, it is expected that older individuals contribute to greater thermal power production than the more immature, even in different species of *holometabolous* insects (Schmolz and Lamprecht 2000; Petz et al 2004). Sung et al (2008) found significant differences in temperature patterns observed in different points measured in the brood area. It is concluded that this was due to the different stages of development in the brood combs of *Trigona ventralis hoozana*. It was believed that temperatures were higher when cells contained more mature larvae or pupae, and lower when cells contained only small eggs or larvae. This view was also defended by Roubik and Peralta (1983), Stabentheiner et al (2010) and Ferreira (2014).

The heat contributions (thermogenesis) by brood was also confirmed by Dantas (2014), which used infrared thermography as a tool precise and non-invasive to measure the surface temperatures of the brood combs of *Melipona subnitida*, under different ambient temperatures (Figure 1). The author found that as pupae and larvae become older, there is a higher metabolic heat production (Figure 2). The study showed that of the thermal treatments, the one with higher experimental temperature (35 °C) was resulting in greater thermogenesis in all categories of age brood.

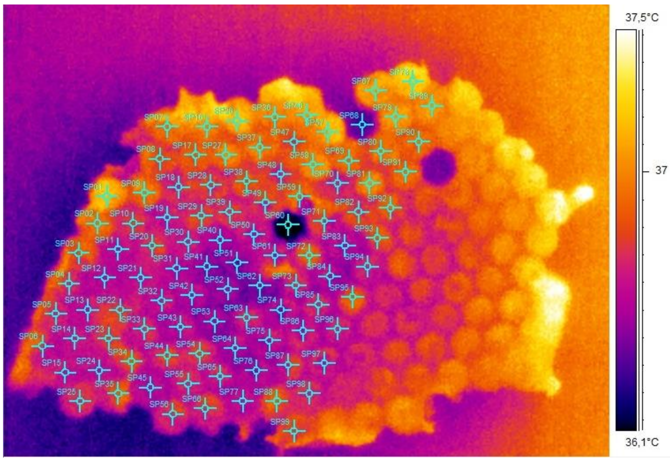

**Figure 1** Thermographic photo to measure the surface temperature to each cell individually (Dantas 2014).

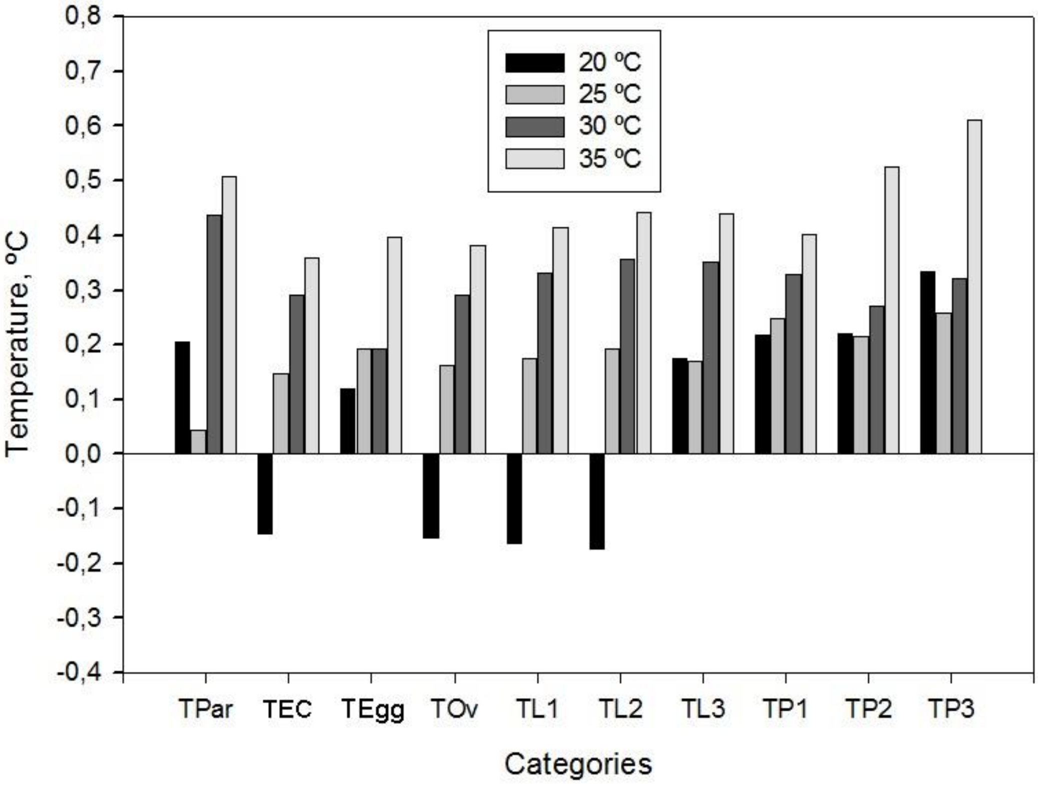

**Figure 2** Variations of means surface temperatures of brood comb by categories for the temperatures ranges. TEgg = egg temperature. TL1 = larval age 1 temperature. TL2 = larval age 2 temperature. TL3 = larval age 3 temperature. TP1 = pupal age 1 temperature. TP2 = pupal age 2 temperature. TP3 = pupal age 3 temperature. T* = dead larva temperature. TEC = empty cells temperature. TPAR = Parasite temperature. Adapted of Dantas (2014).

## Conclusions

Colonial thermoregulation is of paramount importance for the survival and performance of bees, especially for younger individuals, such as brood. The use of active and passive mechanisms is required for these animals to adapt to the environment, combating climate adversities throughout the year, especially the extreme temperatures outside of their thermal tolerance zone. The worker of meliponines, in most species, do not have active mechanisms to thermoregulate, using only the nest and the involucre for it. The brood combs contribute in the colonial thermoregulation with their thermogenesis, and larvae and pupae more mature have higher heat input in the brood comb along its development

## References

Almeida GF (2008) Fatores que interferem no comportamento enxameatório de abelhas africanizadas. Tese, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto.

Angilletta MJ (2002) The evolution of thermal physiology in ectotherms. Journal of Thermal Biology 27:249-268.

Angilletta Jr AF, Bennett H, Guderley CA, Navas CA, Seebacher F, Wilson RS (2006) Coadaptation: a unifying principle in evolutionary thermal biology. Physiological and Biochemical Zoology 79:282-294.

Baêta FC, Souza CF (1997) Ambiência em edificações rurais: conforto animal. Viçosa: UFV.

Camargo JMF (1970) Ninhos e biologia de algumas espécies de Meliponídeos (Hymenoptera: Apidae) da região de Porto Velho, território de Rondônia, Brasil. Revista Biologia Tropical 16:207-239.

Camargo CA (1972) Determinação de castas em Scaptotrigona postica Latreille. Revista Brasileira de Biologia 321:133-138.

Camargo JMF, Wittmann D (1989) Nest architecture and distribution of the primitive stingless bee, Mourella caerulea (Hymenoptera, Apidae, Meliponinae): evidence for the origin of Pleibeia (s. lat.) on the Gondwana continent. Studies on Neotropical Fauna and Environment 24:213-229.

Carvalho MDF (2009) Temperatura da superfície corpórea e perda de calor por convecção em abelhas (Apis mellifera) em uma região semi-árida. Dissertação, Universidade Federal Rural do Semi-árido.

Charabidze D, Bourel B, Gosset D (2011) Larval-mass effect: Characterisation of heat emission by necrophageous blowflies (Diptera: Calliphoridae) larval aggregates. Forensic Science International. doi: 10.1016/j.forsciint.2011.04.016.

Church NS (1959a) Heat loss and the body temperatures of flying insects. I. Heat loss by evaporation of water from the body. Journal of Experimental Biology 37:171–185.

Church NS (1959b) Heat loss and the body temperatures of flying insects. II. Heat conduction within the body and its loss by radiation and convection. Journal of Experimental Biology 37:186–212.

Crailsheim K, Stabentheiner A, Hrassnigg N, Leonhsrd B (1999) Oxygen consumption at different activity levels and ambient temperaturas in isolated honeybees (Hymenoptera: Apidae). Entomologia Generalis 24:001-012.

Couto R, Camillo E (2007) Influência da temperatura na mortalidade de imaturos de Centris (Heterocentris) analis (Hymenoptera, Apidae, Centridini). Iheringia. Série Zoologia 97:51-55.

Dantas MRT (2014) Termogênese e distribuição de calor pela cria de abelhas sem ferrão e sua relação com o estágio de desenvolvimento em ambiente semiárido. Dissertação, Universidade Federal Rural do Semi-árido.

Degrani-Hoffman G, Spivak M, Martin IH (1993) Role of thermoregulation by nestmates on the development time of honeybee (Hymenoptera: Apidae) queens. Annals of the Entomological Society of America 86:165-172.

Dunham WE (1929) The influence of external temperature on the hive temperatures during the Summer. Journal of Economic Entomology 22:798-801.

Engels W, Rosenkranz P, 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. Studies on Neotropical Fauna and Environment 30: 193–205.

Esch H (1960) Über die Körpertemperaturen und den Wärmehaushalt von Apis mellifera. Z. Vergl. Physiol 43:305 –335.

Ferreira NS (2014) Temperatura colonial e tolerância térmica de Melipona subnitida, uma espécie de abelha sem ferrão (Hymenoptera, Apidae, Meliponini) da caatinga. Dissertação, Universidade Federal Rural do Semi-árido.

Fletcher DJC, Crewe RM (1981) Nest structure and thermoregulation in the stingless bee, Trigona (Plebeina) denoiti Vachal (Hymenoptera: Apidae). Journal of the Entomological Society of South Africa 44:183- 196.

Free J, Simpson J (1963) The respiratory metabolism of honeybee colonies at low temperatures. Entomologia Experimentalis et Applicata 8:234-238.

Grodziki P, Caputa M (2005) Social versus individual behavior: a comparative approach to thermal behavior of honeybee (Apis mellifera L.) and the American cockroach (Periplaneta Americana L.). Journal of Insect Physiology 51:315-322.

Halcroft MT, Spooner-Hart RN, Dollin LA (2013a) Australian stingless bees. In: Vit P, Pedro SRM, Roubik DW (ed) Pot Honey: A Legacy of Stingless Bees. Springer Verlag, Berlin, pp 35–72.

Halcroft MT, Haigh AM, Holmes SP, Spooner-Hart RN (2013b) The thermal environment of nests of the Australian stingless bee, Austroplebeia australis. Insectes Sociaux 60:497-506.

Henrich B (1974) Thermoregulation in endothermic insects. Science 185:747-756.

Heinrich B (1979a) Keeping a cool head: Honeybee thermoregulation. Science 205:1269-1271.

Heinrich B (1979b) Thermoregulation of African and European Honeybees during foraging, attack and hive exits and returns. Journal of Experimental Biology 80:217-229.

Heinrich B (1980a) Mechanisms of body-temperature regulation in honeybees, Apis mellifera. I. Regulation of head temperature. Journal of Experimental Biology 85:61-72.

Heinrich B (1980b) Mechanisms of body-temperature regulation in honeybees, Apis mellifera. II. Regulation of thoracic temperature at high air temperatures. Journal of Experimental Biology 85:73-87

Heinrich B (1981) Insect thermoregulation. New York: John Wiley & Sons.

Heinrich B (1993) Hot-blooded insects: Strategies and mechanisms of thermoregulation. Harvard University Press, Cambridge.

Heinrich B, Esch H (1994) Thermorregulation in bees. American Scientist 82:164-170.

Heinrich B (1996) The thermal warriors: strategies of insect survival. Harvard University Press, Cambridge.

Hess WR (1926) Die Temperaturregulierung im Bienenvolk, Z. Vgl. Physiol. 4:465–487.

Himmer A (1927) Der soziale Warmehaushalt der Honigbiene, II, Die Warme der Bienenbrut. Erianger JB. Bienenk 5:1-32.

Huey RB, Kingsolver JG (1989) Evolution of thermal sensitivity of ectotherm performance. Trends in Ecology & Evolution 4:131-135.

Jones JC, Helliwell P, Beekman M, Maleszka R, Oldroyd BP (2005) The effects of rearing temperature on developmental stability and learning and memory in the honey bee, Apis mellifera. Journal of Comparative Physiology A 191:1121-1129.

Jones JC, Oldroyd BP (2007) Nest therorregulation in social insects. Advances in insect Physiology 33:153-191.

Josephson RK (1981) Temperature and the mechanical performance of insect muscle. In: Heinrich J (ed) Insect Thermorregulation. Wiley, New York.

Kerr WE, Sakagami SF, Zucchi R, de Portugal Araujo V, Camargo JMF (1967) Observações sobre a arquitetura dos ninhos e comportamento de algumas espécies de abelhas sem ferrão das vizinhanças de Manaus, Amazonas (Hymenoptera, Apoidea). Atas Simpósio Biota Amazônica 5:255-309.

Kerr WE, Goncalves LS, Blota LF, Maciel HB (1984) Comparative biology of Italian bees (Apis mellifera ligustica), Africanized bees (Apis mellifera adansonii), and their hybrids. Mimeograf paper produced at the Cornell University Entomology Department.

Kerr WE, Carvalho GA, Nascimento VA (1996) Abelha Uruçu: Biologia, Manejo e Conservação – Belo Horizonte-MG: Acangaú: il., (Coleção Manejo da vida silvestre; 2).

Kronenberg F, Heller C (1982) Colonial thermoregulation in honey beee (Apis mellifera). Jornal of Comparative Physiology 148:65-76.

Kukal O, Heinrinch B, Duman JG (1988) Behavioural thermoregulation in the freeze-tolerant arctic caterpillar, Gynaephora groenlandica. Journal of experimental Biology 138:181- 193.

Lindauer M (1955) The water economy and temperature regulation of the honeybee colony. Bee World 364:62-72.

Loli D (2008) Termorregulação colonil e energética individual em abelhas sem ferrão Melipona quadrifasciata Lepeletier (Hymenoptera, Apidae, Meliponini). Tese, Instituto de Biociências, Universidade de São Paulo.

Macías-Macías J, Quezada-Euán J, Contreras-Escareño F, Tapia-Gonzalez J, Moo-Valle H, Ayala R (2011) Comparative temperature tolerance in stingless bee species from tropical highlands and lowlands of Mexico and implications for their conservation (Hymenoptera: Apidae: Meliponini). Apidologie 42:679-689.

Mardan M, Kevan PG (2002) Critical temperatures for survival of brood and adult workers of the giant honeybee Apis dorsata (Hymenoptera: Apidae). Apidologie, Avignon 33:295-301.

May ML (1979) Insect termoregulation. Annu. Review. Entomology 24:313-349.

Michener CD (1974) The social behaviour of bees. A comparative study. Cambridge, Harvard University.

Moo-Valle H, Quezada-Euán JJG, Navarro J, Rodriguez-Carvajal LA (2000) Patterns of intranidal temperature fluctuation for Melipona beecheii colonies in natural nesting cavities. Journal of Apicultural Research 39:3-7.

Moyes CD, Schulte PM (2010) Princípios da fisiologia animal (2ª edição). Artmed, Porto Alegre-RS.

Nããs IA (1989) Princípios de conforto térmico na produção animal. Ícone Editora, São Paulo.

Nieh JC, Sánchez D (2005) Effect of food quality, distance and height on thoracic temperature in the stingless bee Melipona panamica. Journal of Experimental Biology 208:3933-3943.

Petz M, Stabentheiner A, Crailsheim K (2004) Respiration of individual honeybee larvae in relation to age and ambient temperature. Journal of Comparative Physiology B 174:511–518.

Posey DA, Camargo JMF (1985) Additional notes on the classification and knowledge of stingless bees (Meliponinae, Apidae, Hymenoptera) by the Kayapó Indians of Gorotire, Pará, Brazil. Annals of Carnegie Museum 54:247–274.

Roberts S.; Harrison JF (1998) Mechanisms of thermoregulation on flying bees. American Zoologist. 38:459-502.

Roldão YS (2011) Termorregulação colonial e a influência da temperatura no desenvolvimento da cria em abelhas sem ferrão, Melipona scutellaris (Hymenoptera, Apidade, Meliponini). Dissertação, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto.

Roubik DW, Peralta FJA (1983) Thermodinamics in nest of two Melipona species in Brazil. Acta Amazonica 13:452-66.

Roubik DW (1989) Ecology and natural history of tropical bees. Cambridge University Press, New York.

Roubik DW (2006) Stingless bee nesting biology. Apidologie 37:124–143.

Ruf C, Fiedler K (2000) Thermal gains through collective metabolic heat production in social caterpillars of Eriogaster lanestris. Naturwissenschaften 87: 193- 196.

Sakagami SF (1882) Stingless bees. In: Hermann HR (ed) Social Insects, vol 3. Academic Press, New York.

Schwarz HF (1948) Stingless bees (Meliponidae) of the Western Hemisphere. Bulletin of the American Museum of Natural History 90:1–546.

Schmolz E, Schulz O (1995) Calorimetric investigations on thermoregulation and growth of wax moth larvae Galleria mellonella. Thermochimica Acta 251:241–245.

Schmolz E, Lamprecht I (2000) Calorimetric investigations on activity states and development of holometabolous in sects. Thermochimica Acta 349:61–68.

Seeley TD (2006) Ecologia da Abelha: Um Estudo de Adaptação na Vida Social (tradução de C. A. Osowski). Paixão Editores LTDA, Porto Alegre.

Stabentheiner A, Pressl H, Papst T, Hrassnigg N, Crailsheim K (2003) Endothermic heat production in honeybee winter clusters. Journal of Experimental Biology 206:353–358.

Stabentheiner A, Kovac H, Brodschneider R (2010) Honeybee colony thermoregulation – regulatory mechanisms and contribution of individuals in dependence on age, location and thermal stress. Plus One 5:297-308.

Silva RG (2000) Introdução à Bioclimatologia Animal. Nobel, São Paulo.

Southwich EE (1982) Metabolic energy of intact honey bee colonies. Comparative Biochemistry and Physiology 71:277-281.

Southwich EE (1983) The honey bee cluster as a homeothermic superorganism. Comparative Biochemistry and Physiology 75:641-645.

Sung IH, Yamane S, Hozumi S (2008) Thermal characteristics of nests of the Taiwanese stingless bee Trigona ventralis hoozana (Hymenoptera: Apidae). Zoological Studies 47:417-428.

Tautz J, Maier S, Groh C, Rossler W, Brockmann A (2003) Behavioural performance in adult honey bees is influenced by the temperature experienced during their pupal development.

Proceedings of the National Academy of Sciences of the United States of USA 100:7343–7347.

Van Benthem FDJ, Imperatriz-Fonseca VL, Velthuis HHW (1995) Biology of the stingless bee Plebeia remota (Holmberg): observations and evolutionary implications. Insectes Sociaux 42:71-87.

Vollet Neto A (2011) Biologia térmica de Scaptotrigona depilis (Apidae, Meliponini): adaptações para lidar com altas temperaturas. Dissertação, FFCLRP-USP.

Wille A, Michener CD (1973) The nest architecture of stingless bees with special reference to those of Costa Rica (Hymenoptera: Apidae). Revista Biologia Tropical 21:1–278.

Zucchi R, Sakagami SF (1972) Capacidade termoreguladora em Trigona spinipes e em algumas outras espécies de abelhas sem ferrão (Hymenoptera: Apidae: Meliponinae). In: Cruz-Landim C, Hebling NJ, De Lello E, Takahashi CS (eds) Homenagem a Warwick Estevam Kerr. Rio Claro, São Paulo, pp 301-309.