BROOD THERMOREGREULATION BY THE GIANT HONEY BEE
(APIS DORSATA F.)

Michael Burgett* and Manas Titayavan**

ABSTRACT

The brood temperature of a giant honey bee colony, Apis dorsata F., along with the ambient temperature, were recorded for a continuous 35 day period during the hot season in northern Thailand. For the period T_b averaged 33.2°C while T_a averaged 28.4°C. The T_b range was 12°C while the T_a range was 22°C. While the T_a range is greater than that reported for the congener species A. florea, A. cerana and A. mellifera, giant honey bees are capable of regulating the brood nest temperature through a wide range of ambient temperatures.

INTRODUCTION

Within the monophyletic honey bee genus Apis, only the giant honey bee Apis dorsata F., and the dwarf honey bee Apis florea F., build exposed nests consisting of a single comb (RUTTNER, 1988). Giant honey bee workers expend a great deal of time and energy maintaining a curtain of bees over the nest comb that functions for colony defense and protection from weather (SEELEY ET AL., 1982). This "living wall" also serves as the primary mechanism for thermoregulation of the brood nest. To heat the brood nest at low ambient temperatures the bees utilize metabolic heat generated by flight muscles. For brood nest cooling at high ambient temperatures, bees in the curtain use evaporative cooling of honey stomach contents, a process MARDAN & KEVAN (1989) have termed "gobbetting," as well as fanning by bees in the outermost layer of the curtain (DYER & SEELEY, 1991). During periods of high ambient temperatures workers in the curtain will undertake mass defecation flights away from the nest comb (SEELEY ET AL., 1985). This behavioral device also serves to dissipate the corporate heat built up in curtain workers (MARDAN & KEVAN, 1989).

A. dorsata appears less precise in its ability to regulate the brood nest temperature as compared to the cavity nesting Apis species A. mellifera L. and A. cerana F. (DYER & SEELEY, 1991). Extrapolating from the data of DYER & SEELEY (1991), the brood temperature of a free-living A. dorsata colony ranged from a low of 29°C to a high of 37°C over an ambient range of 19°C to 37°C. These data were from 96 temperature measurements of an A. dorsata colony in India. We report here the brood thermodynamics of an A. dorsata colony measured for a continuous 35-day period during the hot season in northern Thailand.

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MATERIALS AND METHODS

The study was conducted during the period 29 April through 3 June 1993 on the campus of Maejo University in Chiang Mai Province, Thailand. 104.6 mm of measurable precipitation fell on 15 days of the 35 day period. The study colony was located 23 m above the ground on a porch roof overhang of a third story dormitory apartment. The bees arrived at the nest site on 23 January 1993. The axis of the colony was oriented in a ENE direction with one side of the colony exposed to afternoon sun while the interior comb side was in constant shade (Fig. 1). The colony measured 1.22 m across the top portion of the comb and was 0.74 m in height. The colony was well populated with adult bees and was in an active brood rearing state throughout the study period.

Brood (T_b) and ambient (T_a) temperatures were recorded for 35 days using an electronic 2-channel temperature recorder (Omnidata Datapod microprocessor DP 212). One of the temperature probes (TP 10 V) was positioned perpendicular to the comb so as to just touch the surface of an area of capped brood. The second probe, used for recording T_a, was positioned ca. 50 cm below the bottom edge of the nest comb. T_b and T_a were automatically recorded at 30-min intervals, with a clock accuracy of ±3 min/mon. T_b measurements were made on both sides of the comb. The temperature measurements on the sun exposed side of the nest comb were made during the period 1030 h April 29 to 1000 h May 20. For the shaded side of the nest, measurements were made from 1030 h May 20 to 1000 h June 3, for a total of 1,678 paired T_b and T_a measurements. This produced a temperature record over a continuous 839-h period.

RESULTS

For the study period the mean T_b was 33.2°C and the mean T_a was 28.42°C. The T_b ranged from 28°C to 39°C. The T_a ranged from 20°C to a maximum of 41°C. The maximum recorded difference between the T_b and T_a was 11°C during a night period when the T_a was 20.5°C and the T_b was 31.5°C. Conversely, at the maximum T_a of 41°C the T_b was 37°C. The T_b maximum of 39°C was recorded when the T_a was 40°C. Interestingly, the T_b minimum of 28°C was recorded 8 May at 1430 h, a time of the diel period when T_b ought to be near the daily maximum. However, in the hour preceding the 28°C low reading, T_b fell from 36.5°C while during the same period T_a plummeted from 35°C to 23°C; obviously some meteorological event precipitated this steep decline in both T_b and T_a. This date (8 May) possessed the maximum recorded daily precipitation of the entire temperature record i.e., 24.0 mm. Table 1 provides a statistical summary of T_b and T_a data.

The diel means derived for each 30-min recording period are shown in Fig. 2. The mean T_b was maintained above the mean T_a for each measured time interval throughout the day. T_b = T_a during the afternoon T_max at 1500 h (T_b = 34.77°C, T_a = 34.72°C). The maximum difference between the mean T_b and T_a occurred at 0600 h (T_b = 31.67°C, T_a = 24.01°C, T_diff = 7.66°C). The mean difference between T_b and T_a for all time periods is 4.79°C. T_a displays an expected cyclical diel pattern. Although higher and much dampened in range, T_b tracks the circadian T_a.

Figure 3 displays the values for the parameter T_b–T_a for the inclusive period 30 April
Table 1. Statistical summary of $T_b$ and $T_a$ data for the period 1030 h 29 April through 1000 h 3 June 1993.

<table>
<thead>
<tr>
<th></th>
<th>mean</th>
<th>standard error</th>
<th>median</th>
<th>mode</th>
<th>standard dev.</th>
<th>min</th>
<th>max</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_b$</td>
<td>33.21°</td>
<td>0.038</td>
<td>33.0</td>
<td>32.5</td>
<td>1.57</td>
<td>28</td>
<td>39</td>
<td>1678</td>
</tr>
<tr>
<td>$T_a$</td>
<td>28.41°</td>
<td>0.104</td>
<td>27.5</td>
<td>24.0</td>
<td>4.26</td>
<td>20</td>
<td>41</td>
<td>1678</td>
</tr>
</tbody>
</table>

Figure 1. *Apis dorsata* colony on the Maejo University campus, Maejo, Thailand. The nest comb measures ~1.22 m in length and ~0.74 m in height.
Figure 2. Diel means for $T_b$ and $T_a$ at the 30 min temperature recording intervals. $N = 35$ for each time interval.
Open bars = $T_b$, closed bars = $T_a$.

Figure 3. Temperature differential between $T_b$ and $T_a$ for the period April 30 through June 2, 1993. Average $T_{	ext{diff}} = 4.79 \pm 0.07^\circ \text{C}$. $T_b > T_a$ for 781 h of 839 h (93.1% of the period).
Figure 4. T_b plotted over a range of T_a. R sq. = 0.84. N = 1681 paired T_b/T_a observations. Line through the origin represents the hypothetical T_b = T_a.

through 2 June. Positive values are produced when T_b > T_a, conversely, negative values are given when T_b < T_a. For the 839 h recording period, T_b was greater than T_a for 781 h (93.1% of the time).

Plotting the individual 1678 T_b recordings against the T_a range of 20° to 41° provides the data base for Fig. 4. The regression formula for T_b is y = 0.338 T_a + 23.59, which is highly significant (P < 0.001). This small slope reflects the colony’s ability to thermoregulate the brood nest.

DISCUSSION

It is intuitively obvious that T_b is not independent of T_a. Regression analysis yields an r^2 value of 0.84. However, it is also apparent that A. dorsata workers are capable of regulating T_b about an optimum of 33.2° through a wide range of ambient temperatures. During the 839 h recording period T_a was below 33° for 696 h (83.0% of the time) and was greater than 33° for 123 h (14.7% of the period). T_b was below 33° 46.4% of the period and was above 33° for 41.7% of the 839 h.

While our data show A. dorsata capable of regulating the temperature of the brood nest, it is not with the precision of the cavity nesting Apis species. Our reported T_b range for A. dorsata is large (≈12°) when compared to its congeners A. florea, A. mellifera and A. cerana (≈3°) and is similar to the ≈9° T_b range for A. dorsata interpolated from Dyer & Seeley (1991).
For A. dorsata brood the temperature limits for thermal death are unknown. Winston (1987) provides a range of 30° to 35° for optimal brood rearing for A. mellifera. The upper limit T_\text{lethal} for A. mellifera brood is ≥ 37° (Seeley & Heinrich, 1981). For the 839 h of our A. dorsata temperature record, T_b ≥ 37° for 16.5 h, i.e. 2% of the time period. It should be noted that this was not a continuous period at T_b ≥ 37°. The effects on brood, if any, of short, episodic periods of T_b ≥ 37° are unknown. For A. mellifera the low lethal is T_b < 26°, however, even brood reared in the range 28° to 30° results in a large number of deformed A. mellifera adults (Himmer, 1927). During our 839 h recording period brood temperatures lower than 30° were experienced for only 4.5 h, and again these low temperature events were episodic. The lower limit for T_\text{lethal} would be rarely experienced by tropical Apis brood in colonies well populated by adult bees. Based on our observations we would suggest that A. dorsata brood can be successfully reared over a broader range of temperatures and is therefore somewhat less stenothermic than A. mellifera.

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REFERENCES