

# Differences in foraging and broodnest temperature in the honey bees *Apis cerana* and *A. mellifera*

Ken TAN<sup>1,2</sup>, Shuang YANG<sup>2</sup>, Zheng-Wei WANG<sup>2</sup>, Sarah E. RADLOFF<sup>3</sup>,  
Benjamin P. OLDROYD<sup>4</sup>

<sup>1</sup>Key Laboratory of Tropical Forest Ecology, Xishuangbanna Tropical Botanical Garden, Chinese Academy of Sciences, Yunnan, People's Republic of China

<sup>2</sup>Eastern Bee Research Institute, Yunnan Agricultural University, Heilongtan, Kunming, Yunnan Province, People's Republic of China

<sup>3</sup>Department of Statistics, Rhodes University, Grahamstown 6140, Republic of South Africa

<sup>4</sup>School of Biological Sciences, University of Sydney, Sydney, NSW 2006, Australia

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**Abstract** – This study aims to explore the effect of ambient temperature on foraging the activity of *Apis cerana* and *Apis mellifera* colonies. We recorded ambient temperature, the time at which foraging commenced, worker thoracic temperature, and brood nest temperature at the same apiary in Kunming, China. We found that *A. cerana* start foraging earlier and at lower temperatures than do *A. mellifera*. *A. cerana* foraging (departures per minute) also peaked earlier and at lower temperature than did *A. mellifera* foraging. At the same ambient temperature, departing *A. mellifera* foragers and workers sampled from the brood nest had a higher thoracic temperature than departing *A. cerana* foragers and brood nest workers. *A. mellifera* colonies also maintained their brood nest temperature significantly higher than did *A. cerana*. Our results suggest that the larger *A. mellifera* foragers require a higher thoracic temperature to be able to forage.

*Apis cerana* / *Apis mellifera* / foraging temperature / thoracic temperature

## 1. INTRODUCTION

The ecological success of honey bees depends in part on their ability to thermoregulate and to thereby forage at lower temperatures than competing bee species (Goulson 2003). The internal temperature of a honey bee, *Apis mellifera*, nest is maintained at a relatively constant temperature around 34.5–35.5 °C (Bujok et al. 2002; Kleinhenz et al. 2003; Jones et al. 2004). This means that honey bee foragers are prewarmed and can commence foraging before most solitary bees or stingless bees (Jones and Oldroyd 2007).

Furthermore, although already warm from the heat generated within their nest, embarking *A. mellifera* foragers further elevate their thoracic temperature ( $T_{Th}$ ) before flight to between 36 and 38 °C by shivering their wing muscles (Heinrich 1979). At low (<20 °C) ambient temperatures ( $T_A$ ), honey bees of several species can maintain their  $T_{Th}$  above 30 °C while foraging (Heinrich 1979; Dyer and Seeley 1987), as a byproduct of flight muscle activity (Heinrich 1993; Dudley 2000), and in some instances utilizing warming zones created by the morphology of the flowers that they visit (Kevan 1975) or selecting flowers with warmer nectar (Dyer et al. 2006; Norgate et al. 2010).

In order to fly, an insect must attain a minimum  $T_{Th}$  (Heinrich 1979; Dyer and Seeley

Corresponding author: B.P. Oldroyd,  
benjamin.oldroyd@sydney.edu.au  
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1987) that is species specific. Thus, the first honey bee colonies in which the foragers can achieve this minimum temperature can commence foraging before competing colonies and solitary bees, potentially benefiting from uncontested access to floral resources. Asian honey bees vary greatly in size and nesting behavior (Ruttner 1988), and this in turn influences their ability to thermoregulate and achieve the minimum  $T_{Th}$  required for flight (Dyer and Seeley 1987). Oldroyd and Wongsiri (2006) argued that the different thermoregulatory abilities of Asian honey bees results in resource partitioning among the species, thereby reducing interspecific competition. Oldroyd et al. (1992) showed that the medium-sized cavity-nesting species *A. cerana* is able to forage earlier than the open-nesting giant bees and dwarf bees, probably because their nests are better thermoregulated (Dyer and Seeley 1991) and because *A. cerana* is able to achieve a greater differential between  $T_{Th}$  and  $T_A$  as a result of endogenous heat production (Dyer and Seeley 1987).

The Western honey bee *A. mellifera* was introduced to China a little more than 100 years ago (Yang 2005). *A. mellifera* has been extensively propagated by beekeepers and is now extant throughout China. In recent years, the number of domestic colonies has surpassed 7 million (Yang 2005). Simultaneously, beekeeping with indigenous *A. cerana* has declined, and there is some evidence that wild populations of *A. cerana* are also in decline, in part because of direct competition with *A. mellifera* (Ji et al. 2003; Yang 2005). This is unfortunate because it has been claimed that the indigenous *A. cerana* is a more efficient pollinator of plants that bloom in early spring than the *A. mellifera* strains present in China. In particular, it has been claimed that *A. cerana* can commence foraging earlier in the morning and at lower ambient temperatures than can *A. mellifera* (Yang 2005).

*A. mellifera* is significantly larger than *A. cerana* (Ruttner 1988). Other things being equal, one would predict that a larger bee species would have greater capacity for endogenous heat production and be able to forage at lower temperatures (e.g., Bartholomew and Heinrich

1981; Dyer and Seeley 1987; Corbet et al. 1993; Bishop and Armbruster 1999). Thus, we predicted that *A. mellifera* should be able to sustain a greater differential between  $T_{Th}$  and  $T_A$  than *A. cerana* and, contrary to the suggestion of Yang (2005), should thereby be able to forage earlier in the morning and on colder days than *A. cerana*.

Here, we explore the relationship between ambient temperature, foraging activity, and bee species at a single location in Kunming, China during winter. Kunming is in the subtropical zone, with winter temperatures in the range of 0–20 °C. Honey bees forage throughout the year in this region.

## 2. MATERIALS AND METHODS

Ten queenright *A. cerana* and 10 queenright *A. mellifera* colonies were placed in an apiary in Yunnan Agricultural University campus, Kunming (102°10'–103°40' longitude, 24°23'–26°22' latitude, 1,890 m elevation), China. All colonies were housed in standard Langstroth hives and we equalized the colonies so that each contained two frames of brood and two frames of honey and pollen. The experiments were conducted in January of 2010 (three pairs of colonies) and 2011 (seven pairs of colonies) in fine weather ( $T_A$  between 2 and 20 °C).

### 2.1. Body and broodnest temperatures

Observations started in the early morning. When the first bees emerged from the hive entrance for foraging, the ambient temperature was recorded. When the ambient temperature reached 6 °C and later when it reached 20 °C, we measured the thoracic temperature of each of 10 randomly selected departing foragers and 10 randomly selected workers from the brood nest from each colony with a digital thermometer (Sensortek, BAT-12, with a resolution of  $\pm 0.1$  °C). To obtain a reading, we grasped a bee with rubber-covered forceps and thrust the copper probe (diameter 1 mm) about 3 mm into the bee's thorax until the highest temperature was encountered (Heinrich 1979). Brood nest temperature was also measured by thrusting the copper probe into the center of the brood nest before brood nest bees were sampled.

## 2.2. Body mass and nectar loads

Body mass was measured for each of the 10 departing and 10 returning foragers caught at the entrance. The mean difference in mass between returning and departing foragers was used as a proxy for the loads carried by returning foragers.

## 2.3. Foraging activity

Foraging activity was measured as the number of exiting bees in a 30-min period for each test colony for test 1 day. Each test ran from 8:30 until 11:30, and fluctuations in the ambient temperature during the test period were recorded on each of the 10 test days.

## 2.4. Statistical analysis

Independent *t* tests were used to test for differences between the two species in body mass, load, minimum foraging temperature, body thoracic temperature, and brood nest temperature. Repeated measures ANOVA was used to test for species differences in the mean number of foragers over time from 8:30 until 11:30. Prior to analysis, homogeneity of variances and normality of the data were examined using Levene's and Shapiro–Wilk's tests (Johnson and Wichern 2002). Homogeneity of the variances was achieved by applying a square-root transformation.

## 3. RESULTS

### 3.1. Body and brood nest temperatures

There was a significant difference in the  $T_A$  at which the *A. cerana* ( $3.42 \pm 0.11$  °C;  $\pm$ SE) and *A. mellifera* ( $6.57 \pm 0.17$  °C) colonies commenced foraging ( $t_{58} = 15.40$ ,  $P < 0.0001$ ). When  $T_A$  was 6 °C,  $T_{Th}$  of *A. mellifera* foragers and brood nest bees was significantly higher than those of *A. cerana*, but when the ambient temperature was 20 °C, there was no significant difference in  $T_{Th}$  between the two species. At the same ambient temperature, *A. mellifera* colonies maintained a significantly higher brood nest temperature than did *A. cerana* colonies (Table 1).

### 3.2. Body mass and forager load

The mass of *A. mellifera* foragers ( $93.3 \pm 1.7$  mg) was significantly greater ( $t_{198} = 12.27$ ,  $P < 0.0001$ ) than that of *A. cerana* foragers ( $69.3 \pm 1.0$  mg). The load carried by *A. mellifera* foragers ( $51.0 \pm 1.9$  mg) was also significantly greater than that carried by *A. cerana* ( $31.3 \pm 1.2$  mg) foragers ( $t_{198} = 8.75$ ,  $P < 0.0001$ ).

### 3.3. Foraging activity

There was a significant difference between the species in the mean number of foragers from 08:30 to 11:30 in each 30-min period (species,  $F_{1,18} = 50.05$ ,  $P < 0.0001$ ; time,  $F_{5,90} = 144.43$ ,  $P < 0.0001$ ; interaction,  $F_{5,90} = 21.01$ ,  $P < 0.0001$ ; Fig. 1). *A. cerana* foraging activity reached its peak around 10:00, at which time the ambient temperature was only about 10 °C. In contrast, *A. mellifera*-foraging activity reached its peak at around 11:30 at which time ambient temperature had reached about 20 °C (Fig. 1).

## 4. DISCUSSION

The ecotype of *A. cerana* that is indigenous to Kunming starts foraging and reaches the peak of foraging activity earlier and at a lower  $T_A$  than does exotic *A. mellifera*. *A. mellifera* foragers apparently require a higher minimum  $T_A$  and  $T_{Th}$  than *A. cerana* foragers before they commence foraging. Thus, we reject our hypothesis that the larger *A. mellifera* should be able to generate higher  $T_{Th}$  than *A. cerana* and thus fly at cooler temperatures. Instead, we support the contention of Yang (2005) that *A. cerana* in the Kunming region forage temperatures than do *A. mellifera*. This suggests that *A. cerana* should outcompete *A. mellifera* during cooler weather. We also support the view of Yang (2005) that if *A. cerana* is driven extinct in the future, *A. mellifera* may not fully replace the pollinating activities of *A. cerana*. Thus, the decline in *A. cerana* populations in China has potential inimical effects on any indigenous flora that is adapted to *A. cerana* pollination

**Table 1.** Mean thoracic temperature, and brood nest temperature (degrees Celcius±SE) in 10 co-located *A. cerana* and *A. mellifera* colonies.

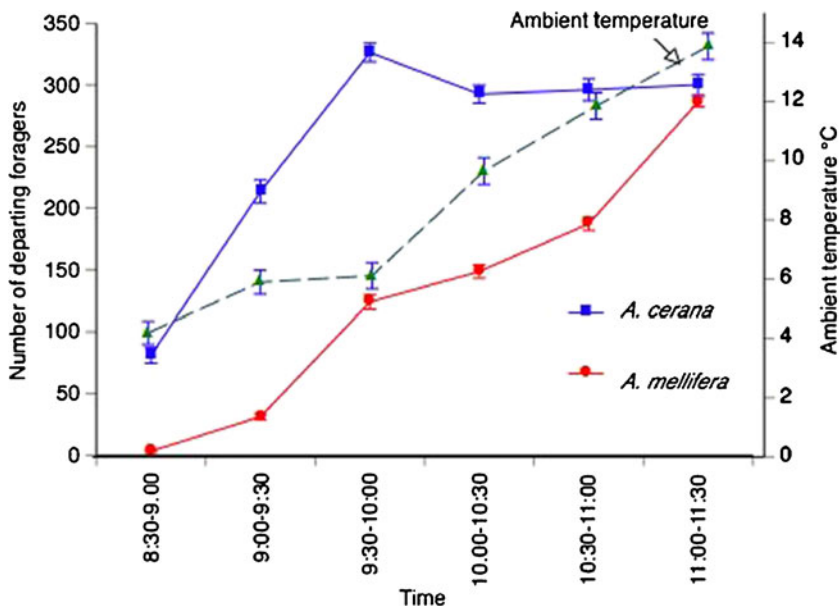
Ambient temperature (°C)	Measurement	<i>A. cerana</i>	<i>A. mellifera</i>	<i>P</i>
6	Departing forager $T_{Th}$	21.8±0.23	23.6±0.22	<0.0001
	Brood nest workers $T_{Th}$	14.5±0.16	19.7±0.16	<0.0001
	Brood nest $T$	33.1±0.05	34.1±0.05	0.001
20	Departing forager $T_{Th}$	30.7±0.3	31.4±0.2	0.052
	Brood nest workers $T_{Th}$	28.9±0.3	29.2±0.2	0.466
	Brood nest $T$	33.7±1.8	34.2±0.9	0.006

(Ji et al. 2003). Some early-flowering crops may also be less well pollinated.

The  $T_{Th}$  of bees in the brood and the overall broodnest temperature was slightly higher for *A. mellifera* than for *A. cerana*, especially at low  $T_A$ . This suggests that *A. cerana* maintains a lower brood nest temperature than *A. mellifera*. There is likely a tradeoff between energy expenditure on nest thermoregulation and the benefits of a higher and more stable brood nest temperature for brood development (Jones et al. 2005). *A. cerana* has apparently evolved to

tolerate a lower and more variable brood nest temperature than *A. mellifera*, perhaps paying a price of less canalized brood development. *A. mellifera* has apparently evolved towards a very stable brood nest temperature, gaining the benefits of uniform brood development, but paying the cost of greater energetic expenditure on maintaining a stable brood nest temperature.

Maintaining an elevated  $T_{Th}$  while foraging requires energy expenditure, but allows foragers to carry heavier loads because they can generate greater mass-specific lift (Harrison and Fewell

**Figure 1.** Mean number of *A. cerana* and *A. mellifera* foragers observed every 30 min from 08:30 to 11:30 ( $n=10$  colonies each) relative to temperature. Error bars are standard error of the mean.

2002). Collectively, thermoregulation by foragers represents a considerable metabolic expense for a colony, which must be balanced against their greater foraging efficiency. It appears that *A. cerana* trades lower foraging efficiency for greater metabolic efficiency, whereas in *A. mellifera* the compromise is reversed.

All honey bee species examined to date maintain a  $T_{Th}$  5–6 °C above  $T_A$  when foraging at cool temperatures (Dyer and Seeley 1987). Coelho (1991) argued that *A. mellifera* require a  $T_{Th} > 28$  °C in order to generate sufficient force to lift off. Heinrich (1979) suggested that departing *A. mellifera* foragers actively warm up their flight muscles before commencing foraging, often achieving  $T_{Th}$  that is greater than workers in the brood nest. We found that departing foragers of both species had lower  $T_{Th}$  than brood nest workers. We cannot account for this difference in findings.

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**Différences de température, pour le butinage et dans le nid à couvain, entre les abeilles *Apis cerana* et *A. mellifera*.**

*Apis cerana* / *Apis mellifera* / température ambiante / début du butinage / température thoracique

**Unterschiede in Sammel- und Brutnesttemperaturen bei den Honigbienenarten *Apis cerana* und *A. mellifera***

*Apis cerana*/*Apis mellifera* / Sammeltemperatur / Thoraxtemperatur

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