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Thermal Characteristics of Nests of the Taiwanese Stingless Bee *Trigona ventralis hoozana* (Hymenoptera: Apidae)

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I-Hsin Sung, Sôichi Yamane, and Satoshi Hozumi (2008) Thermal characteristics of nests of the Taiwanese stingless bee *Trigona ventralis hoozana* (Hymenoptera: Apidae). *Zoological Studies* **47**(4): 417-428. Temperatures in 3 natural nests of the Taiwanese stingless bee *Trigona* (*Lepidotrigona*) *ventralis hoozana* were measured in Dapu and Tsaoshan, Chiayi County, Taiwan from Dec. 2002 to Mar. 2004. The temperature in the brood rearing zone of 2 nests was kept relatively constant in a range of 29-32°C. Even in the morning in Jan., the temperature in the brood area was maintained at 29.5°C, about 21°C higher than the ambient temperature. Healthy nests could tolerate ambient temperatures even lower than 8°C, judging from the elevational distribution limit of this species and corresponding meteorological records. The maintenance of constant temperatures in the brood area is chiefly due to ameliorated thermal conditions in the nesting cavity. This is realized by the thermostatic effect of the thick wood of the living tree enclosing the cavity. The involucrum, which completely encloses the brood combs, may retain thermal energy generated by the adults and partially by the mass of brood in the brood area. http://zoolstud.sinica.edu.tw/Journals/47.4/417.pdf

Key words: Stingless bee, *Trigona ventralis hoozana*, Nest architecture, Nest temperature.

It is well known that highly eusocial bees, such as honeybees (genus *Apis*), bumble bees (genus *Bombus*), and vespine wasps (genera *Vespa* and *Vespula*) have the ability to incubate their nests by generating metabolic heat from their bodies (Heinrich 1993). By maintaining preferable thermal conditions in the nest, these social insects can increase the growth and survival rates of immature stages. This may, in turn, promote successful breeding in their colonies. Among social bees and wasps, honeybee colonies are most capable of controlling the nest temperature with high precision (Heinrich 1996).

Although there are hundreds of stingless bee species in the tribe Meliponini (family Apidae), only a few species are known to maintain relatively constant temperatures in the nest (Sakagami 1982). *Trigona spinipes* (Fabricius), a Brazilian stingless bee, can maintain the temperature of the brood area to between 34.1 and 36.0°C (Zucchi and Sakagami 1972). Another Brazilian species, *Scaptotrigona postica* Latreille, can keep temperatures in the brood area at 32 ± 3°C (Engels et al. 1995). Most stingless bees, however, are thought to lack a notable ability to thermoregulate their nests. This is exemplified by some South American species that build their nest in tree hollows. Brood areas in nests of *Melipona seminigra* Friese and *M. rufiventris* Lepeletier are completely covered by an involucrum, but the temperature of this area changes following changes in the ambient temperature, and is kept at only 2-3°C higher than the temperature outside the involucrum (Roubik and Peralta 1983). *Melipona*

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beecheii Bennet in Mexico (Moo-Valle et al. 2000) and *Tri. laeviceps* Smith in Sumatra (Sakagami et al. 1983) show an unremarkable ability to thermoregulate.

Stingless bees are mostly distributed in the tropics, with a small proportion of species reaching the subtropics (Michener 2000) and only a few species having spread into relatively cool regions (Schwarz 1939, Ortiz-Mora et al. 1995). *Trigona* (*Lepidotrigona*) *ventralis hoozana* Strand is the only stingless bee species distributed on the island of Taiwan, which is located near the northernmost limit of this stingless bee's distribution in the eastern hemisphere (Sakagami and Yamane 1987). Sakagami and Yamane (1984) considered that this species can adapt to a cooler climatic environment than other species that inhabit the tropics. Although most stingless bees inhabit warmer climates, this bee can reach mountainous regions up to 2500 m in elevation on Taiwan, where air temperatures often drop as low as 5°C in winter. Roubik (1989) supposed that such rigorous climatic conditions would lead to diapause or quiescence in stingless bee's colonies. Temperatures change in nests of *Tri. ventralis hoozana* throughout the year, and whether bees have the ability to thermoregulate has not yet been studied.

As a 1st step toward a comprehensive understanding of thermoregulation by *Tri. ventralis hoozana* colonies, this paper deals with the thermal conditions measured in 3 natural nests of this species in submontane areas of Taiwan, where climatic conditions in winter are rigorous for stingless bees. Changes in temperature within the nest, and those inside and outside of the tree hollow were continuously measured by electronic sensors from 2002 to 2004. Based on these measurements, (1) thermal characteristics were examined in comparison with those in some other comb-forming stingless bee species, and (2)

mechanisms for maintaining relatively constant temperatures in the nest are discussed in terms of the nest site, nest structure, and thermogenesis by the colony.

MATERIALS AND METHODS

Nest sites

The 3 nests used for the present study, TV-30, TV-31, and TV-33 were located in submontane areas of Chiayi County, just south of the tropic of Cancer, in southwestern Taiwan. The locality, elevation, species of tree where the nests were found, and some related items are given in table 1. All nests were built in a hollow of trees in secondary forests consisting of betel nut palm *Areca catechu* L., bamboo *Dendrocalamus latiflorus* Munro, and Lauro-Fagaceae association. The inter-nest distance was about 1000 m between TV-31 and TV-33, and about 5000 m between TV-31 and TV-30. The population size of a huge mature colony of this species was estimated to be 10,000 individual adults and 12,000 brood cells (Sakagami and Yamane 1984). The 3 observed nests were regarded as medium to large sized, judging from the trunk size, nest age (Table 1), and flight activities of bees seen at the entrance.

Measuring methods

In order to record temperatures within the nests for a long time, a 4-channel outdoor data logger (HOBO® H08-008-04, Onset Computer Co., Pocasset, MA, USA) with the following specifications was used at each nest: measuring range between -20°C and 70°C, accuracy of ± 0.5°C at 20.0°C, and resolution of ± 0.41°C at 20.0°C. Another type of data logger, H08-004-002, which had an

Table 1. Conditions at 3 natural nests of *Trigona ventralis hoozana* distributed in Dapu and Tsaoshan Villages, Chiayi County, Taiwan

Nest code	Coordinates	Elevation (m)	Species of tree	Trunk diameter at nest entrance height (cm)	Height of entrance (m)	Approximate nest age (yr)
TV-30	Dapu Village, 23°19'N, 120°38'E	350	*Sapindus mukorossi* Gaertner	50	2.5	10
TV-31	Tsaoshan Village, 23°20'N, 120°38'E	650	*Cinnamomum camphora* (L.) Sieb.	70	1	3-5
TV-33	Tsaoshan Village, 23°20'N, 120°38'E	650	*Trema orientalis* (L.) Blume.	85	1	3-5

internal thermosensor, was placed outside the nest out of the direct sun and rain, to measure ambient temperatures.

According to Sakagami and Yamane (1984), the positions of the brood area and storage pot area in the hollow were estimated from the location of the entrance tube (Fig. 1). The entrance tube is usually located near the bottom of the brood area, which is nearly spherical with a diameter of about 20 cm and completely covered by a multilayered involucrum. Storage pots with the same morphology for both pollen and honey are located above the brood area. The entire nest is enclosed by a hard batumen. All cavities had 1 or more open spaces below and/or above the nest, and we also selected such empty spaces for measuring the cavity temperature. First, some 1-cm-diameter holes were bored 0-25 cm above and 0-15 cm below the entrance tube, using a hand drill. Then,

a 0.8-cm-diameter aluminum pipe was carefully inserted into each hole to check for brood or stored food to determine the position at which the thermistor sensors should be inserted. The temperatures measured at each point are indicated as follows (Fig. 1): Tp for the pot area, Tb1-Tb3 for different positions in the brood comb area (2 of these were selected), and Te for an empty space within the cavity. Ambient temperature was labeled Ta.

Temperatures in TV-30 were measured once an hour from 3 Dec. 2002 to 10 Jan. 2004. Due to some trouble, the data logger failed to sample data at 4 points in the nest and the empty space during 2 periods from 11 Aug. to 16 Oct. and 16-30 Nov. 2003. In total, 38,150 records were obtained. In this nest, the sensor for P1 was moved to another point, B3, on 29 Mar. 2003. In TV-31 however, the pretest for checking the locations of the brood
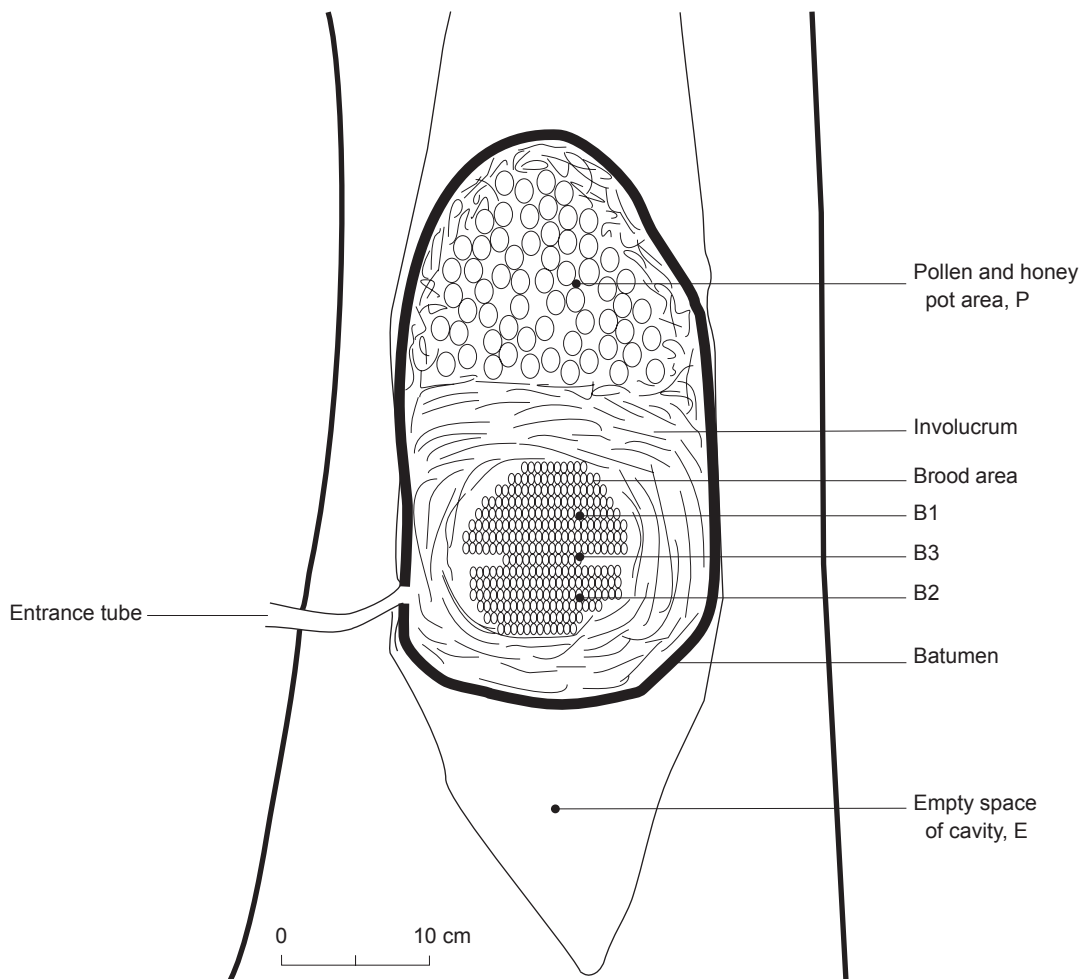
Fig. 1. Schematic drawing of a typical nest of *Trigona ventralis hoozana* (modified from Sakagami and Yamane 1984), with possible positions of the inserted thermosensors.

combs was not so easy, and finally 2 possible points near the combs were selected (Tb1 and Tb2). In TV-31, 49, 200 records covering the period from 9 Feb. 2003 to 25 Mar. 2004 were obtained. In these nests, data stored in the data loggers were transferred to a notebook computer, as a rule, every 2 mo. In TV-33, temperature data were sampled every 10 min from 16:00 on 26 Mar. to 17:00 on 29 Mar. 2004, and 439 data points were obtained. These numerical data were processed by the software BoxCar Pro 4.3 (Onset Computer Co.).

Finally, temperature fluctuations at each point in the nest and outside the nest were calculated by the following formula used by Hozumi et al. (2005):

$$\sum \frac{|X_{i+1} - X_i|}{(N\text{-}1)};$$

where i is the ith record in the trial, and N is the number of records, i.e., 742 records in Jan. and July 2003 for each of TV-30 and TV-31, and 425 in Mar. 2004 for TV-33.

No statistical test, e.g., ANOVA, was applicable to the temperature data measured at different points in each nest, in the tree cavity, and outside, because these sequential data were not mutually independent.

RESULTS

Temperature changes outside the nests

Changes in the weekly mean ambient temperature (Ta) for nests TV-30 and TV-31 over the measured period are shown in figures 2A and B. The average of monthly mean of Ta was 21.3°C for TV-30 (from Jan. to Dec. 2003) and 20.3°C in TV-31 (from Mar. to Feb. 2003). The highest and lowest monthly means of Ta were 25.5 (July 2003) and 15.5°C (Jan. 2003), respectively, for TV-30, while they were 23.1 (Aug. 2003) and 16.7°C (Jan. 2004) for TV-31. When hourly changes of temperatures were examined (partially shown in Figs. 3A, D, 4A), the highest and lowest Ta values for TV-30 were 33.6 (7 May 2003) and 8.6°C (29 Jan. 2003), respectively, and the difference between the extreme temperatures was 25.0°C. Corresponding temperatures for TV-31 were 30.7 (17 Sept. 2003), 7.8 (25 Jan. 2004) and 22.9°C. The daily highest and lowest values of Ta for TV-30 were 25.6 and 8.6°C in Jan. 2003 and 31.9 and 20.2°C in July 2003. Those for TV-31 were 27.5 and 7.8°C in Jan. 2004 and 28.7 and 20.2°C in July 2003. The daily mean differences between the highest and lowest Ta values for TV-30 were 5.3°C in Jan. and 7.2°C in July 2003, while those for TV-31 were 8.9°C in Jan. 2004 and 2.2°C in July 2003.

In both nests, the temperature in the empty space of the cavity (Te) behaved as Ta did (Figs. 2A, B), but weekly mean Te values were slightly higher than those of Ta (21.7 vs. 20.9°C for TV-30 from Dec. to July 2003, and 20.7 vs. 20.4°C for TV-31 from Mar. 2003 to Feb. 2004). When plotted hourly for each month, Te showed daily cyclic changes as Ta did, but with a delay of 4-10 h for TV-30 and 5-11 h for TV-31 (Figs. 3A, B, 4A, B). The range of Te in Jan. was 12.6-20.6°C and in July was 22.1-28.7°C for TV-30 (Figs. 3A, B), and 10.2-19.8 and 23.6-27.1°C for TV-31 (Figs. 4A, B), respectively. The difference between the highest and lowest values of Te was smaller than that of Ta (8.0 vs. 16.9°C (in Jan.) and 6.6 vs. 11.7°C (in July) for TV-30, and 9.6 vs. 19.7°C (in Jan.) and 3.5 vs. 8.1°C (in Aug.) for TV-31) (Figs. 3A, B, 4A, B). The daily mean differences between Te and Ta were +0.9 (in Jan.) and +0.6°C (in July) for TV-30 and +0.4 and +1.6°C for TV-31. A 5 d scale for Feb. and May 2003 showed that the curve of Ta was asynchronous with that of Te, with a delay of 4-9 h (Figs. 3C, D). In a short-term measurement at TV-33 (plotted every 10 min) on 26-29 Mar. 2004, Ta fluctuated between 16.0 and 24.0°C, but Te remained at a constant level of 21-22°C (Fig. 4C).
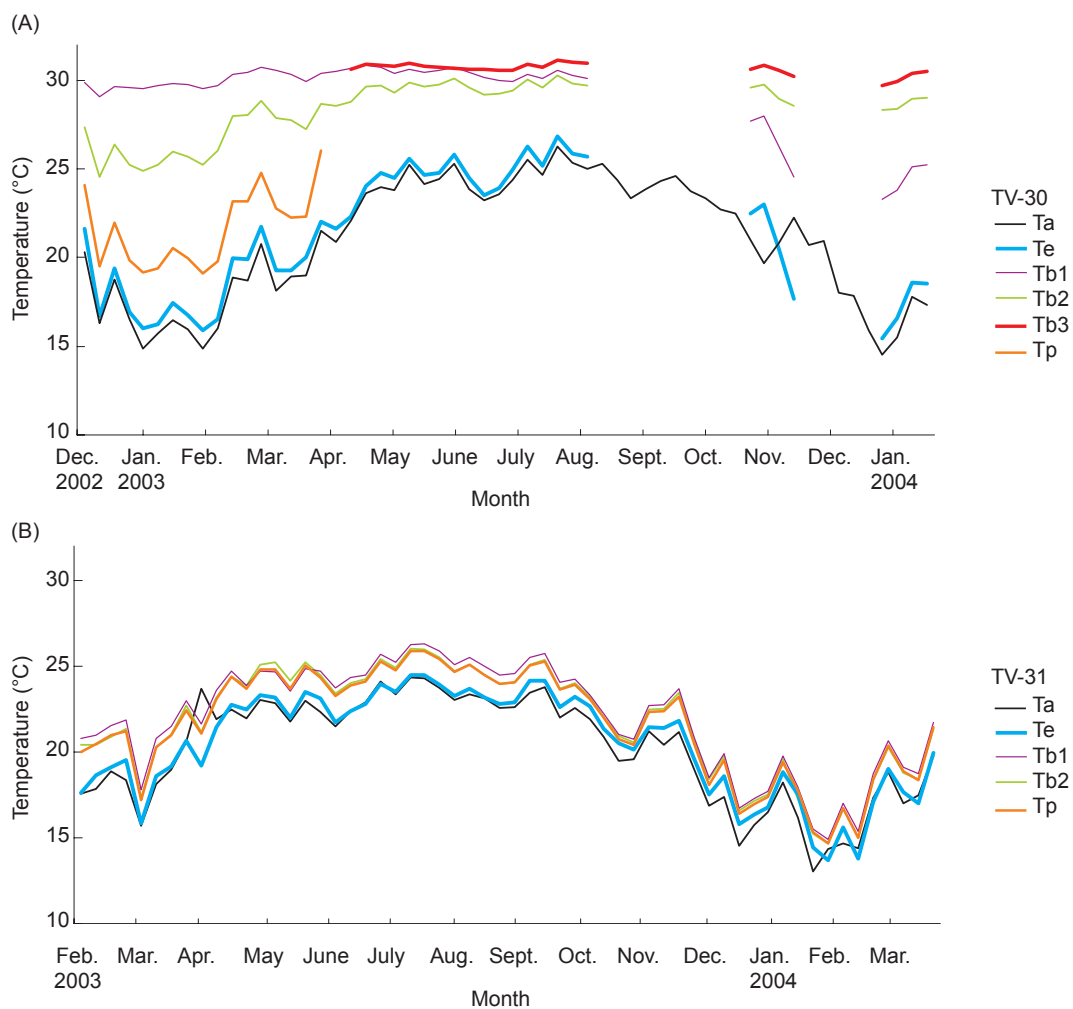
Temperature changes inside the nests

The weekly mean temperature in the storage pot area (Tp) showed changing patterns similar to those for Te and Ta (Figs. 2A, B). At TV-30, Tp was always higher than Te (mean, +2.3-3.5°C) and Ta (mean, +3.2-4.7°C) from Dec. 2002 to Mar. 2003. The difference between the highest and lowest values (24.8 and 19.1°C) of Tp was 5.7°C, nearly comparable to that of Te (6.1°C). On the 5 d scale, Tp showed a pattern synchronous to but higher than that of Te (Fig. 3C). At TV-31, the changing pattern of Tp showed a tendency similar to that for TV-30 (Figs. 4A, B).

Temperatures in the brood area (Tb1-Tb3) in TV-30 were fairly stable, always remaining within a range of 24.0-31.0°C, but the changing patterns differed among the 3 points. Tb1 remained stable at 29-31°C until the end of June 2003, but thereafter, it gradually dropped and reached an average of 23.7°C in Dec. Tb2

remained around 25°C until Feb. 2003, then it gradually increased to 28-30°C from late Apr. to the end of the measurement period (Jan. 2004). Tb3, measured from early Apr., remained around 31.0°C (Fig. 2A). When changes in temperature were plotted hourly, it was shown that Tb1-Tb3 followed Te, but were always higher than Te with smaller amplitudes (Figs. 3A-D). The maximum difference between Tb1 and Ta was 20.9°C on 29 Jan. 2003. The maximum difference between Tb3 and Ta was 20.5°C on the mornings on 16, 29, and 30 Dec. 2003. A short-term measurement in Mar. at TV-33 showed a marked constancy of Tb1-Tb3 which remained in a narrow range of 29-32°C as seen at TV-30. The maximum difference between Tb1 and Ta reached 15.1°C during 01:00-02:00 on 27 Mar. In contrast, changes in Tb values in TV-31

followed the daily and seasonal changes of Te, although at a level slightly higher than Te (Figs. 3B, 4A, B). Since the ambient temperature dropped below 10°C for a considerably prolonged period in Jan., Tp and Tb values also dropped to 11.0°C during these periods at this nest (Fig. 4A).

A few cases showed that the nest temperature was voluntarily controlled from the brood area. In TV-30, when Ta dropped below 15°C and the daily temperature difference was small during 8-9 Mar. 2003, Tb2 and Tp rose rather more than did Te and Ta. Those temperature changes from point a1 to a2 were +0.4°C for Ta, ± 0°C for Te, +0.8°C for Tp, +0.8°C for Tb1, and +1.9°C for Tb2 (Fig. 5A). In the case of TV-31, however, the nest temperature being controlled from the brood area was inconspicuous except for

Fig. 2. Seasonal changes in temperatures in the nest, an empty cavity, and outside the nest from Dec. 2002 to Mar. 2004. (A) Nest TV-30; (B) nest TV-31. Averages of weekly mean temperatures are plotted for each position. Tb1, temperature in brood area 1; Tb2, temperature in brood area 2; Tb3, temperature in brood area 3; Tp, temperature in the storage pot area; Te, temperature in an empty place in the cavity; Ta, ambient temperature.

Tb1. Tb1 rose rapidly following Ta in the daytime, but then dropped following Te and Ta on 10 and 11 Feb. 2003. Changes from point b1 to b2 were +7.6°C for Ta, -0.4°C for Te, +0°C for Tp, +1.5°C for Tb1, and +0.4°C for Tb2, and those from b2 to b3 were -7.6°C for Ta, +1.5°C for Te, +0.4°C for Tp, -1.1°C for Tb1, and -0.4°C for Tb2 (Fig. 5B). On 27 and 28 July 2003, those from c1 to c2 were
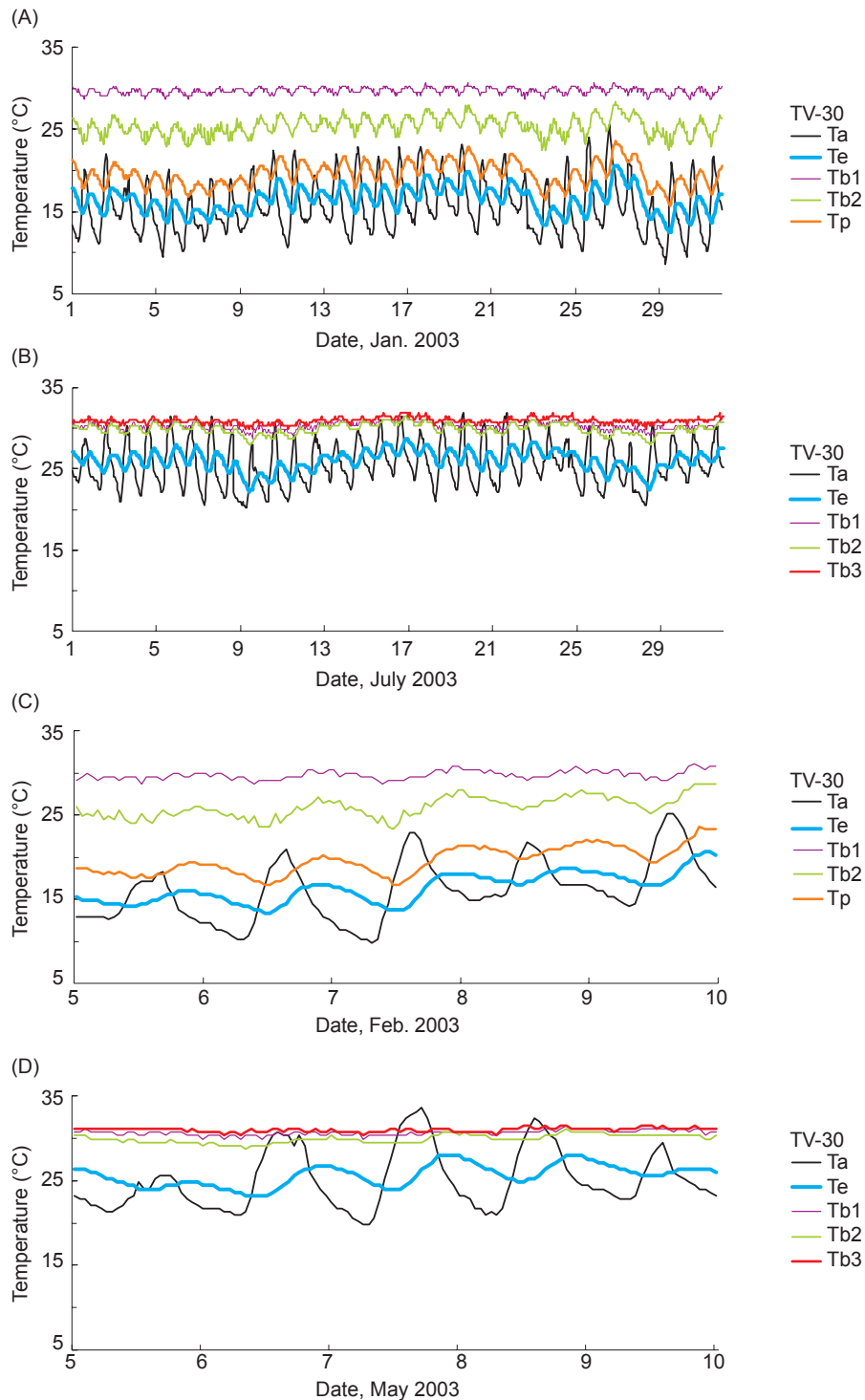
Fig. 3. Changes in temperatures of TV-30 in the nest, an empty cavity, and outside the nest plotted for short periods in 2003. (A) Jan.; (B) July; (C) 5 d in Feb.; (D) 5 d in May. Tb1, temperature in brood area 1; Tb2, temperature in brood area 2; Tb3, temperature in brood area 3; Tp, temperature in the storage pot area; Te, temperature in an empty place in the cavity; Ta, ambient temperature.

+4.6°C for Ta, ± 0°C for Te, +0°C for Tp, +1.2°C for Tb1, and +0°C for Tb2, and those from c2 to c3 were -6.9°C for Ta, -1.2°C for Te, -1.6°C for Tp, -2.3°C for Tb1, and -1.6°C for Tb2 (Fig. 5C).

Temperature fluctuations at each point measured

For TV-30 and TV-31, the value for the monthly fluctuation of Ta was over 0.51 and was greatest among all points measured (Figs. 6A-E). Fluctuations at other points, except Tb2 of TV-30

in Jan. (Fig. 6A), were fairly constant and ranged 0.05-0.24. The value of the fluctuation in Tb2 of TV-30 largely differed between Jan. and July (0.45 vs. 0.11). In a short-term measurement at TV-33, the temperature fluctuation was small at all points measured. The fluctuation of Te was about 0.01, rather smaller than those of Tb (Fig. 6F).

DISCUSSION

First, the ability to thermoregulate the nest
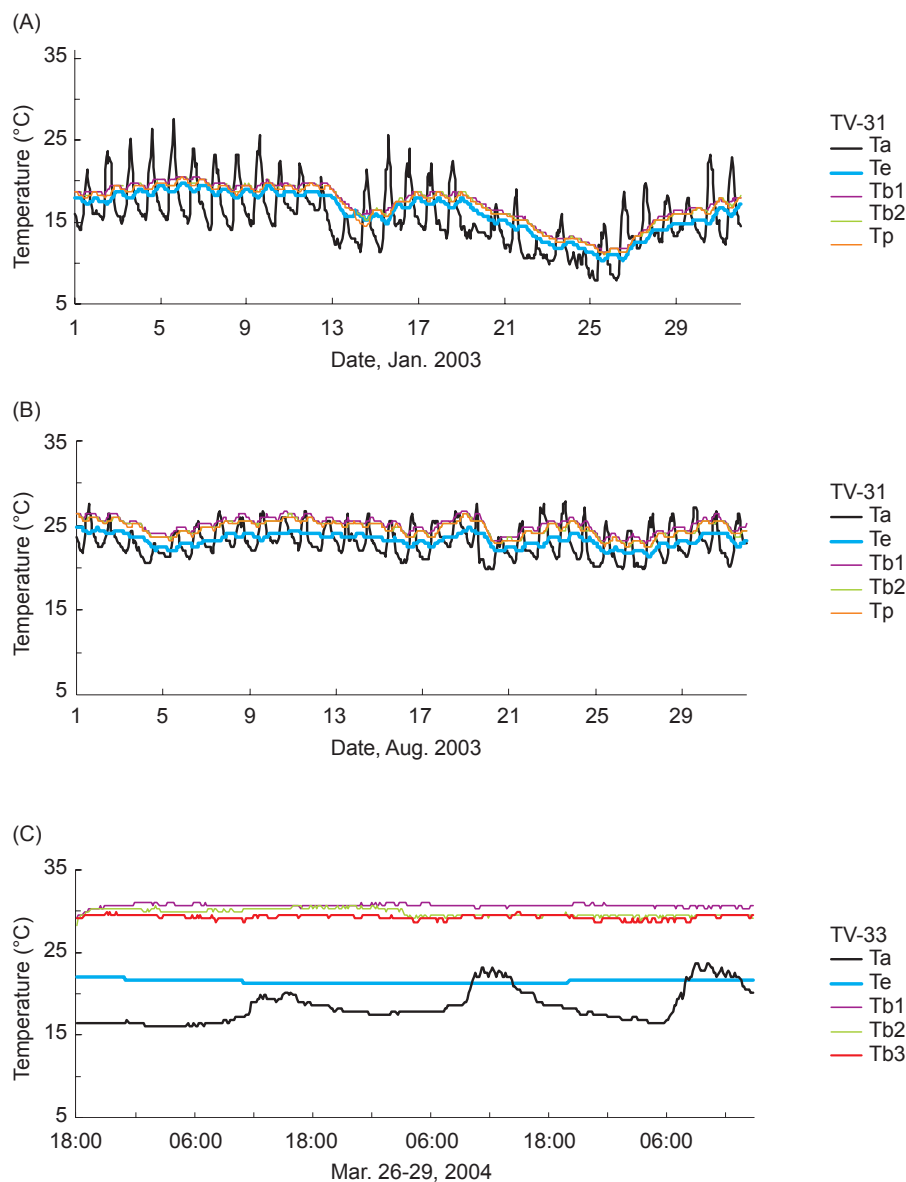
Fig. 4. Changes in temperatures in the nest, an empty cavity, and outside the nest for short periods for TV-31 (A, 2004 and B, 2003) and TV-33 (C, 2004). (A) Jan.; (B) Aug.; (C) 26-29 Mar. 2004. Tb1, temperature in brood area 1; Tb2, temperature in brood area 2; Tb3, temperature in brood area 3; Tp, temperature in the storage pot area; Te, temperature in an empty place in the cavity; Ta, ambient temperature.

of some comb-forming stingless bee species is compared, among which, *Tri. spinipes* seems to maintain a higher nest temperature than do others (Sakagami 1982). It builds huge nest in a tree of which the surface of the nest is exposed to sunlight in the daytime. The nest temperature was maintained at 34-36°C even when the atmospheric temperature varied between 16 and 28°C (Sakagami 1982). In *Scaptotrigona postica*, the nest temperature is ameliorated by a multilayer involucrum that has a high insulating effect (Engels et al. 1995). *Trigona carbonaria* Smith maintained its nest temperature at 24-29°C when the ambient temperature varied between 10 and 23°C (Amano et al. 2000). In the case of *Tetragonisca angustula angustula* Latreille and *Tet. a. fiebrigi* Schwarz, a constant nest temperatures of as high as 28-32°C was thought to be produced by respiratory activities of adults (Proni and Hebling 1996). According to Roubik and Peralta (1983), the temperature in the brood area of *Melipona rufiventris* and *M. seminigra* nests is maintained at 31-32°C, probably by heat generated by the mass of larvae. *Melipona beecheii*, *M. fuliginosa* Lepeletier (=*flavipennis*), and *Partamona cupira* (Smith) maintain nest temperatures at 23-30°C,
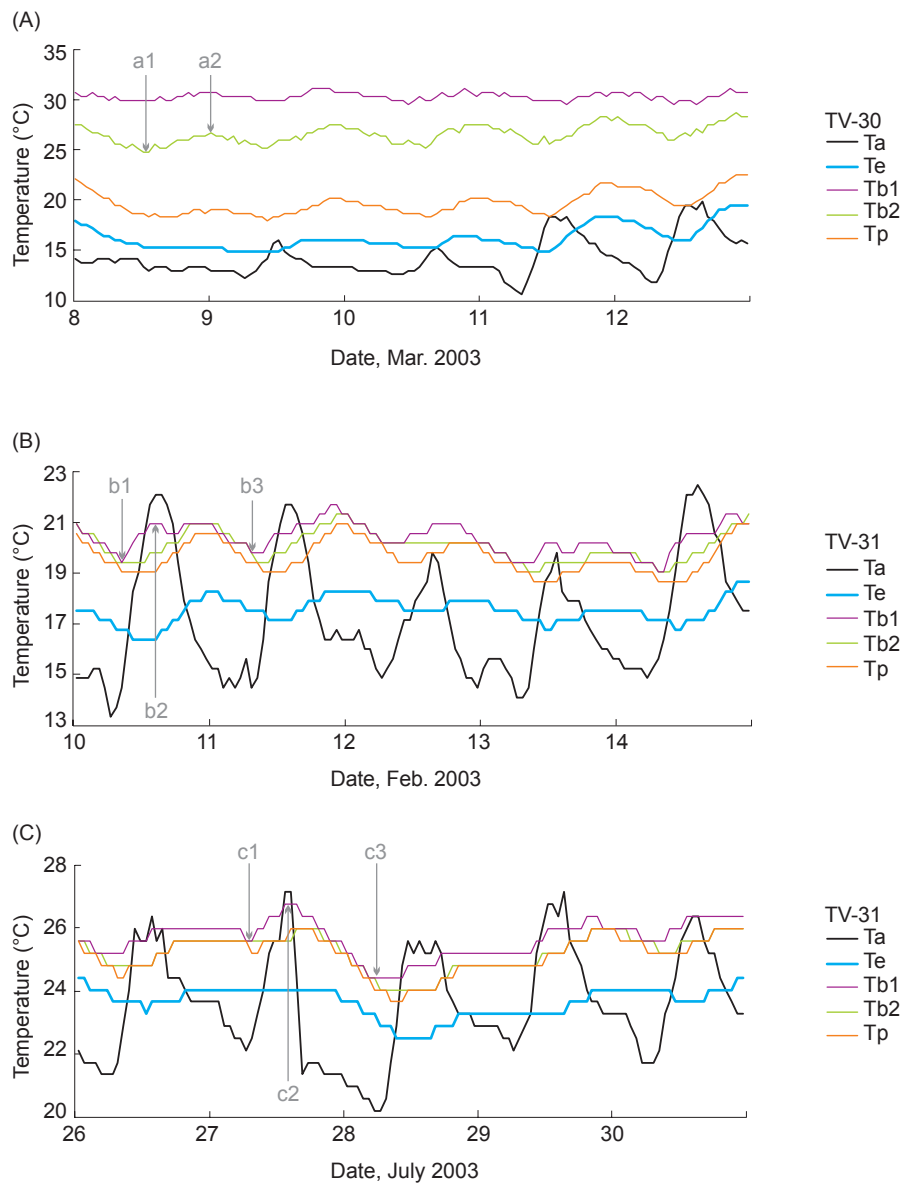

Fig. 5. Changes in temperatures in the nest, an empty cavity, and outside the nest for short periods measured for TV-31 (A and B) and TV-30 (C). Tb1, temperature in brood area 1; Tb2, temperature in brood area 2; Tp, temperature in the storage pot area; Te, temperature in an empty place in the cavity; Ta, ambient temperature. Arrows indicate the period for further calculation (see "Results").

with larger fluctuations than in *M. rufiventris* and *M. seminigra* (Wille and Orozco 1975, Wille 1976, Moo-Valee et al. 2000). These facts suggest that at least in some species of the comb-forming group, some positive mechanisms are operating to maintain preferable temperatures in the brood
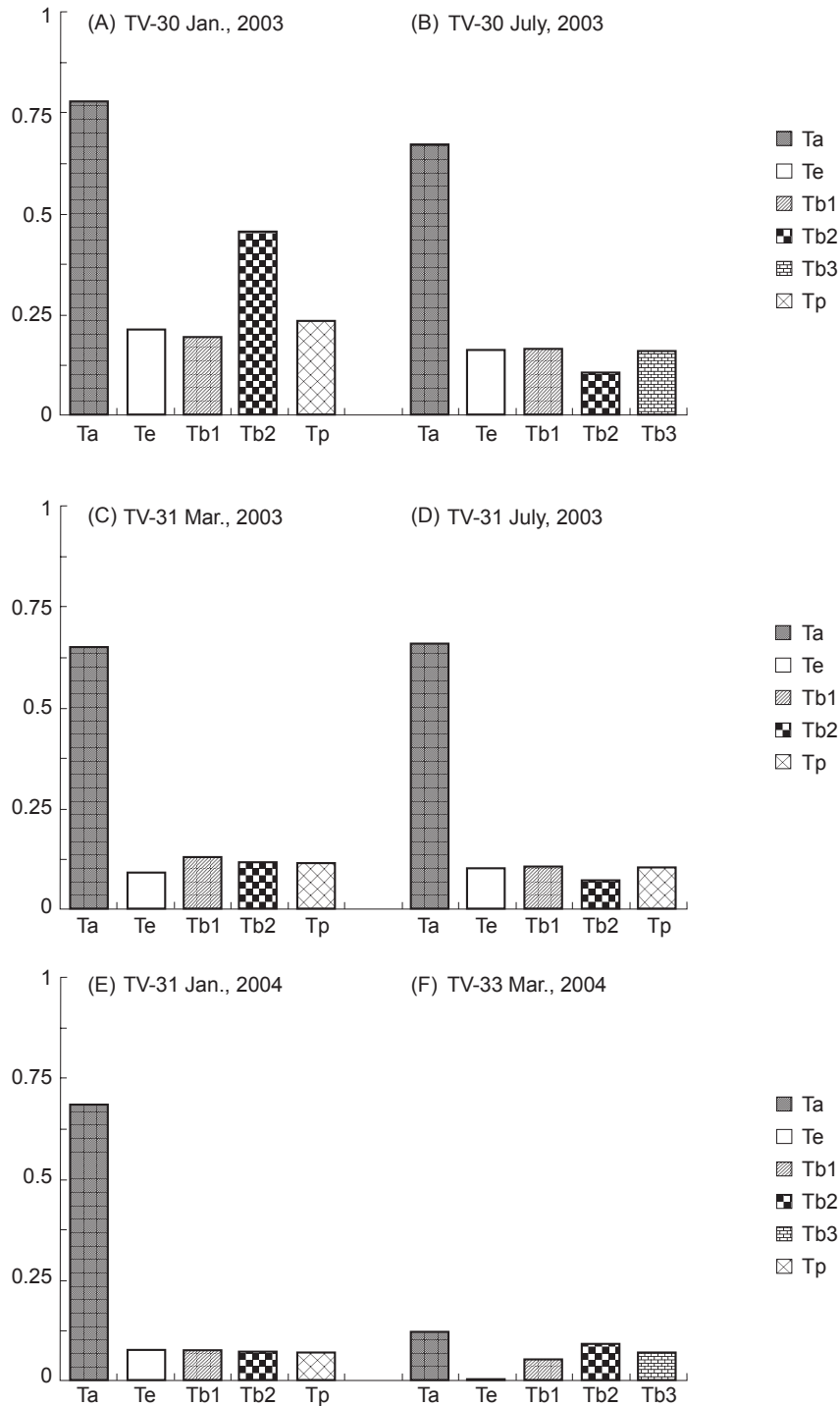
Fig. 6. Temperature fluctuations at each point of nests TV-30, TV-31, and TV-33, in an empty cavity, and outside. (A, B) TV-30 (A, Jan.; B, July 2003); (C-E) TV-31 (C, Mar.; D, July 2003; E, Jan. 2004); (F) TV-33 (Mar. 2004). For calculations, see "Results". Tb1, temperature in brood area 1; Tb2, temperature in brood area 2; Tb3, temperature in brood area 3; Tp, temperature in the storage pot area; Te, temperature in an empty place in the cavity; Ta, ambient temperature.

area. Species of the cluster type, such as *Tri. laeviceps*, lack virtually any thermoregulatory ability (Sakagami et al. 1983).

We consider here how thermal conditions were ameliorated in *Tri. ventralis hoozana* colonies. The following factors seemed to affect the thermal conditions in the nest: (1) microclimatic conditions surrounding the nest site and the nest body, (2) the structure of the nest (e.g., its basic architecture, and the presence of a batumen and involucrum), and (3) metabolic heat generated by immature and adult individuals.

Environment of the nest site

Many stingless bees of the genus *Trigona*, such as *Tri. ventralis hoozana*, *Tri. silvestriana* Vachal, and *Tri. fulviventris fulviventris* Guérin tend to choose closed cavities in large trees (Hubbell and Johnson 1977, Sakagami and Yamane 1984). Johnson and Hubbell (1984) reported that 22 nests belonging to 9 species in Panama were built in hollows of trees with diameters exceeding 95 cm at breast height. Usually, hollows occupied by stingless bee colonies have only 1 or a few small openings, which prevent convection of internal air and interchanges of air between the inside and outside. In the present study, temperature changes of Te followed those of Ta, which rose and fell with a considerable time lag. This phenomenon is due to an effect called the "thermostatic of the tree" (Reynolds 1939). Reynolds mentioned that this phenomenon is affected by various factors, such as the thermal conductivity of the wood, the rate of water absorption/evaporation by the tree, the extent of exposure to the sun, and daily differences in atmospheric temperatures. We consider that Te was stabilized by the thermostatic effect of the wood, and this in turn reduced fluctuations in Tp and Tb values. In the same context for Australian termites *Coptotermes acinaciformis* (Froggatt) and *C. frenchi* Hill, which build nests in living trees, the insulating effect of the wood reduces extreme temperature changes in the nest (Greaves 1964).

Structure of the nest

In most comb-forming species, such as *Tri. ventralis hoozana*, the nest consists of a batumen, an involucrum, brood combs, and storage pots (Fig. 1) (Sakagami 1982, Sakagami and Yamane 1984). The batumen's major function seems to be to seal the cracks of the nesting cavity and waterproofing as seen in an African subterranean species

Plebeina denoiti (Vachal) (Fletcher and Crewe 1981). The involucrum consists of a single or a few layers of thin sheets. It is known to prevent the brood area from being invaded by parasitic insects, such as phorid flies (Sakagami 1982). It also has an insulating effect in some species, e.g., *Ple. denoiti* and *Sca. postica* (Fletcher and Crewe 1981, Engels et al. 1995). It traps metabolic heat generated by immatures in nests of *M. rufiventris* and *M. seminigra* (Roubik and Peralta 1983). In nests of *Polybia paulista* (Ihering) and *Pol. occidentalis* (Olivier) (subfamily Polistinae of the family Vespidae), temperature fluctuations in the nest were smaller than at the surface of its envelope and the outside, showing that even a sheet of envelope which surrounds the combs has a notable insulating effect (Hozumi et al. 2005). In the present study, Tb values showed a tendency to be higher than Tp, indicating that the involucrum had an insulating effect on the brood area in this species.

Generation of metabolic heat

Adult honeybees and vespine wasps can generate large quantities of heat, at least in honeybees, by vibrating their flight muscles (Heinrich 1996). It has been proven that thermogenesis in broodless honeybee clusters is mainly due to endothermic heat produced by bees in the core of the cluster (Stabentheiner et al. 2003). In stingless bees, adults of *M. panamica* Cockerell can maintain their body temperature at a level higher than those outside and inside the nest, by using the thorax as the primary heat source (Nieh and Sánchez 2005). Metabolic heat produced by adults has been positively discussed in other species of stingless bees, such as *Ple. denoiti*, *Sca. postica* and *Tet. angustula* (Fletcher and Crewe 1981, Engels et al. 1995, Proni and Hebling 1996). In *Tet. a. angustula* and *Tet. a. fiebrigi*, the respiration rates of adults increased in proportion with the rise of temperature in the nest (Proni and Hebling 1996). These facts suggest that it is possible for adult stingless bees to generate a quantity of metabolic heat. On the other hand, the occurrence of a mass of larvae seems to stabilize the temperature, as well as to raise the temperature by generating heat in the brood area, because pupae and aged larvae contain much water which has a certain heat capacity. This is consistent with the fact that larvae of a lepidopteran, *Eriogaster lanestris* (Linnaeus) (family Lasiocampidae), can store

thermal energy for a considerable period when forming an aggregation (Ruf and Fiedler 2000). This suggests that if the adult bees act as the main heat generator, the mass of larvae may play a role in keeping the temperature at a constant level. According to Sakagami and Yamane (1984), a mature nest of *Tri. ventralis hoozana* has 2 comb groups, with a total of 20 combs (the number of combs in each group changes with time). In this context, the different changing patterns of temperature seen at different points measured in the brood area may be explained by the developmental stage of immatures occurring at each point (for details of the cell construction cycle, see Sakagami 1982, Sakagami and Yamane 1987). Temperatures may be higher when cells contain grown larvae or pupae, but lower when cells have been vacated or have only eggs or small larvae. This view was supported by Roubik and Peralta (1983).

In the case of TV-31, Tb values basically followed changes in Te, and even dropped to 15°C in Jan. Possible reasons for this are that (1) the thermosensors were positioned at the comb margins, or (2) the condition of the wrap brood area in the involucrum was not good for some reason, and/or the number of adult and immature individuals was not large enough to generate sufficient metabolic heat. We cannot specify which reason is valid. Case studies showed that Tb1 rapidly increased with the rise in the ambient temperature. This phenomenon was studied in *Sca. postica* by Engels et al. (1995); they reported that workers exhibited foraging and fanning activities in the daytime, and through fanning activities, the ventilation of the nest temperature rapidly increased according to the ambient temperature. It was also found that active ventilation of the air controlled the nest temperature in 2 African stingless bees, *Ple. denoiti* and *Hypotrigona gribodoi* Magretti (Moritz and Crewe 1988).

The above considerations suggest that the relative independence of the temperature in the brood area of a *Tri. ventralis hoozana* nest is retained by a composite effect of the following factors. Extreme diel changes in atmospheric temperature are diminished in the cavity by the thermostatic effect of thick wood enclosing the cavity. Inside the nest, the involucrum seems to retain the heat generated in the brood area. From the pattern of temperature distribution in the brood area, the major heat source and the thermoregulator seem to be adults, with a partial contribution by larvae and pupae. The spherical form of the brood combs may decrease the loss of heat generated by the inhabitants. We consider that colonies of *Tri. ventralis hoozana* cannot maintain the nest temperature at a constant level throughout the seasons unless they live in the hollow of a large tree. This possibly explains why nests of this species have never been found in rock cavities or bamboo cylinders.

Trigona ventralis hoozana is mostly distributed at elevations ranging 250-1500 m on the island of Taiwan (Sonan 1927, Sakagami and Yamane 1984, Sung et al. 2006). At the site of colony TV-31, the minimum daily ambient temperature ranged between 8 and 15°C in winter. In Jan. 2003, temperatures of < 16°C continued for 117 h. Such rigorous thermal conditions have never been reported in other species of stingless bees, most of which are distributed in warm tropical areas. The highest elevation at which bees' foraging activities were observed was 2500 m (Sung et al. 2006). This elevation must be the practical distribution limit of their colonies. To extend the distribution area to high mountains in the subtropics, the Taiwanese stingless bee must have some measures to tolerate rigorous climatic conditions during winter, when atmospheric temperatures sometimes drop to 5°C. In such conditions, their colonies can survive only by nesting in tree hollows, which protect them against extremely low temperatures. As in TV-30, preferable thermal conditions can be maintained in the nest even in the cold season, as shown by the temperature of core combs remaining about 20°C higher than the ambient temperature in Jan. and Dec. 2003. However, we do not know how this species endures the winter at the highest point of its distribution. Although stingless bees are basically tropical insects, no records are known from the lowlands of Taiwan. This may be due to the lack of big trees with hollows suitable for nesting, because most of the forests have long been cleared from the lowlands to develop farmland and urban areas (Sung et al. 2006).

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