

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

Helmut Kovac\* and Anton Stabentheiner

Institut für Zoologie, Karl-Franzens-Universität Graz, Universitätsplatz 2, A-8010 Graz, Austria

\*Author for correspondence (he.kovac@uni-graz.at)

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## 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 ( $T_a$ :  $\sim 0$ – $40^\circ\text{C}$ ) where the insects exhibited foraging flights.

Despite the great difference in body weight of *Vespula* (*V. vulgaris*:  $84.1 \pm 19.0$  mg, *V. germanica*:  $74.1 \pm 9.6$  mg) and *Vespa* ( $477.5 \pm 59.9$  mg), they exhibited similarities in the dependence of thorax temperature on  $T_a$  on their arrival (mean  $T_{th} = 30$ – $40^\circ\text{C}$ ) and departure (mean  $T_{th} = 33$ – $40^\circ\text{C}$ ) at the nest entrance. However, the hornets' thorax temperature was up to  $2.5^\circ\text{C}$  higher upon arrival and up to  $3^\circ\text{C}$  lower at departure. The thorax temperature excess

( $T_{th} - T_a$ ) above ambient air of about  $5$ – $18^\circ\text{C}$  indicates a high endothermic capacity in both hornets and wasps. Heat gain from solar radiation elevated the temperature excess by up to  $1^\circ\text{C}$ . 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  $T_{th}$  on the body mass in species weighing less than about 200 mg.

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Key words: Hornet, Wasp, Size, Thermoregulation, Body temperature

## 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 Stabentheiner, 1999; Kovac et al., 2009). In Central Europe, social wasps have a long breeding 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, 1981; Heinrich and Heinrich, 1983; Heinrich, 1993). A positive relationship between thermoregulatory capability and body size was observed 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.

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

Measurements 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 ( $T_a$ :  $\sim 0$ – $40^\circ\text{C}$ ) 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 bit 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 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 ( $\sim 5$  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 fight 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, ThermoCam 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 temperature and emissivity (Stabentheiner and Schmaranzer, 1987; Schmaranzer and Stabentheiner, 1988; Stabentheiner et al., 2012). Thermographic data were stored on a VHS videorecorder at 25 frames  $\text{s}^{-1}$  with the AGA 782 SW, digitally with 14 bit resolution on a portable computer (DOLCH Flexpac-400-XG, Munich, Germany) at a rate of 3–5 frames  $\text{s}^{-1}$  with the SC2000, or digitally (14 bit) on the internal memory card of the i60. The ambient air temperature ( $T_a$ ) was measured with thermocouples near the insects ( $\sim 3$  cm). Thermocouple measurements were corrected for errors caused by solar radiation according to Stabentheiner et al. (Stabentheiner et al., 2012). The solar radiation was measured with a miniature global radiation sensor (FLA613-GS mini spezial, AHLBORN, Holzkirchen,

Germany). The temperature and radiation data were stored every second with ALMEMO data loggers (AHLBORN, Holzkirchen, Germany).

For determination of the body weight, from each colony insects leaving the nest were captured and weighed with a balance to the nearest 0.1 mg (AB104, METTLER-TOLEDO, Greifensee, Switzerland).

### Data evaluation and statistics

The surface temperature of head ( $T_{hd}$ ), thorax ( $T_{th}$ ) and abdomen ( $T_{ab}$ ) 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). Because the SC2000 and i60 infrared cameras work in the long-wave infrared range (7.5–13  $\mu\text{m}$ ) the reflected solar radiation from the wasps' cuticle produced only a small measurement error ( $0.218^\circ\text{C}$  for  $1000 \text{ Wm}^{-2}$ ), which was compensated for (Stabentheiner et al., 2012). In this way we reached an accuracy of  $0.7^\circ\text{C}$  for the insect body surface temperature at a sensitivity of  $0.1^\circ\text{C}$ .

The temperature gradient between the thorax and the ambient air (thorax temperature excess =  $T_{thorax} - T_a$ ) was used as a measure to assess the insects' endothermic capability. To evaluate the influence of the radiative heat gain on the body temperature three classes of solar radiation were established, shade:  $<200 \text{ Wm}^{-2}$ , overcast sky:  $200$ – $500 \text{ Wm}^{-2}$ , and sunshine:  $>500 \text{ Wm}^{-2}$ . For comparing our results of returning insects with results of Heinrich (Heinrich, 1984) and Coelho and Ross (Coelho and Ross, 1996), means or single values of their data were digitized and appropriate functions were fitted.

Activity and behaviour of the hornets at the nest entrance were classified from the infrared video sequences. Means reported for leaving, arriving and foraging insects are average values derived from the fitted regression lines, means of the different hornet activities are calculated means  $\pm$  SD. The relationship between body temperature, temperature excess and ambient temperature ( $T_a$ ) was described by linear, exponential or polynomial regression functions and tested with ANOVA if possible (comparing linear regressions). Data analysis and statistics were performed by using the Statgraphics package (Statistical Graphics Corporation, Warrenton, Virginia) and ORIGIN software (OriginLab Corporation, Northampton, Massachusetts).

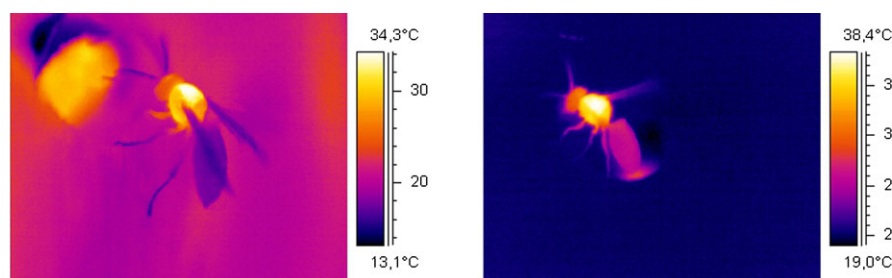
## Results

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

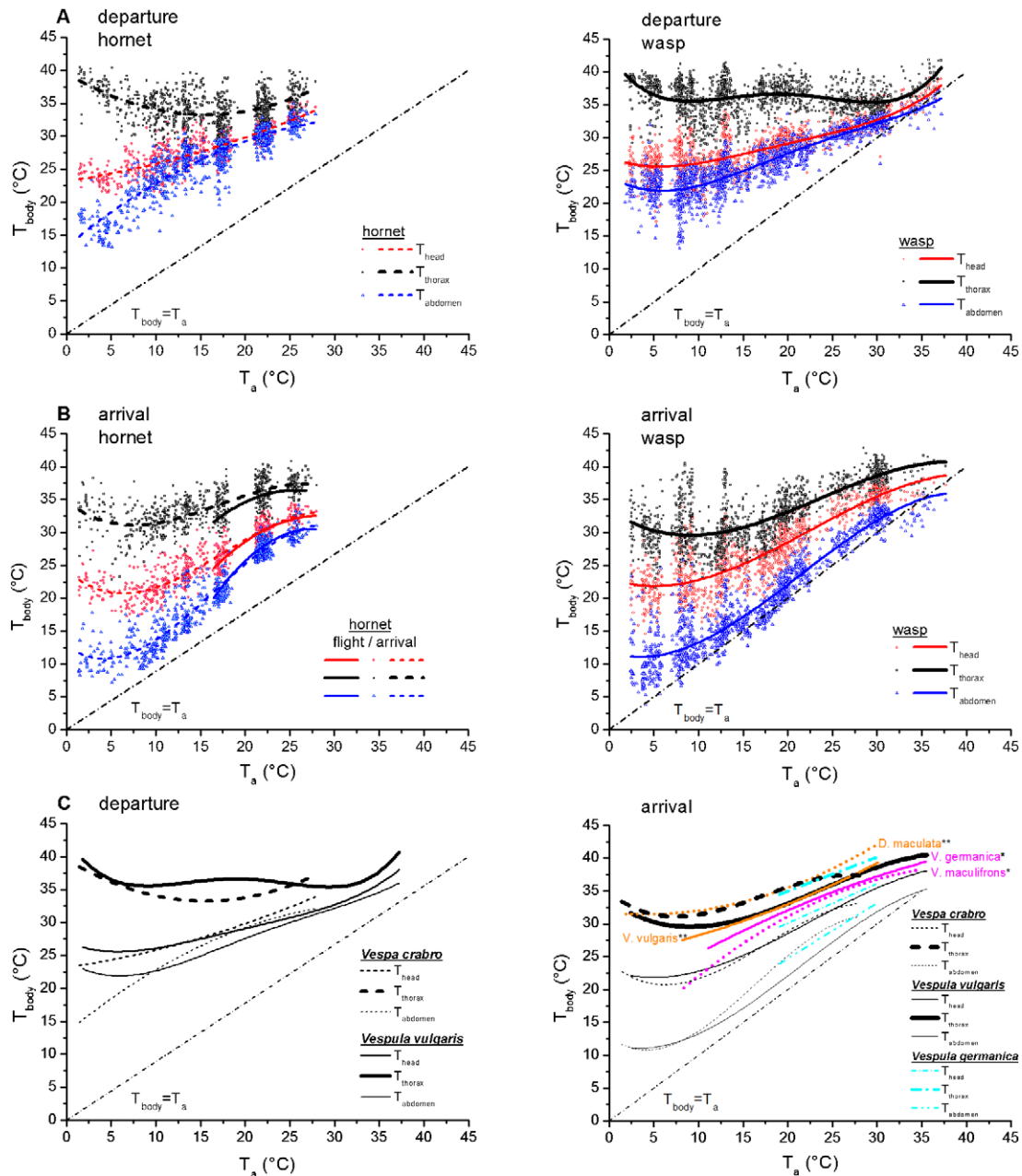
### Departure and arrival measured in shade

#### Departure

Ambient air temperature ( $T_a$ ) in shade during measuring periods ranged from  $\sim 1$  to  $38^\circ\text{C}$  (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



**Fig. 1. Infrared thermograms of a hornet (left) and a wasp (right) at the nest entrance.** Hornet:  $T_a = 15.6^\circ\text{C}$ ,  $T_{head} = 25.8$ ,  $T_{thorax} = 34.3$ ,  $T_{abdomen} = 17.9^\circ\text{C}$ . Wasp:  $T_a = 20.4^\circ\text{C}$ ,  $T_{head} = 30.0$ ,  $T_{thorax} = 38.1$ ,  $T_{abdomen} = 26.0^\circ\text{C}$ .



**Fig. 2.** Surface temperature of thorax, head and abdomen of hornets and wasps in dependence on ambient temperature ( $T_a$ ). (A) Departure at the nest entrance. (B) Arrival at the nest entrance and hornets' flight (left). (C) Comparison of hornets and wasps during departure (left) and arrival (right). Additional regression lines of arrival thorax temperatures from Heinrich (\*\*), and Coelho and Ross (\*) are displayed (Heinrich, 1984; Coelho and Ross, 1996). Equations for linear and non-linear regressions, number of observations and regression statistics are in Table 2.

best with a polynomial regression:

$$T_{\text{body}} = A + B1 \cdot T_a + B2 \cdot T_a^2 \quad (1)$$

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  $T_a = 15^\circ\text{C}$ , and increased again to 36.7°C at  $T_a = 27^\circ\text{C}$ . 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  $T_a = 15^\circ\text{C}$ , 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  $T_a = 2^\circ\text{C}$  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  $T_a = 2^\circ\text{C}$  to 37.7°C at  $T_a = 37^\circ\text{C}$ . 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<sub>a</sub>) 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 <sub>head</sub> (°C)	T <sub>thorax</sub> (°C)	T <sub>abdomen</sub> (°C)	T <sub>a</sub> (°C)	sol.rad.(Wm <sup>-2</sup> )
departure	1210/1210	29.2±3.3	34.5±2.4	27.6±4.7	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	30.8±6.3	25.4±5.0	14.3±4.9	344.9±294.4
bask	100/382	28.0±8.2	31.8±9.5	25.3±7.0	13.5±5.3	118.0±274.6
fight	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<sub>a</sub>) at departure, arrival and flight at the nest entrance. R<sup>2</sup> = coefficient of regression, P = probability, N = number of measurements.**

body part	equations	R <sup>2</sup>	P	N
departure <i>V. crabro</i>				
thorax	T <sub>th</sub> =39.58031-0.81505 *T <sub>a</sub> +0.02625*T <sub>a</sub> <sup>2</sup>	0.21666	<0.0001	862
head	T <sub>hd</sub> =23.18457+0.19641*T <sub>a</sub> +0.00677*T <sub>a</sub> <sup>2</sup>	0.73377	<0.0001	859
abdomen	T <sub>ab</sub> =13.30622+1.10879*T <sub>a</sub> -0.01559*T <sub>a</sub> <sup>2</sup>	0.81289	<0.0001	853
departure <i>V. vulgaris</i>				
thorax	T <sub>th</sub> =42.86411-2.13183*T <sub>a</sub> +0.21115*T <sub>a</sub> <sup>2</sup> -0.00815*T <sub>a</sub> <sup>3</sup> -0.0001*T <sub>a</sub> <sup>4</sup>	0.09069	<0.0001	1537
head	T <sub>hd</sub> =27.16308-0.62231*T <sub>a</sub> +0.0741*T <sub>a</sub> <sup>2</sup> -0.00258*T <sub>a</sub> <sup>3</sup> -0.00003*T <sub>a</sub> <sup>4</sup>	0.61364	<0.0001	1530
abdomen	T <sub>ab</sub> =24.37649-0.94879*T <sub>a</sub> +0.10757*T <sub>a</sub> <sup>2</sup> -0.00334*T <sub>a</sub> <sup>3</sup> +0.00003*T <sub>a</sub> <sup>4</sup>	0.78535	<0.0001	1514
arrival <i>V. crabro</i>				
thorax	T <sub>th</sub> =34.72990-1.06338*T <sub>a</sub> +0.09052*T <sub>a</sub> <sup>2</sup> -0.00176*T <sub>a</sub> <sup>3</sup>	0.50738	<0.0001	680
head	T <sub>hd</sub> =24.23205-1.18979*T <sub>a</sub> +0.11446*T <sub>a</sub> <sup>2</sup> -0.00217*T <sub>a</sub> <sup>3</sup>	0.84548	<0.0001	656
abdomen	T <sub>ab</sub> =12.74708-0.97564*T <sub>a</sub> +0.13389*T <sub>a</sub> <sup>2</sup> -0.00270*T <sub>a</sub> <sup>3</sup>	0.91528	<0.0001	680
flight <i>V. crabro</i>				
thorax	T <sub>th</sub> = -1.23285+2.93678*T <sub>a</sub> -0.05726*T <sub>a</sub> <sup>2</sup>	0.59421	<0.0001	118
head	T <sub>hd</sub> = -12.28619+3.14835*T <sub>a</sub> -0.09052*T <sub>a</sub> <sup>2</sup>	0.79518	<0.0001	118
abdomen	T <sub>ab</sub> = -34.68555+4.73844*T <sub>a</sub> -0.08613*T <sub>a</sub> <sup>2</sup>	0.83691	<0.0001	118
arrival <i>V. vulgaris</i>				
thorax	T <sub>th</sub> =33.58973-0.96143*T <sub>a</sub> +0.06537*T <sub>a</sub> <sup>2</sup> -0.00092*T <sub>a</sub> <sup>3</sup>	0.56570	<0.0001	1302
head	T <sub>hd</sub> =23.00846-0.4795*T <sub>a</sub> +0.05357*T <sub>a</sub> <sup>2</sup> -0.00079*T <sub>a</sub> <sup>3</sup>	0.76378	<0.0001	1259
abdomen	T <sub>ab</sub> =11.79295-0.4341*T <sub>a</sub> +0.06886*T <sub>a</sub> <sup>2</sup> -0.00107*T <sub>a</sub> <sup>3</sup>	0.88601	<0.0001	1296
arrival <i>V. germanica</i>				
thorax	T <sub>th</sub> =27.90989+0.37905*T <sub>a</sub>	0.45182	<0.0001	377
head	T <sub>hd</sub> =21.07564+0.47865*T <sub>a</sub>	0.54369	<0.0001	377
abdomen	T <sub>ab</sub> =14.63780+0.54881*T <sub>a</sub>	0.60703	<0.0001	377

best with a polynomial regression (T<sub>a</sub> ranging from ~1 to 40°C) (Fig. 2B; Table 2):

$$T_{\text{body}} = A + B1 \cdot T_a + B2 \cdot T_a^2 + B3 \cdot T_a^3 \quad (2)$$

This equation fitted the data better than Eqn 1. The hornets' average T<sub>th</sub> after arrival was ~0 to 2.5°C higher than that of *V. vulgaris* (Fig. 2). Their T<sub>th</sub> decreased from ~34°C to ~31°C as T<sub>a</sub> increased from 1°C to 10°C, and increased continuously at higher T<sub>a</sub>. It reached 37.5°C when it was warm (T<sub>a</sub> = 27°C). The

T<sub>th</sub> of *V. vulgaris* upon arrival decreased from ~32 to 30°C in the lowest range of T<sub>a</sub> (1–10°C) and, like in the hornets, increased continuously at higher T<sub>a</sub>. The T<sub>th</sub> reached 40.7°C when T<sub>a</sub> was 37°C. *V. germanica* regulated the T<sub>th</sub> at a similar level as the hornets (T<sub>th</sub> = 34.5–40.1°C; T<sub>a</sub> = 20–30°C) (Fig. 2C). The hornets' T<sub>hd</sub> was ~22.8°C at low T<sub>a</sub> (1–10°C) and increased continuously to 33.0°C at high T<sub>a</sub> (27°C). The T<sub>hd</sub> of *V. vulgaris* was 22.2°C at low T<sub>a</sub> (1–10°C) and increased to 38.6°C at very high T<sub>a</sub> (37°C). The T<sub>ab</sub> of both hornets and wasps depended strongly on ambient air temperature. It was ~2 to 5°C higher than



$T_a$ . 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  $T_{hd}$  of the hornets resembled that of the wasps. The  $T_{ab}$  of the hornets, however, was similar to or warmer than that of the wasps (difference: ~0–3°C) (Fig. 2C).

#### Flight

The  $T_{th}$  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

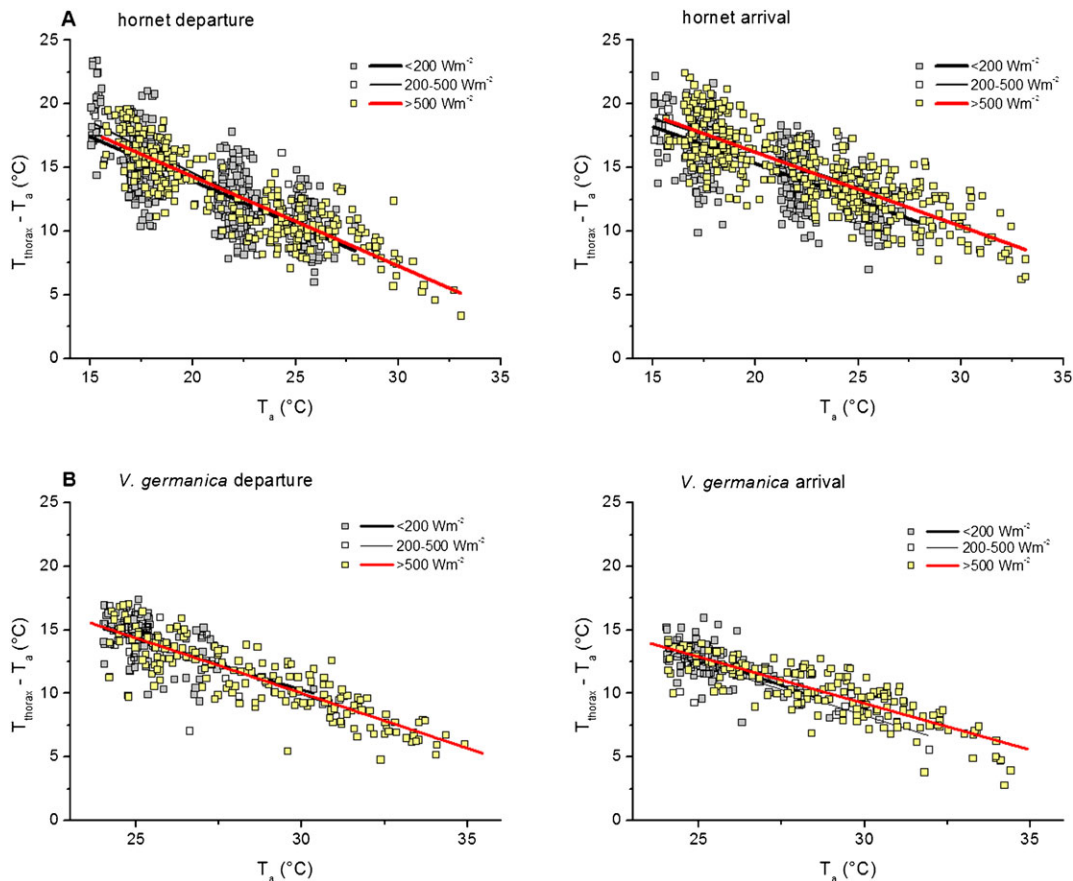
The hornets and wasps were always endothermic at departure and arrival, i.e. their thorax was clearly elevated above the ambient air. The thorax temperature excess depended strongly on  $T_a$  ( $T_{th} - T_a \sim 3\text{--}38^\circ\text{C}$ ) (Fig. 2, Fig. 3; Table 3). To quantify the influence of solar 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:  $< 200 \text{ Wm}^{-2}$ , sunshine:  $> 500 \text{ Wm}^{-2}$ ).

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  $T_{th} - T_a$  in dependence on  $T_a$  revealed significant differences ( $P < 0.0001$ , DF = 3, F-Ratio = 469.38,  $n = 788$ ). The difference in  $T_{th} - T_a$  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 ( $T_{th} - T_a \sim 0\text{--}0.3^\circ\text{C}$ ). 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 ( $T_{th} - T_a \sim 0\text{--}0.7^\circ\text{C}$ ; 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  $T_{th}$  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



**Fig. 3.** Thorax temperature excess ( $T_{th} - T_a$ ) of hornets (*Vespa crabro*) and wasps (*Vespa germanica*) in dependence on ambient temperature ( $T_a$ ) during departure (left) and arrival (right) at the nest entrance. (A) hornets, (B) wasps. Equations of linear regressions, number of observations and regression statistics are in Table 3.

**Table 3. Equations of regressions for the thorax temperature ( $T_{th}-T_a$ ) excess of hornets and *Vespa germanica* (Fig. 3) in dependence on ambient temperature ( $T_a$ ) and solar radiation (sol.rad.) at departure and arrival at the nest entrance.  $R^2$  = coefficient of regression, N = number of measurements.**

sol.rad. ( $Wm^{-2}$ )	equations	$R^2$	P	N
departure <i>V. crabro</i>				
<200	$T_{th}-T_a=27.79163-0.69307*T_a$	0.53978	<0.0001	474
200-500	$T_{th}-T_a=30.68420-0.80536*T_a$	0.57439	<0.0001	27
>500	$T_{th}-T_a=28.29469-0.70065*T_a$	0.76827	<0.0001	314
arrival <i>V. crabro</i>				
<200	$T_{th}-T_a=26.91714-0.58039*T_a$	0.47514	<0.0001	361
200-500	$T_{th}-T_a=27.01601-0.54166*T_a$	0.54114	<0.0001	34
>500	$T_{th}-T_a=27.82557-0.58130*T_a$	0.67363	<0.0001	404
departure <i>V. germanica</i>				
<200	$T_{th}-T_a=34.36011-0.80248*T_a$	0.23492	<0.0001	69
200-500	$T_{th}-T_a=37.63352-0.92471*T_a$	0.48254	<0.0001	48
>500	$T_{th}-T_a=36.05900-0.8681*T_a$	0.75926	<0.0001	177
arrival <i>V. germanica</i>				
<200	$T_{th}-T_a=35.34753-0.89893*T_a$	0.33251	<0.0001	73
200-500	$T_{th}-T_a=32.78261-0.81732*T_a$	0.74751	<0.0001	35
>500	$T_{th}-T_a=31.17292-0.73181*T_a$	0.71277	<0.0001	174

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  $T_{th}$  was fitted with exponential functions in dependence on body mass for three  $T_a$ s (10, 20, 30°C).

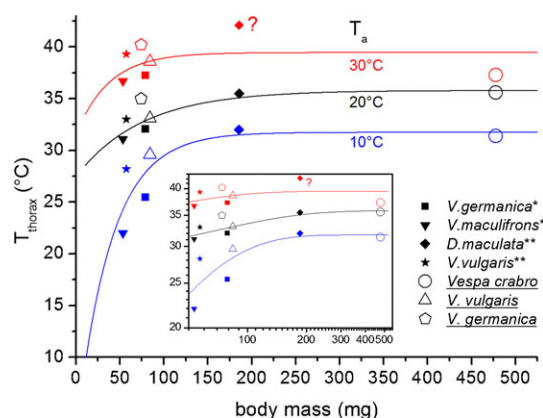
For 10 and 20°C:

$$T_{thorax} = y_0 + A \cdot \exp(B \cdot \text{body mass}) \quad (3)$$

For 30°C:

$$T_{thorax} = y_0 + A \cdot \exp(-\text{body mass}/t_1) + B \cdot \exp(-\text{body mass}/t_2) \quad (4)$$

A dependence of the  $T_{th}$  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,



**Fig. 4. Thorax temperature in dependence on body mass of hornets (*Vespa crabro*) and wasps (*Vespa vulgaris* and *Vespa germanica*) and other vespine wasps of Heinrich (\*\*), and Coelho and Ross (\*) (Heinrich, 1984; Coelho and Ross, 1996). Value with “?” is estimated by extrapolation. Insert: logarithmic scaling. Equations of regressions, number of observations and regression statistics are in Table 4.**

had a somewhat lower  $T_{th}$  than *Dolichovespula maculata* with a medium body mass of 185.5 mg (Heinrich, 1984). The  $T_{th}$  values of the other wasps were mostly below that of *D. maculata* and *V. crabro*. For statistical details see Table 4.

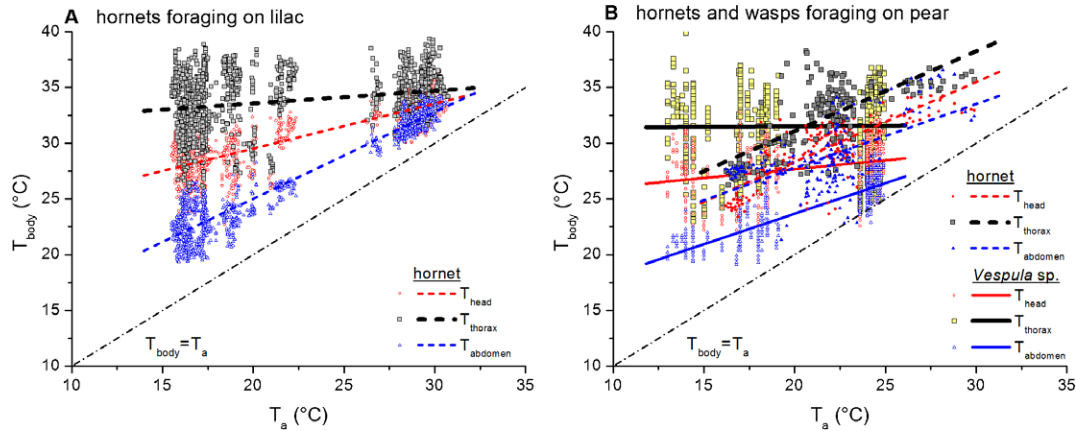
#### Foraging and other activities

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  $T_{th}$  was regulated nearly independent of  $T_a$  ( $T_a = 15^\circ\text{C}$ :  $T_{th} = 33.0^\circ\text{C}$ ;  $T_a = 30^\circ\text{C}$ :  $T_{th} = 34.7^\circ\text{C}$ ). The head was cooler and exhibited a stronger dependence on  $T_a$  ( $T_a = 15^\circ\text{C}$ :  $T_{hd} = 27.6^\circ\text{C}$ ;  $T_a = 30^\circ\text{C}$ :  $T_{hd} = 33.6^\circ\text{C}$ ). The abdomen was the coolest body part. It was  $\sim 3$  to  $5^\circ\text{C}$  warmer than  $T_a$ . The temperature increased nearly parallel to  $T_a$  ( $T_a = 15^\circ\text{C}$ :  $T_{ab} = 21.2^\circ\text{C}$ ;  $T_a = 30^\circ\text{C}$ :  $T_{ab} = 32.9^\circ\text{C}$ ).

By contrast, foraging hornets on pears exhibited a strong dependence of all body parts on  $T_a$  (Fig. 5B, regression lines; Table 5). The thorax was the warmest body part ( $T_a = 15^\circ\text{C}$ :  $T_{th} = 27.5^\circ\text{C}$ ;  $T_a = 30^\circ\text{C}$ :  $T_{th} = 38.0^\circ\text{C}$ ), followed by the head ( $T_a = 15^\circ\text{C}$ :  $T_{hd} = 24.8^\circ\text{C}$ ;  $T_a = 30^\circ\text{C}$ :  $T_{hd} = 35.5^\circ\text{C}$ ), and the abdomen ( $T_a = 15^\circ\text{C}$ :  $T_{ab} = 24.9^\circ\text{C}$ ;  $T_a = 30^\circ\text{C}$ :  $T_{ab} = 33.5^\circ\text{C}$ ). However, wasps foraging on pears showed no dependence of  $T_{th}$  on  $T_a$  ( $T_a = 13^\circ\text{C}$ :  $T_{th} = 31.5^\circ\text{C}$ ;  $T_a = 25^\circ\text{C}$ :  $T_{th} = 31.6^\circ\text{C}$ ). A weak dependence on  $T_a$  was measured in  $T_{hd}$  ( $T_a = 13^\circ\text{C}$ :  $T_{hd} =$

**Table 4. Equations of regressions for the thorax temperature ( $T_{th}$ ) of hornets and wasps (Fig. 4) in dependence on body mass for three ambient temperatures ( $T_a$ ).  $R^2$  = coefficient of regression, N = number of measurements.**

$T_a$ (°C)	equations	$R^2$	P	N
10	$T_{th} = 31.75396 - 29.1466^{-0.02551} \cdot \text{body mass}$	0.68137	<0.001	6
20	$T_{th} = 35.80331 - 8.32914^{-0.01324} \cdot \text{body mass}$	0.85670	<0.0001	7
30	$T_{th} = 39.46219 - 3.95754^{(-\text{body mass}/37.41529)}$ $- 3.95754^{(-\text{body mass}/37.41529)}$	0.16207	0.0720	7



**Fig. 5.** Temperature of thorax, head and abdomen of hornets (*Vespa crabro*) and wasps (*Vespula* sp.) foraging from natural sources in dependence on ambient temperature ( $T_a$ ). (A) Hornets foraging on lilac. (B) Hornets and wasps foraging on pear. Equations of linear regressions, number of observations and regression statistics are in Table 5.

26.6°C;  $T_a = 25^\circ\text{C}$ :  $T_{hd} = 28.5^\circ\text{C}$ ), and a strong dependence on  $T_a$  in  $T_{ab}$  ( $T_a = 13^\circ\text{C}$ :  $T_{ab} = 19.9^\circ\text{C}$ ;  $T_a = 25^\circ\text{C}$ :  $T_{ab} = 26.4^\circ\text{C}$ ).

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  $\sim 2.5^\circ\text{C}$  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				
thorax	$T_{th} = 31.32101 + 0.11260 * T_a$	0.06176	<0.0001	1312
head	$T_{hd} = 21.46458 + 0.40305 * T_a$	0.66458	<0.0001	1312
abdomen	$T_{ab} = 9.49536 + 0.77635 * T_a$	0.91605	<0.0001	1312
hornet pear				
thorax	$T_{th} = 16.71841 + 0.71806 * T_a$	0.49876	<0.0001	190
head	$T_{hd} = 13.99229 + 0.71671 * T_a$	0.60759	<0.0001	190
abdomen	$T_{ab} = 16.28067 + 0.57452 * T_a$	0.35836	<0.0001	190
wasp pear				
thorax	$T_{th} = 31.29097 + 0.01136 * T_a$	0.00018	0.66117	1077
head	$T_{hd} = 24.49777 + 0.15877 * T_a$	0.07172	<0.0001	1076
abdomen	$T_{ab} = 12.71658 + 0.54804 * T_a$	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  $\sim 31.5^\circ\text{C}$ ) was regulated constantly high and nearly independent from  $T_a$  (Fig. 5B). By contrast, the hornets'  $T_{th}$  (mean  $\sim 28$  to  $38^\circ\text{C}$ ) showed a strong increase with  $T_a$ . On the other hand, the  $T_{th}$  of hornets foraging on lilac (mean  $\sim 33$  to  $35^\circ\text{C}$ ) 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  $37.2^\circ\text{C}$ ) (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  $T_a$ s. The result revealed a significant 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  $T_a = 22^\circ\text{C}$  (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  $3^\circ\text{C}$  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,  $10^\circ\text{C}$  and  $20^\circ\text{C}$ ). 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. crabro* 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  $28^\circ\text{C}$ ) *Vespula* exhibited distinctly higher thoracic temperatures (mean  $T_{th}$   $35.5$ – $37.5^\circ\text{C}$ ) than *Polistes* (mean  $T_{th}$   $28.5$ – $35.5^\circ\text{C}$ ). *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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