SYSTEMATICS, MORPHOLOGY AND PHYSIOLOGY

Promotion of Thermoregulatory Insulation in Nests of Neotropical Wasps by Building Extra-Combs with Empty Cells

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Promoção de Isolamento Térmico em Ninhos de Vespas Neotropicais pela Construção de Favos com Células Vazias

RESUMO - Examinou-se a hipótese de que os favos vazios dos ninhos de *Polybia occidentalis* Olivier (Hymenoptera: Vespidae) atuam como isolamento térmico dos elementos internos da colônia. Para avaliar essa hipótese dois tipos de medidas de temperatura foram tomadas: 1) com o favo externo intacto (Controle) e 2) removido (Tratamento), usando um ninho grande e um ninho menor. As temperaturas diárias no ninho grande (parte externa T_{n1}; parte interna T_{n2}), no Controle, foram 0,6°C (T_{n1}) e 1,2°C (T_{n2}) mais baixas que aquelas do Tratamento, devido à temperatura ambiente (T_a) mais alta durante todo o período avaliado. Entretanto, a temperatura excedente ($T_n - T_a$) no Controle foi mais alta que no Tratamento. O valor foi 0,7°C mais alto em T_{n1} e 0,1°C em T_{n2}. No ninho menor, a temperatura excedente na parte externa foi semelhante entre os experimentos, e na parte interna a temperatura do Controle foi inferior à do Tratamento. A flutuação térmica nos ninhos foi menor no Controle que no Tratamento, tanto na parte externa quanto interna dos favos. Conclui-se que o favo sem uso é ecologicamente muito importante para criar ou proteger a cria das alterações extremas de temperatura ambiente no inverno, uma vez que ele auxilia na manutenção de temperatura alta no ninho e também no decréscimo da flutuação de temperatura ao redor dos favos de cria. Além disso, essas temperaturas mais altas influenciam as atividades dos adultos.

PALAVRAS-CHAVE: Polistinae, *Polybia occidentalis*, termoregulação, inverno

ABSTRACT - We examined the hypotheses that the empty combs of *Polybia occidentalis* Olivier (Hymenoptera: Vespidae) nest insulate the inside of the nest. To examine this hypotheses, two kinds of temperature measurements were carried out: 1) with the outer comb of the nest intact (Control) and 2) removed (Treatment), using a large and a small nest. In the large nest, the daily nest temperatures (outer part, T_{n1}; inner part, T_{n2}) in Control were lower by 0.6°C (T_{n1}) and 1.2°C (T_{n2}) than those in Treatment, because of a higher ambient temperature (T_a) throughout temperature assessment in Treatment. However, the excess temperature ($T_n - T_a$) in Control was higher than that in Treatment. The value was higher by 0.7°C at T_{n1} and 0.1°C at T_{n2}. In the small nest, the excess temperature in outer part was similar between experiments, while that in inner part of Control was lower than that of Treatment. The temperature fluctuation in the nests was lower in the Control than that in Treatment both the outer and inner part of the comb. We conclude that the unused comb is ecologically invaluable for raising and protecting the brood from extreme changes in ambient temperature during the winter period, because it helps not only keeping a higher nest temperature but also decreasing the temperature fluctuation around the brood combs. In addition, such a high temperature may influence the performance of adult wasps.

KEY WORDS: Polistinae, *Polybia occidentalis*, nest architecture, thermoregulation, winter in neotropics

Nests of social insects serve as incubators for raising the broods by reducing the effects of external temperature fluctuations in the environment (Heinrich 1993). Many studies on nest thermoregulation have been conducted in temperate and cold regions. It is well known that honeybee colonies maintain moderate temperature inside their nests by both heating with metabolically-generated heat and cooling by ventilation and sprinkling water (Seeley & Heinrich 1981).

In the case of social wasps, thermal conditions are also improved in various ways, such as choice of nest sites (Morimoto 1953, Jeanne & Morgan 1992), heating with metabolic heat of adult wasps (Himmer 1927, Ishay *et al*. 1967, Gibo *et al*. 1974a, b, 1977), and cooling by fanning and sprinkling with extraneous water (Steiner 1929, Ishay *et al.* 1967, Yamane 1971). In addition to these behavioral thermoregulations, a stable temperature is achieved by nest insulation. In the nests of many vespine wasps, the combs are enclosed by envelopes, and the nest temperatures are kept at a certain level by the insulation effect of envelopes (Himmer 1927, Spradbery 1973, Kojima 1991). Furthermore, a paper wasp, *Polistes riparius* Yamane & Yamane (Hymenoptera: Vespidae), inhabiting in cold climate improves the thermal condition of their nests by building empty cells around the brood cells and extending the depth of brood cells (Hozumi & Yamane 2001). Such a nest homeothermy is also effective in terms of the colony defense. When the nest is attacked by predators, a high temperature condition enables the colony to intercept immediately (Heinrich 1981, 1984).

In tropics and subtropics, the adaptation to achieve a stable nest temperature is also seen in the nests of social bees and wasps. Some authors investigated the thermoregulation ability of colonies, such as heat generation and nest cooling when the nest is over heated (Martin 1992, Engels *et al*. 1995), while few studies have dealt with the thermoregulatory nest architecture.

Polybia occidentalis Olivier (Hymenoptera: Vespidae) is a swarm-founding wasp commonly seen in the Neotropical ecozone. The wasps build characteristic nests in modules, with each module consisting of a comb of cells plus the envelope covering the comb. Each envelope serves as the substrate for the cells of a next comb. The nest architecture is called phragmocyttarous (Richards & Richards 1951, Jeanne 1975). Recently, it was reported that *P. occidentalis* (Jeanne & Bouwma 2004) builds empty combs at the outer part of the nest and the wasps rear the brood at the inner part. In the tropics and subtropics, two thermal problems may occur in the nests with the seasonal changes. One is nest over heating in summer, and the other is low nest temperature in winter, both of which are related with normal development of brood. Hozumi *et al*. (2005) investigated the thermal conditions of the nests of *P. occidentalis* in summer, showing that they were well insulated with a phragmocyttarous architecture with little temperature fluctuation in nests where the brood was raised. On the other hand, no studies on thermoregulation in the *Polybia* nests have been carried out during the winter.

We examined whether the extra-combs seen in the nest of *P. occidentalis* insulate the inside of the nest and keep the nest temperature higher during winter. We measured the nest temperatures with the extra-combs intact (Control) and removed (Treatment). If extra-combs insulate the nest, the internal temperature in the Control should be higher and more stable than that of the Treatment. In addition, to know the relationship between temperature and wasp activity, we also assessed the number of flights the wasps took. Our results indicated that the outer extra-combs had an insulation effect, since the removal of the extra-combs caused a decrease of the temperature in the remaining combs, also resulting in a higher variability between the minimum and maximum temperature. The flight number of wasps was closely related to the temperature around the nest surface, suggesting that higher nest temperatures may promote adult wasp activities.

Material and Methods

Temperature measurements were carried out during winter (from July 12 to 24, 2005) in subtropical climates, when a large fluctuation of ambient temperature occurs during the day (from 10°C to 30°C). In mid-July, *P. occidentalis* wasps continued their nesting activity in spite of the extreme climate. We used two nests for temperature measurements, a large and a small nest (Fig. 1). The two nests observed were found on the concrete wall of a building at the Ribeirão Preto Campus of the Universidade de São Paulo (21°11' S, 47°48' W), São Paulo State.

The large nest was 120 × 150 × 80 mm (L × W × H) and consisted of nine layers of combs and one constructing envelope. It was built at 2.5 m above the ground on a north-facing concrete wall, located just below the eaves and did not receive direct sunlight during daytime, although the wall received direct sunlight up to 1 m below the nest. The small nest was 60 × 60 × 55 mm (L × W × H) and consisted of seven layers of combs. It was built at 2.5 m above the ground on a south-facing concrete wall just below the eaves and did not receive direct sunlight during daytime. When the nests were collected after the whole measurements were taken, 1254 and 200 adult individuals were captured in the large and the small nests, respectively. Immature wasps were found in the 3rd to 7th comb in the large nest and 2nd to 5th in the small one.

Two kinds of temperature measurements were carried out to calculate the insulation effect of the extra-combs. Nest temperatures (T_n) were measured with copper-constantan thermocouples (ø = 0.32 mm), and the temperatures were read to the nearest 0.1°C on a data logger (Keyence, NR1000). The thermocouples were placed between the 7th and 8th comb (T_{n1}) counted from the wall and between the 3rd and 4th comb (T_{n2}) in the large nest, and between the 2nd and 3rd (T_{n3}) and between the 4th and 5th in the small nest (Fig. 1). In addition, a thermocouple was placed around the outermost nest entrance to gauge the surface temperature of the large nest (T_{s1}, T_{s2}) and the small one (T_{s3}, T_{s4}). First, the measurement was done with the nests whose envelope was intact (untreated condition, called Control). When the outer extra layers were removed after a 3-day interval, the temperature measurement was repeated (treated condition, called Treatment). No immature stages were present on the outer surface of the nest when the extra outer layer was removed (Fig. 1). Ambient temperature and surface temperature of the substratum wall were simultaneously measured near the nests. All the temperatures were measured every second for 10 minutes (600 records of temperature data), and the temperature was shown by an averaged value (n = 600).

The measurements of each experiment were repeated five times, and measurement of the Control and the Treatment was done from 12th July to 16th July and from 20th July to 24th July,

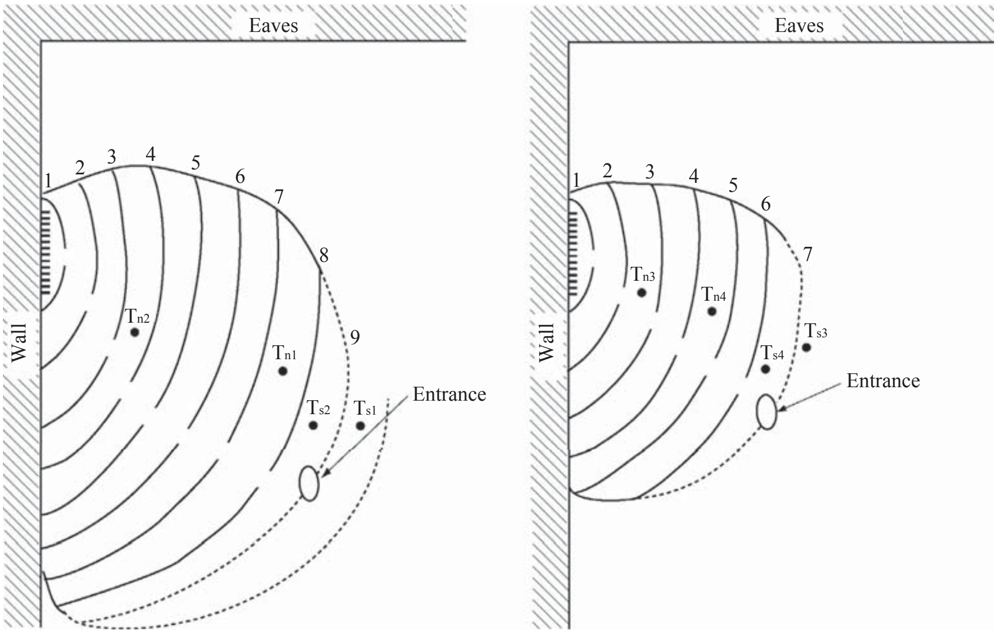

Fig. 1. Schemes of cross-sectioned nest of *P. occidentalis* used for the present study; a, Large nest; b, Small nest. The innermost comb-like bars mean the first sessile comb built on the wall of the building. The thickness of the envelope was less than 1 mm, and the depth of cells was about 6-10 mm. Numbers in the figure represent the location of the combs from the wall; T_{n1-4} and T_{s1-2} represent the positions of thermocouples.

respectively. All the measurements were carried out from hour 7 to 17, i.e., from just after sunrise to just before sunset; with the exception of the measurement on 12th July, when it was interrupted at hour 16. The wasps attempted to build the envelope during the course of the Treatment, but it was removed as often as possible after the daily measurement.

Temperature fluctuation at each point of the nest was calculated by the following formula:

$$\sum|x_{i+1} - x_i|/(N - 1),$$

where *i* indicates the *i*th record in this trial, and *N* means the number of records, i.e., 600 records each for the hourly measurement. The formula represents the rate of temperature change in a second (°C/s). To know the relation between nest temperature and flight activity of wasps, the number of wasps leaving the nest was counted at 10-min intervals every hour simultaneously with the temperature measurements.

In order to increase statistical power, data of temperatures and flight number of adult wasps were pooled over each experiment. Mann-Whitney U-test was used to establish significant differences between results obtained for the two experiments. Multiple regression analysis was used to test the effect of temperatures on the flight activity of wasps.

Results

Nest temperatures of Control and Treatment. All the temperatures showed similar changes during the experimental period in both nests (Fig. 2). The temperature gradually increased from hour 7 to 9, and then rose steeply and peaked at hour 14. The temperature then decreased until the end of the measurement period. The temperature at the outer part tended to be higher than that at the inner part in each nest. In the large one, T_{n1} in the Control was always higher than T_{n2}, while they reversed in the morning (from hour 7 to 9) in the Treatment (Fig. 2a,b). In the small nest, T_{n3} was always lower than T_{n4} in the morning (Fig. 2c,d). The changes of surface temperature were almost similar to those of outer part, although surface temperature was lower than the outer part in the morning and early in the evening. The temperature of the substratum wall was always lower than the ambient temperature except during early morning (Table 1). In both nests, the mean temperature in the Treatment was higher by approximately 1°C than that of the Control at each measuring point.

To standardize the nest temperatures taken under the different daily weather conditions, excess temperature (nest temperature minus ambient temperature, T_e) was calculated. In the nests with extra layers (Control), the excess temperature in the outer measuring points were kept higher than that of the nest that had the extra layers removed (Treatment). In the large nest, at the point of T_{n1}, excess temperature in the Control was consistently higher than those of the Treatment throughout the measurements (Fig. 3a). When excess temperature was compared at each measurement hour between the experiments, values of the Control were significantly higher than those of the Treatment from hours 7 to 10 and hour 17. On the other hand, the values of excess temperature at the point of T_{n2} were similar between the experiments (Fig. 3b). In the T_{n2}, the excess temperature in the Control was significantly higher than that of the Treatment at hour 7. In the small nest, at the point of

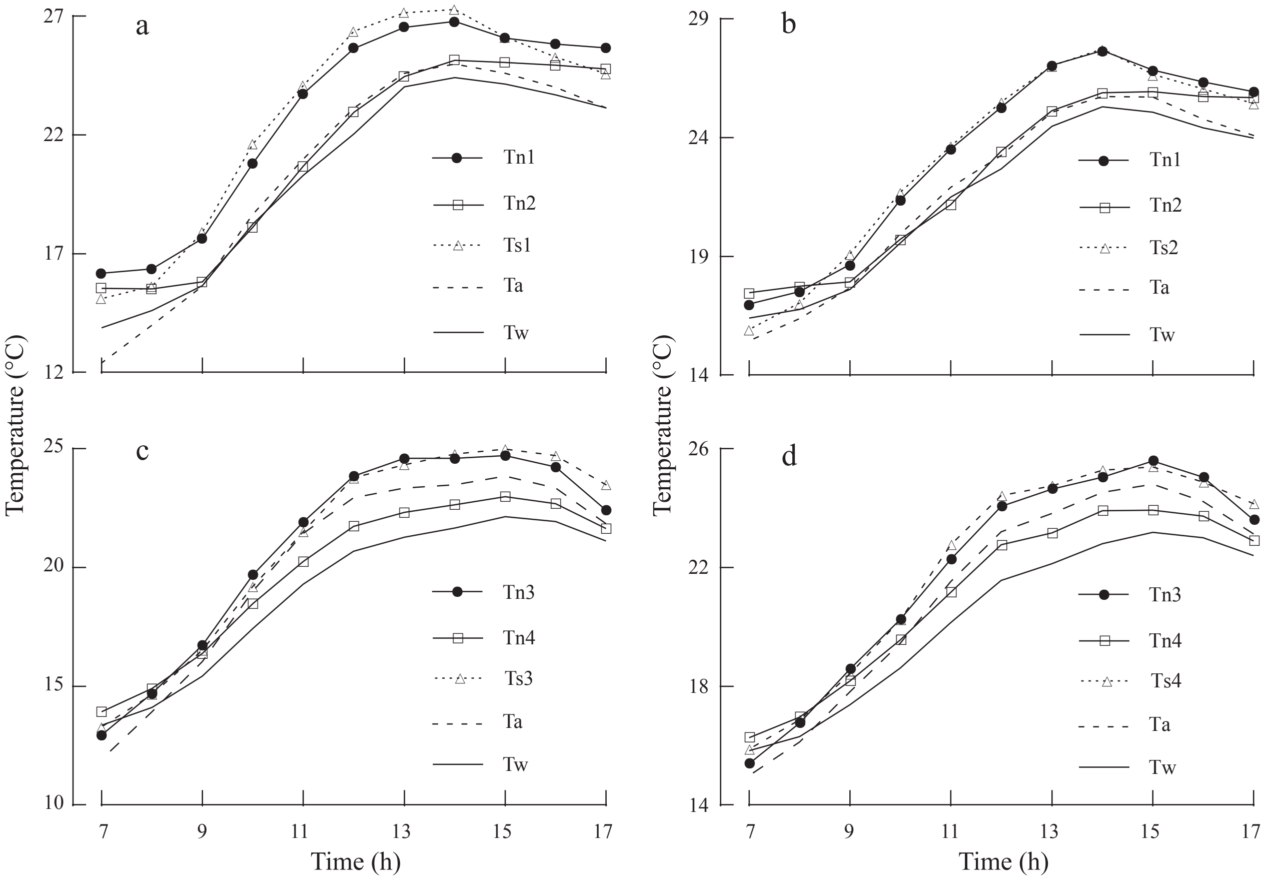

Fig. 2. Temporal changes of mean temperature in *P. occidentalis* nest, ambient, and wall temperatures; a, Control large nest; b, Treatment large nest; c, Control small nest; d, Treatment small nest. The temperatures are averaged (each measurement, n = 5) every measurement hour. In the Control, temperature was measured in the nest with an intact envelope, and in the Treatment, temperature was measured in the nest with removed envelope and combs.

Table 1. Mean (± SE) nest temperatures and environmental temperatures.

Large nest	T_{n1}	T_{n2}	T_s	T_a	T_w
Control	22.75 ± 0.60	21.60 ± 0.60	22.78 ± 0.62	20.50 ± 0.62	20.31 ± 0.55
Treatment	23.37 ± 0.58	22.76 ± 0.55	23.25 ± 0.60	21.81 ± 0.57	21.61 ± 0.54
Small nest	T_{n3}	T_{n4}	T_s	T_a	T_w
Control	20.90 ± 0.58	19.77 ± 0.45	20.97 ± 0.58	20.06 ± 0.58	18.90 ± 0.45
Treatment	21.93 ± 0.54	21.13 ± 0.45	22.09 ± 0.53	21.23 ± 0.53	20.30 ± 0.44

$T_{n1\text{-}4}$, nest temperature at each point (see Fig. 1); T_s, surface temperature of the nest; T_a, ambient temperature; T_w, wall temperature where the nest was built. In both nests, the number of samples in Control and Treatment were 54 and 55, respectively.

T_{n3}, excess temperature in the Control was similar between the experiments (Fig. 3c). Excess temperature in the Control was significantly higher than that of the Treatment at hour 7. At the point of T_{n4}, excess temperature in the Control was lower than those of the Treatment throughout the measurements, but the value of Control at hour 7 was higher than that of Treatment (Fig. 3d). The excess temperature in Control was higher than that of the Treatment at hour 7, while the values of the Control were lower than those of the Treatment from 10 to 12. The mean daily value of excess temperature was higher in the Control than in the Treatment, except for T_{n4} (Table 2). When the mean values of excess temperature were compared between the large and the small nests, all values in the large nest were higher than that in the small one (Table 2).

The temperature fluctuation was larger in Treatment than in Control nest at each measuring point, and the temperature fluctuation in the Control was higher than that in the

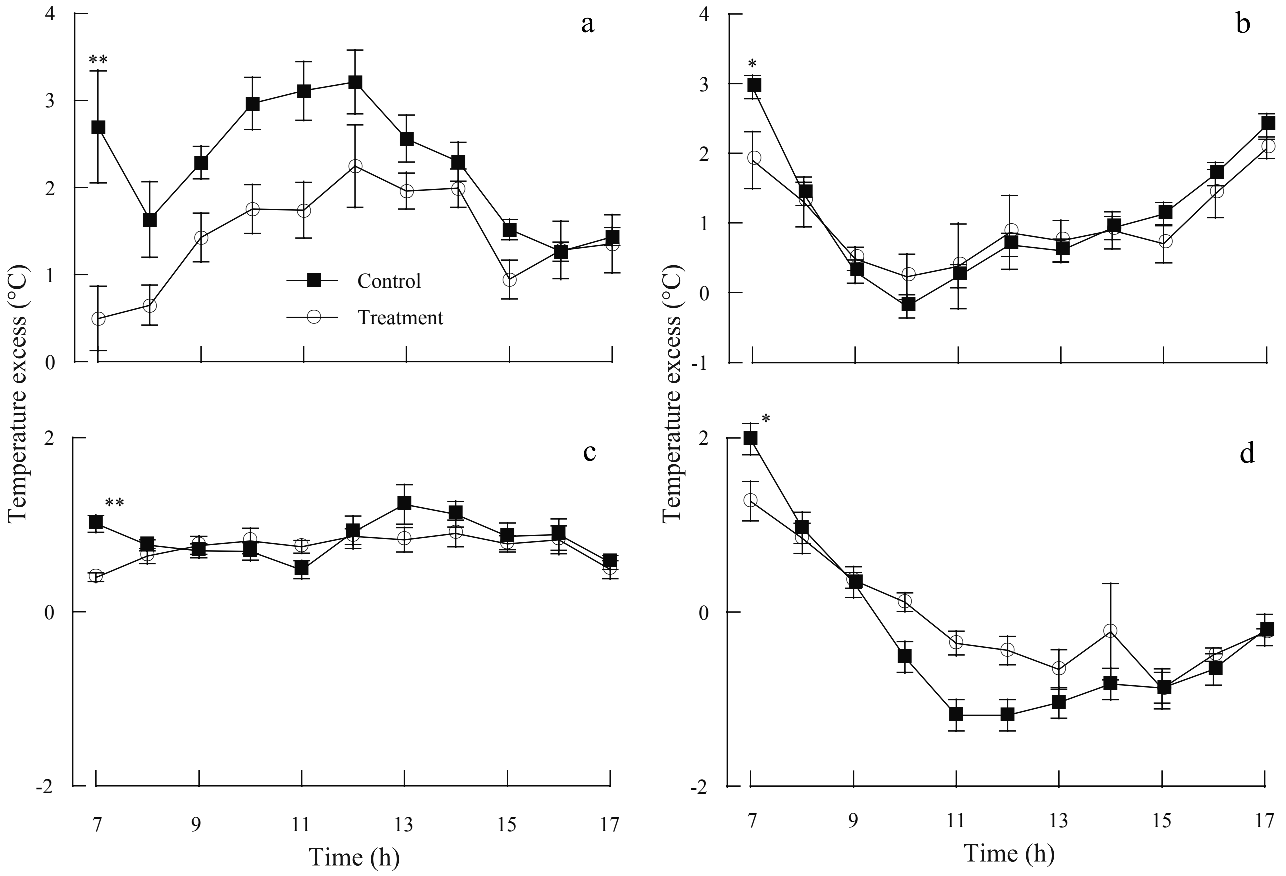

Fig. 3. Mean ± S.E. (n = 5) of the excess temperature (nest temperature minus ambient temperature) in *P. occidentalis* nests; a, excess temperature at T_{n1} in large nest; b, excess temperature at T_{n2} in large nest; c, excess temperature at T_{n3} in small nest; d, excess temperature at T_{n4} in small nest. Black square and open circle mean the Control and the Treatment, respectively. Significant differences between trials by a Mann–Whitney U-test are indicated by asterisks; *P < 0.05; **P < 0.005.

Table 2. Temperature excess (mean ± SE, °C) of the Control and the Treatment. (n. of samples = 109)

		Control	Treatment
Large nest	T_{n1}	2.28 ± 0.13	1.56 ± 0.08
	T_{n2}	1.10 ± 0.14	0.95 ± 0.13
Small nest	T_{n3}	0.84 ± 0.05	0.72 ± 0.03
	T_{n4}	-0.29 ± 0.14	-0.10 ± 0.10

T_{n1-4} (see Fig. 1)

Treatment at the inner points. In the large nest, at the point of T_{n1}, the fluctuation was significantly lower in the Control than that in the Treatment (Table 3). The fluctuation at T_{n2} was also lower in the control, while the difference was not significant. In the small nest, a significant difference was found at T_{n3}, but the values were not different at T_{n4} (Table 3). When the values of temperature fluctuation were compared between the two nests, they were similar and no significant difference was found between the nests (T_{n1} vs T_{n3} and T_{n2} vs T_{n4}, see Table 3).

Nest temperature and flight activity. In both nests, the flight activity of wasps was seen from hour 9 in all the measurements, and the activity continued until sunset (hour 17). In the morning, at hour 7, only a few wasps were found on the surface of the outermost envelope, and no flight was observed. In all the observations, as the surface temperature rose, many wasps appeared on the nest surface at hour 9. The wasps stayed around the nest entrance, and then left the nest with a weak flap or sometimes failed to fly. The flight increased in proportion to the changes of T_s until hour 14. Then, their activity decreased from hour 15. The number of inflight wasps was larger in the Treatment (79.4 individuals/10 min) than in Control (55.2) in the large nest, but with no differences observed in the small one (5.6 in Control and the 6.0 in Treatment). The measured temperatures i.e., T_n, T_s, T_a and T_w, had enough effect on the flight activity of wasps (multiple regression done with no activity extrapolated; whole model: large nest, Control, $R^2 = 0.79$, N = 40, P < 0.0001; Treatment, $R^2 = 0.73$, N = 43, P < 0.0001; small nest Control, $R^2 = 0.59$, N = 37, P < 0.0001). Among the temperatures, surface temperature had the primal effect on the flight activities in the Control (T_{s1}

Table 3. Comparison of temperature fluctuation (mean ± SE) between the Control and the Treatment. (n. of samples = 109)

	Control	Treatment	Statistical value	Statistical significance (P)
T_{n1}	2.80 ± 0.12	5.39 ± 0.24	7.638	< 0.0001
T_{n2}	2.91 ± 0.10	3.07 ± 0.12	-0.576	0.5759
T_{n3}	2.79 ± 0.10	4.73 ± 0.20	6.449	< 0.0001
T_{n4}	3.22 ± 0.11	3.28 ± 0.18	-1.055	0.2912

$T_{n1\text{-}4}$ (see Fig. 1); statistics: Mann-Whitney U-test.

$P < 0.05$, T_{s3} $P < 0.05$), while its effect tended to be small in the Treatment (T_{n1} $P < 0.0001$, T_{s2} $P < 0.05$), and in the small nest, T_{s4} was of marginal importance (Treatment, $R^2 = 0.39$, $N = 38$, $P < 0.0001$, T_{s4} $P = 0.09$). The flight activity did not occur when surface temperature was under 18.0°C in all the measurements.

Discussion

It is clear from our experiments that the outer empty combs, i.e., the extra layers on the *P. occidentalis* nest, provides an insulation effect against the fluctuation of environmental temperatures. The nest temperatures of this study may be influenced by two heat sources, such as the ambient air and the wall of the extra layers. The ambient heat was insulated by the outer combs; and the heat, once conducted, was stored around the outer combs. The heat from the wall was stored within the nest by layers of combs that were directly attached to the wall, and the thermal effect of the wall was large in the inner part of the nest. The heat generated by colony also affected the nest temperature, but it is presumed that the heat is small or negligible in the nest of *P. occidentalis* (Hozumi *et al.* 2005).

When the nest temperatures were compared between the two nests, the large nest attained higher temperature than that of the small one. At the outer part of the large nest (T_{n1}), notable insulation effect by the extra layer was observed. The values of excess temperature in the Control were higher than those of the Treatment throughout the measuring hours. It is perhaps due to the large heat-flow through the outer surface and the insulation effect by combs at the outer part. The surface area of a comb becomes gradually large from the inner to the outer part of the nest (see Fig. 1A), and the outermost envelope sometimes encloses more than half of the nest. Such a large surface receives more heat radiation from the ambience, and the heat once conducted was stored between the adjacent combs at the outer part of the nest. On the other hand, at the internal part of the nest (T_{n2}), the values of excess temperature were similar between the experiments except in the morning. In this part of the nest, the thermal conditions may be mainly influenced by the heat from substratum—concrete wall in this study—since the inner part is well insulated from the fluctuation of ambient temperature by many layers of combs. At hour 7, the surface temperature of the wall was higher than that of ambient temperature, and the heat was stored by the outer extra layers in the Control, showing higher excess temperature than those of the Treatment. In the small nest, unlike the case of the large one, the temperature in the inner part was largely influenced by a layer of comb, while excess temperature at the outer part did not differ between the experiments. This difference between the nests was possibly caused by the small surface area and the small number of the combs in the small nest. Thus, it is suggested that a large surface area introduce more heat into the outer part of the nest and many layers of combs moderate the inner part of the nest, i.e., the larger the nest, the higher the insulation effect and the thermal stability were.

Generally, the thermal requirement in social insect nest is different in ecozones, such as temperate, tropic and subtropic. In the temperate ecozone, the ambient temperature is cool in spring and fall, and the temperature largely varies in a day even in summer; wasps hibernate during the winter. In this ecozone, because of the low ambient temperature, the wasps strive to warm the nests for an early development of brood and for a promotion of activity of adults. On the other hand, in the tropical ecozone, the ambient temperature is stably high in summer, and the lowest temperature is much milder in winter. In this ecozone, the primal thermal problem will be nest overheating during the daytime. In the subtropical ecozone, where the climate is cool in winter and hot in summer, warming and avoidance of overheating of the nests are required in each season. Since swarm founding *Polybia* wasps hardly seen in temperate, we focus on the thermal effect of the nests under subtropical and tropical ecozone.

The ecological significance of thermal effect of the extra-combs is to reduce the fluctuation of nest temperature throughout the cool winter and hot summer in the subtropical ecozone. In *P. occidentalis* nests, as shown above, excess temperature in the Control was higher than that in the Treatment during winter, suggesting that nest temperature will be high in the Control than in the Treatment if ambient temperature is the same in both experimental conditions. This means that broods are reared with warmer condition in the nest with extra-combs even under the low ambient temperature during the winter. Unfortunately we do not have physiological data of *Polybia* species, but such a high temperature will generally shorten the developmental period of brood. In addition, higher temperatures by extra-combs may influence the performance of adults under the cool environment, since the flight activity of wasps is closely related to the thermal environment (Heinrich 1984, Lima & Prezoto 2003, Nascimento & Nascimento 2005).

The nest temperature promotes adult activity, which may contribute to the colony defense against enemies and increase the wasps' ability to engage in extranidal activities from the early morning. In the summer period, on the other hand, ambient temperature may exceed 40°C during the daytime. In this situation, it is expected that the nest temperatures will become extremely high, and consequently brood may be exposed to thermal injury. However, such a high ambient temperature can be prevented by outer layers of combs where no or few broods are present. In the previous study (Hozumi *et al*. 2005) that was conducted in the summer, the nest temperature at the brood combs were below 33°C even when ambient temperature was 42°C in spite of the lack of thermoregulation by adult wasps. Thus, it is suggested that the immature individuals were protected from high ambient temperature and large fluctuations of temperatures, and it may be an unlikely occurrence that immature stages are exposed to lethal temperatures. This insulation effect will be also effective in the tropical ecozone.

On the building of outer empty combs, Jeanne & Bouwma (2004) proposed five potential selective factors, such as "maximization of productivity," "work group efficiency," "brood protection," "adult protection," and"reproductive competition." In addition to these five factors, we propose the thermal effect of the empty combs, and it is one of the aspects of the ecological features of the nest building behavior. The building behavior of the extra-combs is also seen in other *Polybia* species, such as *P. paulista* von Ihering (Kudô, personal observation), a consubgeneric species of *P. occidentalis*. It is supposed that temperature in *P. paulista* nests are also regulated with the same mechanism that in *P. occidentalis* nest. We suggest that the building of extra comb is one of the measures to protect the nest from the fluctuation of temperature and to maintain a stable microenvironment for brood rearing.

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