Does size matter? – Thermoregulation of ‘heavyweight’ and ‘lightweight’ wasps (Vespa crabro and Vespula sp.)

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Introduction

Flying insects that can elevate their body temperature can forage with some independence of ambient air temperature and in this way extend their activity range (Heinrich, 1993). The vespine wasps are capable of endothermic heat production by means of their thoracic muscles (Heinrich, 1984; Stabentheiner and Schmaranzer, 1987). This improves their flight performance and allows a better exploitation of food resources (Kovac and Schmaranzer, 1987). This improves their flight performance and allows a better exploitation of food resources (Kovac and Schmaranzer, 1987). In Central Europe, social wasps have a long breading season from the spring till the autumn, where they have to cope with a vast variation of thermal conditions challenging their thermoregulatory capability.

In members of the family Vespidae a great variability of the body mass occurs. The hornet (Vespa crabro) is the largest species of vespine wasps in Central Europe. They may weigh up to 580 mg. Species of the genus Vespula are much smaller, weighing about 40–130 mg. Flying insects with small body size or mass can operate with relatively low thoracic temperatures, large insects must generally have higher thoracic temperatures (Heinrich, 1974; Heinrich, 1993). An obvious advantage of the greater body mass and the higher temperature is the ability to hunt larger prey and to carry heavier loads of food. The thermoregulatory capacity of insects is often a function of their body mass (Bartholomew and Heinrich, 1973), beetles (Bartholomew and Heinrich, 1978), 18 species of Alaskan bees (Bishop and Armbruster, 1999) and Alaskan dragonflies (Sformo and Doak, 2006), in wasps (Heinrich, 1984; Coelho and Ross, 1996) and in solitary bees (Stone and Willmer, 1989; Stone, 1993a; Stone, 1993b). In general, small bees initiate flight at lower thoracic temperatures than larger ones (Stone, 1993a; Stone, 1993b). However, in an interspecific comparison of endothermy in moths (Bartholomew and Heinrich, 1973), beetles (Bartholomew and Heinrich, 1978), 18 species of Alaskan bees (Bishop and Armbruster, 1999) and Alaskan dragonflies (Sformo and Doak, 2006), in wasps (Heinrich, 1984; Coelho and Ross, 1996) and in solitary bees (Stone and Willmer, 1989; Stone, 1993a; Stone, 1993b). In general, small bees initiate flight at lower thoracic temperatures than larger ones (Stone, 1993a; Stone, 1993b). However, in an interspecific comparison of endothermy in honeybees (Apis), Dyer and Seeley observed deviations from the expected size-related patterns (Dyer and Seeley, 1987).

The knowledge concerning the thermal biology of the European hornet is very sparse. Only a few measurements of body temperature of hornets foraging honey at an artificial feeding place exist (Stabentheiner and Schmaranzer, 1987). The aim of this study was to investigate the thermoregulatory capacity and strategies of this big flying insect in detail. We assumed that hornets have advantages in thermoregulation due to their large body mass. To verify this hypothesis we compared the body temperature of hornets (Vespa crabro) with that of smaller native vespine wasps (Vespula vulgaris, Vespula germanica) living in the same habitat within the same climatic environment. The temperature of leaving and arriving insects was chosen for the assessment of the thermoregulatory performance. The comparison with similar investigations of wasps of different size (Heinrich, 1984; Coelho and Ross, 1996) promised general conclusions.

Summary

In insect groups with the ability of endothermy, the thermoregulatory capacity has a direct relation to body mass. To verify this relationship in vespine wasps, we compared the thermoregulation of hornets (Vespa crabro), the largest species of wasps in Central Europe, with two smaller wasps (Vespula vulgaris and Vespula germanica) in the entire range of ambient temperature (Ta: ~0–40°C) where the insects exhibited foraging flights.

Despite the great difference in body weight of Vespula (V. vulgaris: 84.1±19.0 mg, V. germanica: 74.1±9.6 mg) and Vespa (477.5±59.9 mg), they exhibited similarities in the dependence of thorax temperature on Ta on their arrival (mean Tth = 30–40°C) and departure (mean Tth = 33–40°C) at the nest entrance. However, the hornets’ thorax temperature was up to 2.5°C higher upon arrival and up to 3°C lower at departure. The thoracic temperature excess (Tth−Ta) above ambient air of about 5–18°C indicates a high endothermic capacity in both hornets and wasps. Heat gain from solar radiation elevated the temperature excess by up to 1°C. Results show that hornets and wasps are able to regulate their body temperature quite well, even during flight. A comparison of flight temperature with literature reports on other vespine wasps revealed a dependence of the Tth on the body mass in species weighing less than about 200 mg.

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In order to assess the thermoregulatory performance it is of great advantage to investigate the insects’ thermoregulation in their natural environment where they are exposed to the variation of several environmental factors like ambient air temperature, solar radiation and convection, influencing their body temperature. If the greater body mass delivers advantages in thermoregulation this has to be especially expected at low ambient temperatures. Therefore, our experiments covered the entire range of environmental conditions the wasps are likely to be exposed to in their season of activity. Infrared thermography allowed behavioural observations in addition to the non-invasive, undisturbed measurement of body temperature.

Materials and Methods

Animals, field site and measuring conditions
Measures were conducted on four hornet colonies (Vespa crabro, Vespidae, Hymenoptera) and six wasp colonies, five Vespula vulgaris and one Vespula germanica (Vespidae, Hymenoptera). The hornet nests were located in tree hollows or abandoned bird nest boxes. The wasps nested in wall hollows or lofts (V. vulgaris) and in a ground nest (V. germanica). Data were collected on 16 days from July till October in the years 2009 and 2010, and on 2 days in October and November 1989. The entire range of ambient temperature (Tb ~ 0–40°C) where the insects exhibited foraging flights was investigated in V. crabro and V. vulgaris. The insects’ body surface temperature was investigated during take-off, landing, and other activities at the nest entrance. To ensure similar environmental conditions for the comparison of hornet (V. crabro) and wasp (V. vulgaris) thermoregulation only measurements conducted in shade were taken into consideration in this case. The influence of solar radiation on body temperature of leaving and arriving insects was investigated in another set of experiments comparing hornets with wasps (V. germanica) when the nest entrance was in sunshine. Foraging wasps and hornets on fruits (pear) or lilac were investigated in an orchard. The hornets foraging on lilac bitted open the bark of the lilac branches and sucked the sap. Hornets and wasps foraging on pears sucked the sap of the fruits or gnawed off the fruit pulp. The insects were observed during their whole foraging stay. Infrared recordings were started immediately after landing and ran until the insects’ take-off. Foraging stays lasted from a few seconds (~ 5 s) to maximal 15 minutes. After departure of the observed insect the next arriving forager was chosen for measurement. Hornets preying on honeybees were also observed in the orchard. Patrolling hornets were followed until they were in the focus of the infrared camera. The flight between hornets was observed and measured on the ground in the vicinity of a nest.

Measurements
The insects were filmed with an infrared camera (AGA 782 SW, ThermaCam SC2000 NTS or i60, FLIR, Stockholm, Sweden). The infrared cameras were calibrated periodically by slotting in a precision-calibrated AGA1010 reference source (FLIR) or a self-constructed peltier-driven reference source of known sensitivity (FLIR) or a self-constructed peltier-driven reference source of known sensitivity (FLIR, Stockholm, Sweden) or a self-constructed peltier-driven reference source of known sensitivity (FLIR, Stockholm, Sweden). The infrared cameras were measured on the ground in the vicinity of a nest.

Data evaluation and statistics
The surface temperature of head (Thd), thorax (Tth) and abdomen (Tab) was calculated from the infrared thermograms (Fig. 1) by means of proprietary software in the AGA 782 SW, or by the AGEMA Research software (FLIR, Stockholm, Sweden) controlled by a proprietary Excel VBA-macro (Microsoft Corporation, Santa Rosa, California) in the other two cameras. Values were taken from pictures immediately before take-off, after landing or during flight (if the insects were in focus) at the nest entrance. From foraging insects values were evaluated immediately after landing and subsequently in intervals of about five seconds. The surface temperature of the three body parts was calculated with an infrared emissivity of 0.97, determined for the honeybee cuticle (Stabentheiner and Schmaranzer, 1987; Schmaranzer and Stabentheiner, 1988; Stabentheiner et al., 2012). To avoid a wrong measurement of body temperature (Tb) on the background we have to choose the maximum temperature of each foraging insect. This was especially important at low temperatures. If the greater body mass delivers advantages in thermoregulation this has to be especially expected at low ambient temperatures. Therefore, our experiments covered the entire range of environmental conditions the wasps are likely to be exposed to in their season of activity. Infrared thermography allowed behavioural observations in addition to the non-invasive, undisturbed measurement of body temperature.

Results
The difference in the body mass of the three investigated Vespidae was significant (t-test, P < 0.05). Vespula vulgaris weighed on average 84.1 ± 19.0 mg (n = 147), Vespula germanica weighed 74.1 ± 9.6 mg (n = 23) and the hornets had a mean weight of 477.5 ± 59.9 mg (n = 50). The hornets weighed the 5.7 fold of V. vulgaris and the 6.4 fold of V. germanica.

Departure and arrival measured in shade

Departure
Ambient air temperature (Tₐ) in shade during measuring periods ranged from ~ 1 to 38°C (Fig. 2A; Tables 1, 2). The relation of body surface temperatures and ambient temperature of hornets (V. crabro) and wasps (V. vulgaris) could be fitted and described...
best with a polynomial regression:

$$T_{\text{body}} = A + B_1 T_a + B_2 T_a^2$$  \hspace{1cm} (1)

The hornets’ thorax surface temperature ($T_{\text{th}}$; derived from the regression line) was 38.0°C at a low $T_a$ of 2°C. With increasing $T_a$ it first declined to 33.3°C at $T_a = 15$°C, and increased again to 36.7°C at $T_a = 27$°C. By contrast, the wasps had a more constant $T_{\text{th}}$ during departure. When leaving the nest at a low $T_a$ of 2°C we measured a $T_{\text{th}}$ of 39.4°C, which decreased to 36.4°C at $T_a = 15$°C, and increased again to 40.4°C at a high $T_a$ of 37°C. The temperature of the head exhibited a stronger dependence on $T_a$.

In the hornets it was 23.6°C at $T_a = 2$°C and increased to 33.5°C at a high $T_a$ of 27°C, and in the wasps it increased from 26.2°C at $T_a = 2$°C to 37.7°C at $T_a = 37$°C. The abdomen was the coolest body part. Its temperature depended strongly on $T_a$. In the hornets $T_{\text{ab}}$ increased from 15.5°C to 31.9°C, and in the wasps from 22.8°C to 35.8°C in the investigated range of $T_a$ (Fig. 2A; Table 2).

**Arrival**

The relationship of body surface temperatures and ambient temperature of hornets and wasps could be fitted and described...
Table 1. Summary statistics of the hornets’ surface temperature (T) of head, thorax and abdomen, and ambient temperature (T_a) and solar radiation (sol.rad.) for different activities at the nest entrance and during foraging (* mean values of Fig. 5). Data presented as means ± SD. N = number of measurements.

| activity       | hornets/N | T_head (°C) | T_thorax (°C) | T_abdomen (°C) | T_a (°C) | sol.rad (Wm⁻²) |
|----------------|-----------|-------------|---------------|----------------|---------|----------------|
| departure      | 1210/1210 | 29.2±3.3    | 34.5±2.4      | 27.6±7.4       | 17.5±6.9| 252.1±320.5   |
| arrival        | 1128/1128 | 27.9±4.7    | 35.3±3.3      | 23.1±6.9       | 18.4±6.7| 328.2±352.1   |
| flight         | 152/152   | 30.8±4.0    | 35.7±2.8      | 28.1±4.7       | 22.8±3.6| 241.1±326.8   |
| walk           | 123/246   | 30.5±4.3    | 35.0±3.7      | 28.5±5.1       | 20.9±5.9| 239.8±296.6   |
| build          | 14/64     | 26.5±6.9    | 29.6±6.7      | 23.5±6.6       | 15.3±5.5| 374.5±321.2   |
| fanning        | 65/459    | 29.8±5.5    | 33.0±5.4      | 27.9±5.3       | 19.4±6.6| 415.4±313.0   |
| feed           | 2/15      | 27.3±0.3    | 31.2±2.3      | 23.8±1.0       | 17.0±0.5| 47.2±12.7     |
| examine        | 3/74      | 32.0±1.8    | 34.0±1.8      | 30.3±1.6       | 23.9±3.0| 148.3±215.0   |
| move           | 55/106    | 26.9±5.7    | 30.3±6.3      | 25.4±5.0       | 14.3±4.9| 344.9±294.4   |
| bask           | 100/382   | 28.0±8.2    | 31.0±9.5      | 25.3±7.0       | 13.5±5.3| 118.0±274.6   |
| flight         | 6/443     | 33.1±1.0    | 37.2±1.0      | 30.2±1.0       | 22.1±2.4| 113.9±75.0    |
| attack         | 20/79     | 33.3±1.2    | 36.8±1.9      | 31.8±1.1       | 24.7±0.5| 581.1±63.0    |
| foraging pear* | 18/190    | 29.5±2.8    | 32.2±3.1      | 28.7±2.9       | 21.6±1.2| 548.8±60.5    |
| foraging lilac*| 220/1313  | 30.3±2.8    | 33.8±2.6      | 26.5±4.6       | 22.0±6.1| 49.7±66.6     |
| hunting bees   | 40/162    | 30.4±2.2    | 35.8±2.7      | 23.1±3.3       | 18.1±2.4| 328.7±225.9   |

Table 2. Equations of regressions for the body temperature of hornets and wasps (Fig. 2) in dependence on ambient temperature (T_a) at departure, arrival and flight at the nest entrance. R² = coefficient of regression, P = probability, N = number of measurements.

| body part       | equations                                      | R²    | P       | N  |
|-----------------|------------------------------------------------|-------|---------|----|
| thorax V. crabro| T_th=39.58031–0.81505*T_a+0.02625*T_a²         | 0.2166| <0.0001 | 862|
| head            | T_th=23.18457+0.00677*T_a–0.0001559*T_a²      | 0.7377| <0.0001 | 859|
| abdomen         | T_th=13.30622+1.0879*T_a–0.01559*T_a²         | 0.8128| <0.0001 | 853|
| thorax V. vulgaris| T_th=4.2.86411–2.12183*T_a–0.000952*T_a²–0.000176*T_a³ | 0.09069 | <0.0001 | 1537|
| head            | T_th=27.16308–0.52231*T_a–0.00258*T_a–0.000033*T_a³ | 0.61364 | <0.0001 | 1530|
| abdomen         | T_th=24.37649–0.94879*T_a–0.000334*T_a³       | 0.78535 | <0.0001 | 1514|
| thorax V. crabro| T_th=34.72990–1.06338*T_a–0.005726*T_a²       | 0.50738 | <0.0001 | 680 |
| head            | T_th=24.23205–1.18970*T_a–0.000217*T_a²      | 0.84545 | <0.0001 | 658 |
| abdomen         | T_th=12.74708–0.97564*T_a–0.000270*T_a²      | 0.91582 | <0.0001 | 680 |
| thorax V. vulgaris| T_th=3.58973–0.96143*T_a–0.06537*T_a²–0.009902*T_a³ | 0.56570 | <0.0001 | 1302|
| head            | T_th=23.00846–0.4795*T_a–0.000797*T_a³       | 0.76378 | <0.0001 | 1259|
| abdomen         | T_th=11.79295–0.4341*T_a–0.06886*T_a–0.00107*T_a³ | 0.88601 | <0.0001 | 1296|
| thorax V. germanica| T_th=27.09089+0.37905*T_a  | 0.45182 | <0.0001 | 377 |
| head            | T_th=21.07564+0.47865*T_a        | 0.54369 | <0.0001 | 377 |
| abdomen         | T_th=14.63780+0.54881*T_a    | 0.60703 | <0.0001 | 377 |

best with a polynomial regression (T_a ranging from −1 to 40°C) (Fig. 2B; Table 2):

\[ T_{body} = A + B1 \cdot T_a + B2 \cdot T_a^2 + B3 \cdot T_a^3 \] (2)

This equation fitted the data better than Eqn 1. The hornets’ average T_th after arrival was ~0 to 2.5°C higher than that of V. vulgaris (Fig. 2). Their T_th decreased from ~34°C to ~31°C as T_a increased from 1°C to 10°C, and increased continuously at higher T_a. It reached 37.5°C when it was warm (T_a = 27°C). The T_th of V. vulgaris upon arrival decreased from ~32 to 30°C in the lowest range of T_a (1–10°C) and, like in the hornets, increased continuously at higher T_a. The T_th reached 40.7°C when T_a was 37°C. V. germanica regulated the T_th at a similar level as the hornets (T_th = 34.5–40.1°C; T_a = 20–30°C) (Fig. 2C). The hornets’ T_th was ~22.8°C at low T_a (1–10°C) and increased continuously to 33.0°C at high T_a (27°C). The T_th of V. vulgaris was 22.2°C at low T_a (1–10°C) and increased to 38.6°C at very high T_a (37°C). The T_th of both hornets and wasps depended strongly on ambient air temperature. It was ~2 to 5°C higher than
Only at very low \( T_a \) the abdominal temperature elevation reached a maximum of 10°C above the ambient air in both species. At high \( T_a \) (27°C) the hornets’ abdomen was only slightly elevated above \( T_a \) and the wasps had an abdominal temperature ~2°C lower than the ambient air (Fig. 2B; Table 2). The \( T_{\text{th}} \) of the hornets resembled that of the wasps. The \( T_{\text{th}} \) of the hornets, however, was similar to or warmer than that of the wasps (difference: ~0–3°C) (Fig. 2C).

**Flight**

The \( T_{\text{th}} \) of hornets in flight was ~1 to 2°C lower than immediately after landing at a \( T_a \) of 16 to 27°C (Fig. 2B). Linear regression lines of flying and landing hornets differed significantly in this range of ambient temperature (ANOVA, \( P<0.0001 \), DF = 3, F-Ratio = 85.27, \( n=447 \)).

**Thorax temperature excess and solar radiation**

The hornets and wasps were always endothermic at departure and arrival, i.e. their thorax was clearly elevated above the ambient air. The thorax temperature excess depended strongly on \( T_a \) (\( T_{\text{th}} - T_a \) = 3–38°C) (Fig. 2, Fig. 3; Table 3). To quantify the influence of solar radiation on the body temperature, measurements were conducted also in sunshine. For hornets and *V. germanica* the values of the thorax temperature excess were partitioned according to our classification of solar radiation (Fig. 3; Table 3) (shade: <200 Wm\(^{-2}\), sunshine: >500 Wm\(^{-2}\)).

The hornets leaving the nest in sunshine had a ~0.2–0.4°C higher temperature excess than in the shade. An ANOVA comparing regressions of \( T_{\text{th}} - T_a \) in dependence on \( T_a \) revealed significant differences (\( P<0.0001 \), DF = 3, F-Ratio = 469.38, \( n=788 \)). The difference in \( T_{\text{th}} - T_a \) at arrival was ~1°C. An ANOVA comparing regressions also revealed significant differences (\( P<0.0001 \), DF = 3, F-Ratio = 364.88, \( n=765 \)).

The wasps leaving the nests in the sun had a similar temperature excess than in the shade (\( T_{\text{th}} - T_a \) ~ 0–0.3°C). However, the regression lines differed significantly (ANOVA, \( P<0.0001 \), DF = 3, F-Ratio = 224.82, \( n=246 \)). In arriving wasps the difference in temperature excess between sunshine and shade was smaller than in the hornets (\( T_{\text{th}} - T_a \) ~ 0–0.7°C; ANOVA: \( P<0.0001 \), DF = 3, F-Ratio = 209.58, \( n=247 \)).

**Thorax temperature and body mass**

The thorax temperature of arriving insects of each colony was plotted in dependence on ambient temperature. From the calculated regressions functions the mean \( T_{\text{th}} \) was determined for three \( T_a \)s (10, 20, 30°C) and afterwards related with the colonies’ mean body mass. An ANOVA revealed a dependence on \( T_a \) (\( P<0.05 \), DF = 1, F-Ratio = 74.26, \( n=13 \)), but no dependence on colony or body mass. For a further comparison with data from the literature our values were pooled for each species (because values for different colonies were not available in these papers) and analysed in the same way. Fig. 4 shows the
Thermoregulation of wasps

| sol.rad. (Wm⁻²) | equations | R²  | P    | N   |
|-----------------|-----------|-----|------|-----|
| <200            | Tₘₐₜ−Tₚ = 27.7916³−0.69307*Tₚ | 0.53978 | <0.0001 | 474 |
| 200–500         | Tₘₐₜ−Tₚ = 30.68420−0.80536*Tₚ | 0.57439 | <0.0001 | 27  |
| >500            | Tₘₐₜ−Tₚ = 28.29469−0.70065*Tₚ | 0.76827 | <0.0001 | 314 |

Table 3. Equations of regressions for the thorax temperature (Tₘₐₜ−Tₚ) excess of hornets and Vespula germanica (Fig. 3) in dependence on ambient temperature (Tₚ) and solar radiation (sol.rad.) at departure and arrival at the nest entrance. R² = coefficient of regression, N = number of measurements.

For statistical details see Table 4.

Foraging and other activities

Linear regression lines were fitted for the temperature values of thorax, head and abdomen of foraging hornets on lilac. The results revealed differences in the dependence of body part temperatures on ambient temperature as expected (Fig. 5A; Table 5). The Tₘₐₜ was regulated nearly independent of Tₚ (Tₘₐₜ = 15°C: Tₚ = 33.0°C; Tₘₐₜ = 30°C: Tₚ = 34.7°C). The head was cooler and exhibited a stronger dependence on Tₚ (Tₘₐₜ = 15°C: Tₘₐₜ = 27.6°C; Tₘₐₜ = 30°C: Tₘₐₜ = 33.6°C). The abdomen was the coolest body part. It was ~3 to 5°C warmer than Tₖ. The temperature increased nearly parallel to Tₖ (Tₘₐₜ = 15°C: Tₘₐₜ = 21.2°C; Tₘₐₜ = 30°C: Tₘₐₜ = 32.9°C).

By contrast, foraging hornets on pears exhibited a strong dependence of all body parts on Tₖ (Fig. 5B, regression lines; Table 5). The thorax was the warmest body part (Tₘₐₜ = 15°C; Tₚ = 27.5°C; Tₘₐₜ = 30°C; Tₕ = 38.0°C), followed by the head (Tₘₐₜ = 15°C: Tₕ = 24.8°C; Tₘₐₜ = 30°C: Tₕ = 35.5°C), and the abdomen (Tₘₐₜ = 15°C: Tₘₐₜ = 24.9°C; Tₘₐₜ = 30°C: Tₘₐₜ = 33.5°C). However, wasps foraging on pears showed no dependence of Tₘₐₜ on Tₖ (Tₘₐₜ = 13°C: Tₖ = 31.5°C; Tₘₐₜ = 25°C: Tₖ = 31.6°C). A weak dependence on Tₖ was measured in Tₖ (Tₘₐₜ = 13°C: Tₖ = 27.0°C).

Table 4. Equations of regressions for the thorax temperature (Tₘₐₜ) of hornets and wasps (Fig. 4) in dependence on body mass for three ambient temperatures (Tₚ). R² = coefficient of regression, N = number of measurements.

For statistical details see Table 4.

Relation of thorax temperature and body mass, comparing our results with results of Heinrich, and Coelho and Ross (Heinrich, 1984; Coelho and Ross, 1996). The Tₘₐₜ was fitted with exponential functions in dependence on body mass for three Tₚs (10, 20, 30°C).

For 10 and 20°C:

\[ T_{\text{thorax}} = y + A \exp(-\text{body mass}) \]  (3)

For 30°C:

\[ T_{\text{thorax}} = y + A \exp(-\text{body mass/11}) + B \exp(-\text{body mass/22}) \]  (4)

A dependence of the Tₘₐₜ on body mass could be detected, but it was small and more distinct at lower temperatures (ANOVA, P<0.01, DF = 6, F-Ratio = 6.18, n = 20). However, the heaviest species (V. crabro, this paper), weighing 477.5 mg on average, had a somewhat lower Tₘₐₜ than Dolichovespula maculata with a medium body mass of 185.5 mg (Heinrich, 1984). The Tₘₐₜ values of the other wasps were mostly below that of D. maculata and V. crabro.
26.6°C; $T_a = 25$ °C; $T_{thd} = 28.5$ °C), and a strong dependence on $T_a$ in $T_{ab}$ ($T_a = 13$ °C; $T_{ab} = 19.9$ °C; $T_a = 25$ °C; $T_{ab} = 26.4$ °C).

The hornets’ mean body temperatures for the observed activities at the nest entrance, in the vicinity of the nest and during foraging and hunting are summarized in Table 1. The highest $T_{th}$s were measured in fighting (37.2 °C) and attacking (36.8 °C) hornets. The $T_{th}$ during hunting, flight and arrival after flight was somewhat lower (35.8, 35.7 and 35.3 °C, respectively) and they were lowest during nest-building activities at the entrance (29.6 °C). The mean $T_{th}$ during foraging was in the intermediate range (compare with Fig. 5). Guards examining other hornets at the nest entrance could be observed in three individuals. In one case the examined hornet exhibited a heating bout similar to a typical thermal behaviour observed in honeybees involved in such guard – examinee interactions (Stabentheiner et al., 2002). After some seconds of inspection the examined hornet started to heat up the thorax very strongly, without making any attempts to escape. The thorax temperature at the beginning of inspection was 26 °C. After about 80 seconds the guard stopped the inspection and the $T_{th}$ of the examined hornet reached the maximum of 31 °C. When the guard left the inspected hornet the $T_{th}$ decreased strongly to 28 °C. In honeybees such heating bouts are presumed to improve the recognition of examined individuals (Stabentheiner et al., 2002; Stabentheiner et al., 2007).

Discussion

Our results demonstrate that hornets (Vespa crabro) and wasps (Vespula sp.) are capable of pronounced and similar endothermy and thermoregulation despite the large difference in body mass. Both maintained their thorax surface temperature ($T_{th}$) not only elevated but also relatively constant in a vast range of $T_a$ (Figs 2, 3, 5). A high thermal performance (large temperature excess, i.e. gradient between thorax and ambient air) was exhibited especially at low ambient temperatures. The decline of the thoracic temperature excess with increasing $T_a$ in the landing insects revealed that both hornets and wasps were able to regulate their body temperature even during flight. Measuring the insects immediately after landing provided values comparable with the flight temperature (Fig. 2B). The somewhat lower $T_{th}$ of hornets during flight than after landing was possibly due to a higher convective cooling of the thorax surface in flight. The hornets’ mean thorax temperature after arrival was maximal ~2.5°C higher than that of V. vulgaris and similar to that of V. germanica (Fig. 2C). In contrast to the arrival, V. vulgaris had a similar or a somewhat higher $T_{th}$ than the hornets during departure from the

Table 5. Equations of linear regressions for the body temperature of hornets and wasps (Fig. 5) in dependence on ambient temperature ($T_a$) during foraging on lilac and pear. $R^2$ = coefficient of regression, $N$ = number of measurements.

| body part | equations | $R^2$ | $P$  | $N$ |
|-----------|-----------|-------|------|-----|
| hornet lilac | $T_{th} = 31.32101 + 0.11260 \times T_a$ | 0.06176 | <0.0001 | 1312 |
| head | $T_{hd} = 21.46458 + 0.40305 \times T_a$ | 0.66458 | <0.0001 | 1312 |
| abdomen | $T_{ab} = 9.49536 + 0.77635 \times T_a$ | 0.91605 | <0.0001 | 1312 |
| hornet pear | $T_{th} = 16.71841 + 0.71806 \times T_a$ | 0.49876 | <0.0001 | 190 |
| head | $T_{hd} = 13.99229 + 0.71671 \times T_a$ | 0.60759 | <0.0001 | 190 |
| abdomen | $T_{ab} = 16.28067 + 0.57452 \times T_a$ | 0.35836 | <0.0001 | 190 |
| wasp pear | $T_{th} = 31.29097 + 0.01136 \times T_a$ | 0.00018 | 0.66117 | 1077 |
| head | $T_{hd} = 24.49777 + 0.15877 \times T_a$ | 0.07172 | <0.0001 | 1076 |
| abdomen | $T_{ab} = 12.71658 + 0.54804 \times T_a$ | 0.77735 | <0.0001 | 1076 |
nest (Fig. 2C). Perhaps they need a higher $T_{th}$ for take-off to compensate for a higher heat loss in the initial phase of flight due to their more unfavourable relation of body surface area to mass. However, during foraging the results were not so consistent. In wasps foraging on pears, the $T_{th}$ (mean $\sim$31.5°C) was regulated constantly high and nearly independent from $T_a$ (Fig. 5B). By contrast, the hornets’ $T_{th}$ (mean $\sim$28 to 38°C) showed a strong increase with $T_a$. On the other hand, the $T_{th}$ of hornets foraging on lilac (mean $\sim$33 to 35°C) was regulated at a relatively high level and rather independent from $T_a$ (Fig. 5A). These results confirm that the body temperature in wasp species depends not only on physiological requirements but also on other parameters like motivation, type of activity and behavioural context (Kovac and Stabentheiner, 1999; Eckles et al., 2008; Kovac et al., 2009). The dependence of thermoregulation on the behavioural context is pronounced by the great differences in the hornets’ body temperature observed during different activities at the nest entrance (mean $T_{th}$ 29.6 to 37.2°C) (Table 1).

The investigated hornets had more than fivefold the body mass ($M_b$) of the wasps. However, this great difference in body mass was only partly reflected in the measured thorax temperatures. In Fig. 2C we compare our results of arriving hornets and wasps with similar measurements of other authors (Heinrich, 1984; Coelho and Ross, 1996). The investigated species cover nearly the entire range of body mass occurring in vespine wasps (mean $M_b$ $\sim$ 53–477 mg). Comparing our $T_{th}$s of arriving hornets and wasps with measurements of Heinrich revealed an astonishing coincidence (Heinrich, 1984). The $T_{th}$s of our hornets ($M_b$ = 477.5 mg) and of $D$. maculata ($M_b$ = 185.5 mg) from Heinrich were quite similar and the values of $V$. vulgaris from Heinrich were nearly the same as the $T_{th}$s of our $V$. vulgaris (Heinrich, 1984). However, the $V$. vulgaris ($M_b$ = 57.2 mg) from Heinrich had a lower body mass than our $V$. vulgaris ($M_b$ = 84.1 mg). By contrast, our $V$. germanica ($M_b$ = 74.1 mg) exhibited a similar thorax temperature as the hornets. However, the thorax temperatures of $V$. germanica ($M_b$ = 78.7 mg) and $V$. maculifrons ($M_b$ = 53.4 mg), measured by Coelho and Ross, were lower than in the other wasps (Coelho and Ross, 1996), although the body mass of $V$. germanica was similar to our wasps’ mass (Fig. 2C). These results demonstrate that investigations on the same or related species in varying geographical and climatic areas (Europe, USA) may reveal different results. These differences in the flight body temperature may be caused by local adaptation of strains of this species as well as by differences in foraging motivation.

To show the relationship between thorax temperature and body mass of all the aforementioned species, the temperature was plotted against the mass for three different $T_{th}$s. The result revealed a significantly dependence of the $T_{th}$ on the body mass (Fig. 4) (ANOVA: $P<0.01$). However, $T_{th}$ at a given mass varied considerably. A similar relationship between metathoracic temperature and body mass of flying dung beetles was obtained by Bartholomew and Heinrich (Bartholomew and Heinrich, 1978). Beetles did not show appreciable endothermy in continuous flight until they reached a body mass of $\sim$100 mg. Methathoracic temperature of beetles with a mass between $\sim$100 and 250 mg was strongly correlated with body mass. The critical mass for obvious endothermy in beetles seems to be about 50 mg. A further comparison of the $T_{th}$ with body mass of 12 species of moths from Costa Rica (Bartholomew and Heinrich, 1973) (range $M_b$ $\sim$70 to 1200 mg) also showed a strong correlation of $T_{th}$ with mass.

There are some studies investigating the relationship between body mass and thermoregulatory performance in bees (Apoidea). They show that large bees can generally regulate $T_{th}$ better than small ones. Stone and Willmer reported a positive correlation between body mass (range $M_b$ $\sim$10 to 1300 mg) and thoracic temperature in flight in a comparison of 55 species of bees at $T_a$ = 22°C (Stone and Willmer, 1989). A similar result was obtained by Stone, who investigated endothermy in the solitary bee Anthophora plumipes (Stone, 1993a). Thoracic temperatures measured during free flight in the field correlated positively with the bees’ body mass (range $M_b$ $\sim$120 to 220 mg). In another study of Stone on thermoregulation of tropical solitary bees, he could show that in Coelioxys frontalis and Amegilla sapiens thoracic temperatures correlated positively with both ambient temperature and body mass (Stone, 1993b). A similar result was obtained by Bishop and Armbruster with regression analysis of species and family means of 18 Alaskan bees (Bishop and Armbruster, 1999). Thermoregulatory capability, and minimum thoracic temperature necessary for initiating flight, increased with body size. Bees having a dry mass smaller than 15 mg ($\sim$46 mg fresh mass) showed no appreciable ability to regulate their thorax temperature. This is probably due to the extreme increase of cooling constants at a mass below 50 mg fresh weight (Bishop and Armbruster, 1999). Heinrich and Heinrich reported a similar relationship in bumblebees (Heinrich and Heinrich, 1983). In large queens foraging $T_{th}$ did not decrease much in the mass range of 750 to 300 mg. Only the smaller workers, ranging in mass from about 150 to 90 mg, showed about 1 to 3°C lower thorax temperatures. This coincided with a steep increase of cooling constants at a fresh mass below 200 mg.

These results of bees, beetles and moths are partly in agreement with our results of wasps. However, from our analysis of own and literature data (Heinrich, 1984; Coelho and Ross, 1996) we obtained no simple linear correlation between $T_{th}$ and body mass (Fig. 4) as shown in the solitary tropical bee Anthophora by Stone (Stone, 1993a). Even a double logarithmic plot does not show a linear relationship as shown in a comparison of 55 species of bees by Stone and Willmer (Stone and Willmer, 1989). Extrapolation of curves of Fig. 4 to body masses below 50 mg suggests a critical mass of about 40 to 50 mg for a pronounced endothermic performance to be also valid for wasps. However, all vespine wasps investigated so far were heavier than $\sim$50 mg. The $V$. maculifrons (Coelho and Ross, 1996) with a mean weight of $\sim$53 mg has the lowest thorax temperature especially at low ambient temperatures (Fig. 4, 10°C and 20°C). With increasing mass the $T_{th}$ increases to a plateau at $M_b$ $\sim$180 mg. Above this value occurs no appreciable increase in $T_{th}$ between the intermediate species ($D$. maculata with $M_b$ = 185.5 mg) (Heinrich, 1984) and the largest species ($V$. crabo with $M_b$ = 477.5 mg).

In contrast to these findings there are investigations with results deviating from the expected size-related patterns. Kovac et al. reported in water foraging wasps (Vespinae and Polistinae) a great difference in their thermoregulatory behaviour (Kovac et al., 2009). At moderate $T_a$ (22 to 28°C) Vespuila exhibited distinctly higher thoracic temperatures (mean $T_{th}$ 35.5–37.5°C) than Polistes (mean $T_{th}$ 28.5–35.5°C). Polistinae showed only a weak endothermic activity, despite their larger size and body mass. In honeybees Heinrich found two races of Apis mellifera, A. m. adansonii and A. m. mellifera, to have the same average thorax temperature excess, even though A. m. mellifera is about
30% larger in mass than *A. m. adansonii* (Heinrich, 1979). Dyer and Seeley made an interspecific comparison of endothermy in honeybees (*Apis*) arriving at the nest (Dyer and Seeley, 1987). The smallest species, *A. florea*, showed the lowest thorax temperature excess above ambient air, but the intermediate-sized *A. cerana* and *A. mellifera* both showed a higher excess temperature than the largest species, *A. dorsata*. They found that the rate of passive convective heat loss from the thorax scales linearly and inversely with body size in the four species and there was no anatomical evidence for differences in efficiency with which heat flow from the thorax to the abdomen may be restricted. Dyer and Seeley reported that wing-loading was disproportionately high in *A. cerana* and *A. mellifera* relative to *A. dorsata* and *A. florea* (Dyer and Seeley, 1987). A higher $T_{th}$ in flight may be necessary to improve muscular efficiency (Coelho, 1991), and this way compensate for the higher wing loading. Such parameters could also be responsible for the small differences in flight $T_{th}$ of the vespine wasps.

Concluding we can say that thermoregulation in vespine wasps depends on body mass, but not in a simple linear relation. The great variability in the $T_{th}$ especially in the smaller sized wasps, confirms a statement of Dyer and Seeley: “… general scaling relationships based on body mass alone may fail to predict qualitative physiological differences even within a closely related group of species” (Dyer and Seeley, 1987).

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Competing Interests

The authors have no competing interests to declare.

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