



Thermoregulation of water foraging wasps (*Vespula vulgaris* and *Polistes dominulus*)

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ABSTRACT

A comparison of the thermoregulation of water foraging wasps (*Vespula vulgaris*, *Polistes dominulus*) under special consideration of ambient temperature and solar radiation was conducted. The body surface temperature of living and dead wasps was measured by infrared thermography under natural conditions in their environment without disturbing the insects' behaviour. The body temperature of both of them was positively correlated with T_a and solar radiation. At moderate T_a (22–28 °C) the regression lines revealed mean thorax temperatures (T_{th}) of 35.5–37.5 °C in *Vespula*, and of 28.6–33.7 °C in *Polistes*. At high T_a (30–39 °C) T_{th} was 37.2–40.6 °C in *Vespula* and 37.0–40.8 °C in *Polistes*. The thorax temperature excess ($T_{th}-T_a$) increased at moderate T_a by 1.9 °C (*Vespula*) and 4.4 °C (*Polistes*) per $\text{kW}^{-1} \text{m}^{-2}$. At high T_a it increased by 4.0 °C per $\text{kW}^{-1} \text{m}^{-2}$ in both wasps. A comparison of the living water foraging *Vespula* and *Polistes* with dead wasps revealed a great difference in their thermoregulatory behaviour. At moderate T_a (22–28 °C) *Vespula* exhibited distinct endothermy in contrast to *Polistes*, which showed only a weak endothermic activity. At high T_a (30–39 °C) *Vespula* reduced their active heat production, and *Polistes* were always ectothermic. Both species exhibited an increasing cooling effort with increasing insolation and ambient temperature.

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1. Introduction

The capability of endothermic heat production by means of the thoracic flight muscles has been developed by several insect groups. Flying insects with the ability to elevate their thorax temperature above ambient air temperature can forage with some independence of the thermal environment (Heinrich and Heinrich, 1983). During resource collection, foraging endothermic insects have high energetic costs because flight muscles must achieve a minimum threshold temperature (e.g. Heinrich, 1979; Harrison and Hall, 1993; Harrison et al., 1996; Coelho and Ross, 1996; Kovac and Schmaranzer, 1996; Woods et al., 2005). The foraging strategies of social insects balance the energy expenditure of individual foragers with the net energetic gains to the colony (Seeley et al., 1991). For example, the value of carbohydrates (sucrose concentration) influences foraging behaviour and thermoregulation of bees and wasps. The foragers can minimize thermoregulatory costs during foraging by varying their thorax temperature in response to the carbohydrate content of the food source (Dyer and Seeley, 1987; Schmaranzer and Stabentheiner, 1988; Waddington, 1990; Stabentheiner and Hagmüller, 1991; Underwood, 1991; Kovac and Stabentheiner, 1999; Stabentheiner,

2001; Nieh and Sanchez, 2005; Nieh et al., 2006). Water collection does not provide a gain in energy. At first sight there is just energy expenditure. However, it is nevertheless essential for the survival of the colonies during heat stress. Wasps use water in conjunction with wing fanning for evaporative cooling of the nest (Steiner, 1930; Weyrauch, 1936; Akre, 1982; Greene, 1991) and in this way prevent overheating of the nest that could result in damage to the brood. In addition, they need water for providing their larvae or for processing plant fibre material for nest construction (Jeanne, 1996).

Variation in ambient air temperature can greatly affect the energy expended by foragers to maintain their flight threshold temperature. Thus, some wasps and bees alter their metabolic or activity rates to respond to changes in ambient temperature (Heinrich, 1993). The ability to regulate above ambient temperature and maintain a positive relationship between ambient and body temperature is a form of thermoregulation (Coelho and Ross, 1996).

Beside the ambient air temperature the influence of solar radiation on insect thermoregulation is not negligible. The effect of solar radiation on body temperature has been investigated in the Western honeybee (Heinrich, 1979) and Indian honeybees (Underwood, 1991) and in wasps of the subfamily Vespinae in a small range of ambient temperatures (Stabentheiner et al., 2004). These measurements showed that part of the heat gained from the sun is used to increase the insects' thorax temperature. Foragers can minimize the thermoregulatory costs and nevertheless keep flight muscle temperature at a high level.

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Concerning Central European wasps (Vespidae) two different strategies of individual thermoregulation seem to exist. The members of the subfamily Vespinae are known to have thermoregulatory abilities comparable to those of the honeybee. They are capable of intense endothermy and modulate their body temperature during food collection. They use this ability to keep their body temperature well above the ambient level to increase foraging efficiency (Heinrich, 1984; Stabentheiner and Schmaranzer, 1987; Kovac and Stabentheiner, 1993, 1999; Coelho and Ross, 1996; Eckles et al., 2008) and to regulate the temperature of their nests (Himmer, 1932; Ishay and Ruttner, 1971; Ishay, 1973; Gibo et al., 1974; Makino and Yamane, 1980; Martin, 1988; Klingner et al., 2005; Klingner et al., 2006). In contrast to the Vespinae, very little is known about the individual thermoregulation of the Polistinae. Preliminary measurements suggested that they are not or only weakly endothermic during their foraging trips on natural food sources (Kovac and Stabentheiner, 2001). Water foraging Polistinae have not yet been investigated. The purpose of this study was to give a comprehensive comparison of the thermoregulatory behaviour of Vespinae and Polistinae during water foraging, with special consideration of the influence of the environmental factors ambient air temperature and solar radiation.

2. Materials and methods

2.1. Animals, field site and measuring conditions

Measuring location was an orchard on a farm in Gschwendt/Austria, middle Europe. On 5 days in 2 different years we investigated wasps (*Vespula vulgaris* and *Polistes dominulus*) foraging water on a rainwater barrel. In order not to impair their behaviour during foraging we refrained from marking the individuals. We presume at least about 15–20 water collecting individuals of *Vespula* and about 5–10 individuals of *Polistes* to be included in this study. One of the measuring days in August 2003 was one of the hottest days of the year, with ambient air temperatures (T_a) above 30 °C (~30–40 °C). On the other days we had moderate temperatures in the range of ~20–30 °C. In addition to water foragers, Polistine wasps foraging nectar on raspberry and gathering sap on rhubarb, and another Vespine wasp, *Dolichovespula saxonica*, also foraging nectar on raspberry blossoms were measured for comparison.

2.2. Measurements

The wasps were filmed during their complete foraging stay at the water barrel with an infrared camera (ThermaCam SC2000 NTS, FLIR) without disturbing them. The infrared camera was

calibrated periodical by slotting in a self-constructed peltier driven reference source or an AGA1010 reference radiator of known temperature and emissivity (for details of calibration see Stabentheiner and Schmaranzer, 1987; Schmaranzer and Stabentheiner, 1988). Thermographic data were stored digitally with 14 bit resolution on a portable computer (DOLCH Flexpac-400-XG) at a rate of 3–5 frames s^{-1} . *Dolichovespula* and *Polistes* foraging nectar and plant sap were measured solely in the shade at a rate of 25 frames s^{-1} because the infrared camera AGA 782 SW, which we used at that time, was not appropriate for measurements in the sunshine.

To take into consideration the effects of ambient air temperature, solar radiation and air convection on the measurement site, we determined the insects' operative (environmental) temperature (T_e ; Bakken, 1976, 1980, 1992; Bishop and Armbruster, 1999). Freshly killed dead wasps (*Vespula* and *Polistes*) were fixed with needles on their wings about 1 cm above a wooden board beside the foraging wasps and measured simultaneously with them. During the measurements there were only a few foraging *Polistes* at the barrel, thus we did not catch and kill any for estimating the T_e . We fetched these measurements of the T_e at a later time with two individuals of *Polistes* in comparison with two *Vespula* to compensate for possible differences of air convection and other micro climatic effects between measurement days (Fig. 1B).

The ambient air temperature (T_a) was measured near the foraging and dead wasps with NTC-sensors or thermocouples. The solar radiation was measured with a Dirmhirm-global radiation-pyranometer (range: 0.3–3.3 μm ; NP-42, NEO Inc.) or with a global radiation sensor (FLA613-GS mini spezial, AHLBORN) in the immediate vicinity of the insects. The temperature and radiation data were stored every 2 s with ALMEMO data loggers (AHLBORN). During body temperature calculation from the infrared thermograms they were automatically extracted from the logger files.

2.3. Data evaluation and statistics

The temperature of the three body parts, and of the water surface (in close vicinity to the spot where the wasps' mouthparts were in contact with the wet substrate), was calculated from the infrared thermograms by means of the AGEMA Research software (FLIR) controlled by a self written Excel VBA-macro (Microsoft Corporation). Values of the body temperature during foraging were taken in regular intervals of about 3 s immediately after the landing of the insects until they took off. The surface temperatures of head (T_{hd}), thorax (T_{th}) and abdomen (T_{ab}) were calculated with an infrared emissivity of 0.97, determined for the honeybee cuticle (Stabentheiner and Schmaranzer, 1987; Schmaranzer and Stabentheiner, 1988; Kovac and Stabentheiner, 1999). Because the

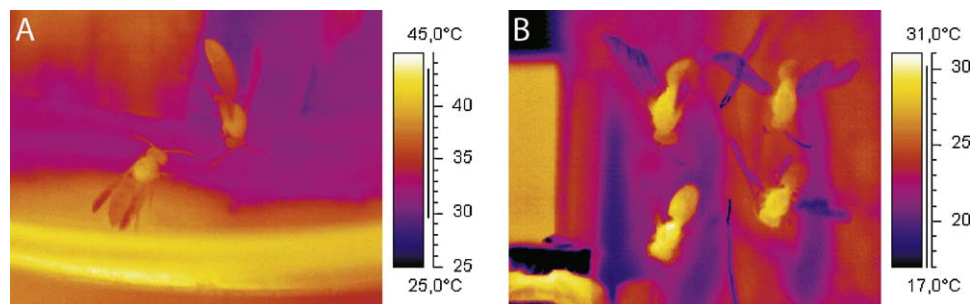


Fig. 1. Thermograms of living wasps (A) and dead wasps fixed with needles (B) beside the foraging site of the wasps (top: *Polistes*, bottom: *Vespula*). (A) At an ambient temperature of 36.1 °C the body surface temperature of the water foraging *Vespula* on the left was $T_{thorax} = 41.5$, $T_{head} = 38.8$, $T_{abdomen} = 38.6$ °C, and of the *Polistes* on the right was $T_{thorax} = 39.7$, $T_{head} = 36.7$, $T_{abdomen} = 38.8$ °C. (B) Body temperature of dead *Polistes* on top left: $T_{thorax} = 29.5$, $T_{head} = 26.1$, $T_{abdomen} = 27.6$ °C; top right: $T_{thorax} = 29.0$, $T_{head} = 27.0$, $T_{abdomen} = 26.6$ °C; dead *Vespula* on bottom left: $T_{thorax} = 30.9$, $T_{head} = 29.3$, $T_{abdomen} = 29.3$ °C; bottom right: $T_{thorax} = 29.8$, $T_{head} = 28.5$, $T_{abdomen} = 26.1$ °C at an ambient temperature of 21.6 °C. Left-hand rectangle: reference radiator; between wasps: thermocouples for measurement of T_a (their warming by sunlight was compensated for by special calibrations).

ThermaCam works in the long-wave infrared range (7.5–13 μm) the reflected radiation from the wasps' cuticle produced only a small measurement error (0.2 °C for 1000 Wm⁻²) which was compensated for. In this way we reached an accuracy of 0.7 °C for the body surface temperature of the wasps at a sensitivity of <0.1 °C.

The gradient between the thorax and the ambient temperature (thorax temperature excess = $T_{thorax} - T_a$) is often used as a measure to judge the endothermic capability of insects. In sunshine, however, this is not a reliable measure of the endogenously generated temperature excess. Therefore, we compared the living wasps' temperature excess of thorax, head and abdomen with that of the dead wasps (operative temperature excess = $\Delta(T_{body} - T_a)$ [living-dead wasps]).

The relationship between body temperature, temperature excess and T_a or solar radiation was described by simple linear regression and tested with an ANOVA. Data analysis and statistics were conducted using the Statgraphics package (Statistical Graphics Corporation) and ORIGIN software (OriginLab Corporation).

3. Results

Fig. 1A shows a thermogram of water foraging wasps (*V. vulgaris* and *P. dominulus*), and Fig. 1B of dead wasps (*V. vulgaris* and *P. dominulus*) fixed at the foraging site on a board. Body surface temperature values of head, thorax and abdomen were evaluated from 1509 thermograms for temperature curves of living wasps (Fig. 2), and 1476 thermograms were used for all body parts of dead wasps. In addition, 357 evaluated thermograms of wasps (*Dolichovespula saxonica* and *P. dominulus*) foraging nectar on raspberry and plant sap on rhubarb supplied body temperature

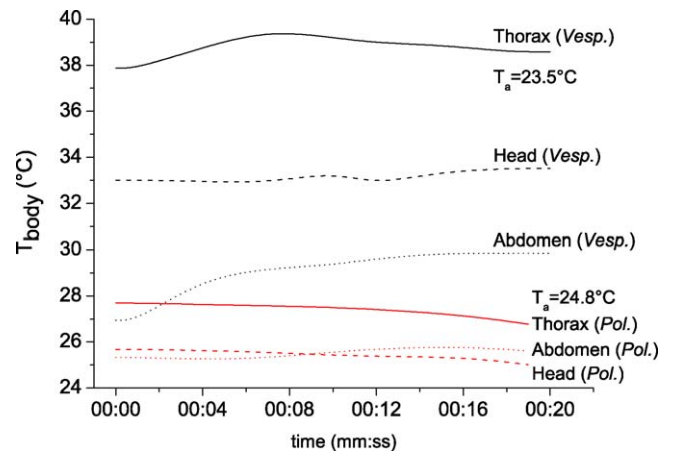


Fig. 2. Temperature curves of thorax, head and abdomen of water foraging *Vespula* (top) and *Polistes* (bottom) from arrival till departure at the water barrel.

data for the following analysis. An average foraging stay at medium ambient air temperature (T_a : 20–30 °C) lasted 21 ± 10 (SD) seconds for *Vespula* ($N = 82$) and 16 ± 6 s for *Polistes* ($N = 7$). At high T_a (30–40 °C) *Vespula* ($N = 78$) needed 16 ± 4 and *Polistes* ($N = 68$) 16 ± 6 s for collecting the water.

3.1. Body temperature and ambient temperature

The relation of body temperature and ambient air temperature (T_a) is described with simple linear regressions shown in Fig. 3A–D. For statistical details see Table 1. At medium T_a (20–30 °C) the temperature of the thorax (T_{th}), head (T_{hd}) and abdomen (T_{ab}) of

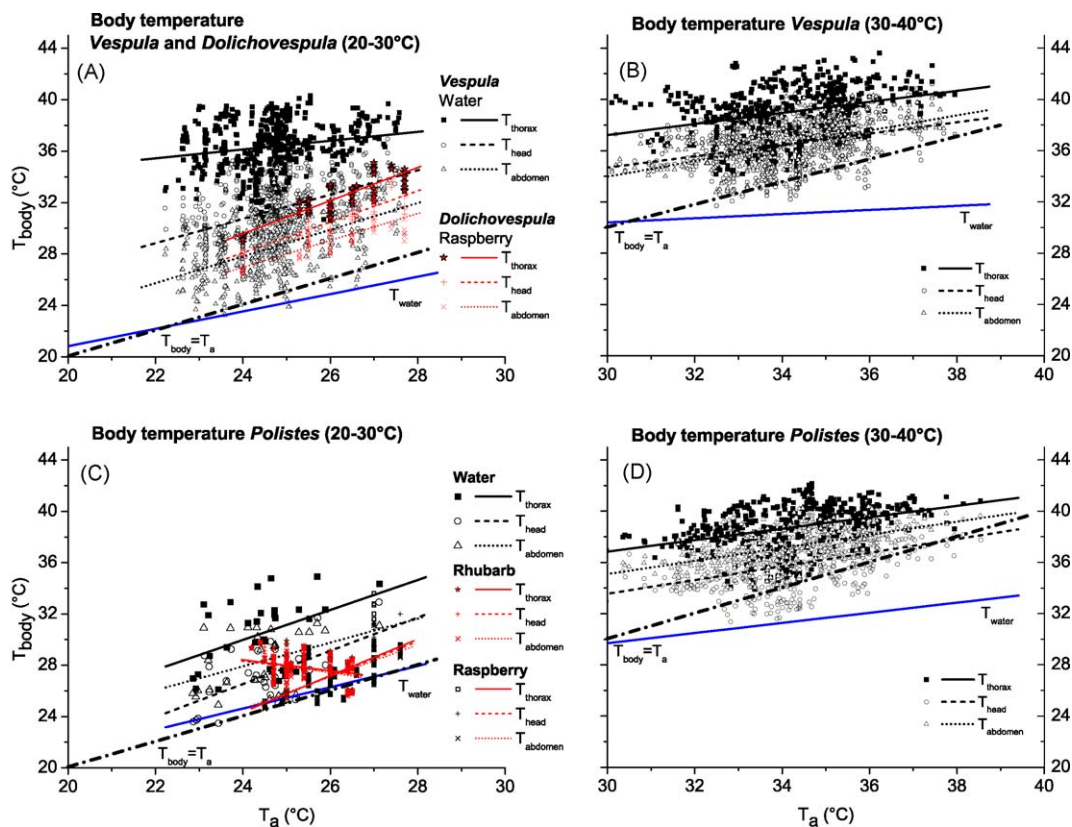


Fig. 3. Water temperature and body temperature of Vespinae (*Vespula*, *Dolichovespula*) and Polistinae (*Polistes*) during water collecting and foraging on raspberry and rhubarb in dependence on ambient temperature (T_a) at two different levels of T_a (A and C: 20–30 °C, B and D: 30–40 °C). For number of observations and regression statistics see Table 1.

Table 1
Equations of regressions, coefficients of regressions (*R*), number of measurements (*N*) and probabilities (*P*) for the water temperature and the body temperature of Vespinae (*Vespula*, *Dolichovespula*) and Polistinae (*Polistes*) during water foraging, and on raspberry and rhubarb in dependence on ambient temperature (T_a) at two levels of T_a (Fig. 2A and C: 20–30 °C, Fig. 2B and D: 30–40 °C).

T_a (°C)		Equations	<i>R</i>	<i>N</i>	<i>P</i>
Vespula – water					
20–30	Thorax	$T_{th} = 27.41175 + 0.36209 * T_a$	0.20178	522	< 0.0001
	Head	$T_{hd} = 8.39917 + 0.93079 * T_a$	0.45513	522	< 0.0001
	Abdomen	$T_{ab} = 3.31422 + 1.02167 * T_a$	0.50668	522	< 0.0001
	Water	$T_{water} = 7.3329 + 0.67507 * T_a$	0.54315	181	< 0.0001
30–40	Thorax	$T_{th} = 24.29328 + 0.43083 * T_a$	0.32296	515	< 0.0001
	Head	$T_{hd} = 21.38082 + 0.44313 * T_a$	0.35296	511	< 0.0001
	Abdomen	$T_{ab} = 16.10936 + 0.59591 * T_a$	0.48795	515	< 0.0001
	Water	$T_{water} = 25.54591 + 0.1619 * T_a$	0.14942	514	< 0.0001
Polistes – water					
20–30	Thorax	$T_{th} = 1.91764 + 1.1688 * T_a$	0.42543	30	0.01909
	Head	$T_{hd} = -4.49277 + 1.29297 * T_a$	0.56875	30	0.00104
	Abdomen	$T_{ab} = 5.58229 + 0.93007 * T_a$	0.39501	30	0.03074
	Water	$T_{water} = 4.70129 + 0.83004 * T_a$	0.64233	28	< 0.0001
30–40	Thorax	$T_{th} = 23.47161 + 0.44577 * T_a$	0.38489	442	< 0.0001
	Head	$T_{hd} = 17.52134 + 0.53413 * T_a$	0.43880	438	< 0.0001
	Abdomen	$T_{ab} = 19.76665 + 0.51086 * T_a$	0.53307	440	< 0.0001
	Water	$T_{water} = 17.83922 + 0.3951 * T_a$	0.34866	364	< 0.0001
Dolichovespula – raspberry					
20–30	Thorax	$T_{th} = -1.29307 + 1.28641 * T_a$	0.85973	74	< 0.0001
	Head	$T_{hd} = -0.7887 + 1.20336 * T_a$	0.86174	74	< 0.0001
	Abdomen	$T_{ab} = 1.83391 + 1.04714 * T_a$	0.76102	74	< 0.0001
Polistes – raspberry					
20–30	Thorax	$T_{th} = -9.79247 + 1.42237 * T_a$	0.66113	129	< 0.0001
	Head	$T_{hd} = -8.21547 + 1.35957 * T_a$	0.70978	129	< 0.0001
	Abdomen	$T_{ab} = -5.33647 + 1.24764 * T_a$	0.69689	129	< 0.0001
Polistes – rhubarb					
20–30	Thorax	$T_{th} = 38.41846 - 0.41693 * T_a$	-0.28278	154	0.0004
	Head	$T_{hd} = 38.30495 - 0.4162 * T_a$	-0.27034	154	0.0007
	Abdomen	$T_{ab} = 40.65034 - 0.50875 * T_a$	-0.35157	154	< 0.0001

Vespula and *Polistes* water foragers was on average always elevated above T_a and increased with T_a . The regressions were always significantly different from 0 ($P < 0.05$, Table 1). In *Vespula* the regression line indicated an increase of the mean T_{th} from 35.5 to 37.5 °C, of the T_{hd} from 29.1 to 34.1 °C, and of the T_{ab} from 26.0 to 31.5 °C. In *Polistes* the T_{th} increased from 28.6 to 33.7 °C, the T_{hd} from 25.0 to 30.7 °C and the T_{ab} from 26.8 to 30.8 °C in this range of T_a (20–30 °C). The abundance of foraging *Vespula* at this T_a was much higher than that of *Polistes*, which is expressed in a disproportionately higher number of measured foraging stays for the Vespinae (*Vespula* $N = 82$, *Polistes* $N = 7$).

In *Vespula* foraging under warm conditions the T_{th} increased on average from 37.2 to 40.6 °C as T_a increased from 30 to 40 °C. The T_{hd} increased from 34.7 to 38.2 °C, and the T_{ab} from 34.0 to 38.7 °C, respectively. In *Polistes* the T_{th} increased from 37.0 to 40.8 °C, the T_{hd} from 33.7 to 38.2 °C and the T_{ab} from 35.3 to 39.5 °C. The abundance of foraging species was well-balanced at these conditions (*Vespula* $N = 78$, *Polistes* $N = 68$ measured foraging stays).

At medium T_a we also measured *Dolichovespula* foraging nectar on raspberry (in the shade), and in this case the T_{th} increased on average from 29.6 to 34.4 °C, the T_{hd} from 28.1 to 32.5 °C and the T_{ab} from 27.0 to 30.8 °C as T_a increased from 24.0 to 27.7 °C (Fig. 3A). The increase of body temperature with T_a was always significant ($P < 0.0001$, statistical details in Table 1). Comparing the regression lines of T_{th} of *Dolichovespula* with *Vespula*, ANOVA indicated significant differences (intercepts: F-ratio = 358.89, $P < 0.00001$; slopes: F-ratio = 18.06, $P < 0.00001$).

In *Polistes* gathering nectar on raspberry (in the shade) a positive correlation between T_a and body temperature was observed, with T_{th} increasing from 25.0 to 29.5 °C, T_{hd} from 25.0 to 29.4 °C and T_{ab} from 25.2 to 29.1 °C as T_a increased from 24.5 to

27.6 °C ($P < 0.0001$, Fig. 3C, statistical details in Table 1). However, *Polistes* foraging sap on rhubarb (in the shade) revealed a negative correlation between body temperature and increasing ambient temperature. The T_{th} decreased on average from 28.4 to 27.4 °C, the T_{hd} from 28.2 to 27.3 °C and the T_{ab} from 28.3 to 27.2 °C as T_a increased from 24.2 to 26.5 °C ($P < 0.001$, Fig. 3C, statistics in Table 1). Comparing the regression lines of T_{th} of water foraging and nectar gathering *Polistes* on raspberry revealed no significant differences between slopes (F-ratio = 0.40, $P = 0.5270$), but significant differences between intercepts (F-ratio = 167.27, $P < 0.00001$) could be detected. The regression lines of T_{th} of water foraging and sap gathering *Polistes* on rhubarb differed significantly in intercepts (F-ratio = 87.26, $P < 0.00001$) and slopes (F-ratio = 29.19, $P < 0.00001$; ANOVA).

The median T_{th} of water foraging *Vespula* and *Polistes* (*Vespula*: 36.5 and 36.7 °C, *Polistes*: 31.9 and 31.3 °C, respectively; Fig. 4) did not differ between arrival and departure at moderate T_a ($P > 0.05$). However, at high T_a in both species the T_{th} decreased significantly from the landing until take off (*Vespula*: 39.5 and 38.7 °C; $P < 0.002$; *Polistes*: 39.7 and 38.1 °C; $P < 0.00001$, Mann–Whitney/Wilcoxon test).

The temperature of the collected water was positively correlated with the T_a under all conditions (Fig. 3, statistics in Table 1). The slope of the regression lines, however, was considerably flatter at high T_a (30–40 °C).

3.2. Thorax temperature excess and solar radiation

The T_{th} of living and dead wasps (*Vespula* and *Polistes*) was elevated above T_a at medium ambient temperature, and increased in all cases significantly with solar radiation (Fig. 5A, statistics in Table 2). The thorax temperature excess ($T_{th} - T_a$, mean values of

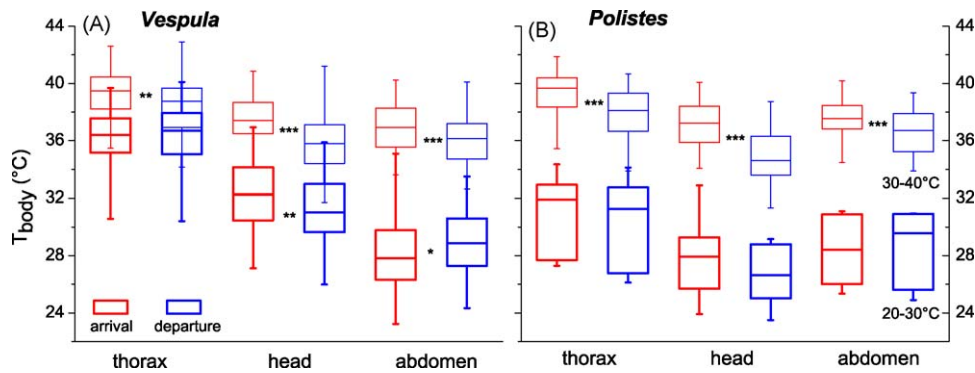


Fig. 4. Temperature of thorax, head and abdomen of *Vespula* (A) and *Polistes* (B) during arrival (red, left boxes) and departure (blue, right boxes) at the water barrel. Shown in the box plots are median, 25–75 percentile and minimum and maximum (Mann–Whitney/Wilcoxon test: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$).

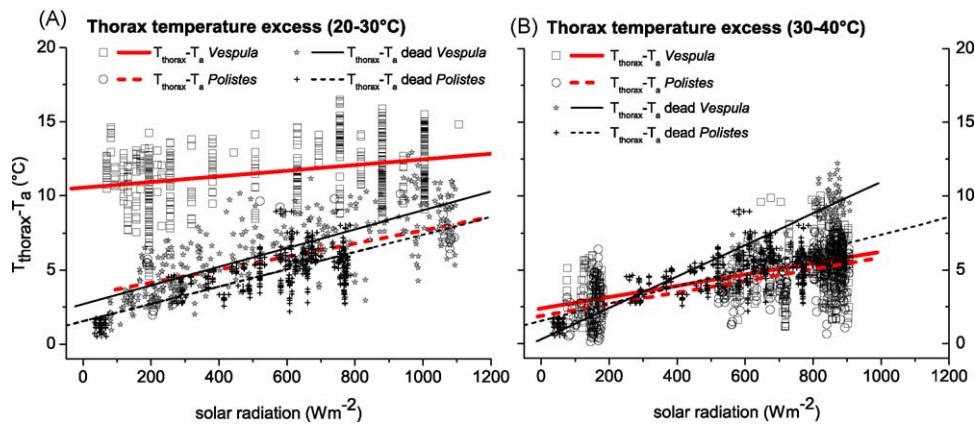


Fig. 5. Thorax temperature excess (gradient between thorax and ambient temperature = $T_{th} - T_a$) of living *Vespula* and *Polistes* during water foraging and dead wasps in dependence on solar radiation at two levels of ambient temperature (A: 20–30 °C, B: 30–40 °C). For number of observations and regression statistics see Table 2.

regression lines) increased in *Vespula* from 10.6 to 12.6 °C (1.9 °C per $\text{kW}^{-1} \text{m}^{-2}$), and in *Polistes* from 4.1 to 8.1 °C (4.4 °C per $\text{kW}^{-1} \text{m}^{-2}$) as solar radiation increased from 35 to 1104 Wm^{-2} (T_a : 20–30 °C). In dead *Vespula* it increased from 3.2 to 9.6 °C (6.3 °C per $\text{kW}^{-1} \text{m}^{-2}$), and in dead *Polistes* from 1.8 to 6.2 °C (6.1 °C per $\text{kW}^{-1} \text{m}^{-2}$). Comparing the four linear regressions with each other, with one exception (dead *Vespula* against dead *Polistes*), all differed significantly in intercepts and slopes ($P < 0.05$, statistics in Table 3).

Under very warm conditions the T_{th} of living and dead wasps was also elevated above T_a (Fig. 5B). The thorax temperature excess increased with increasing solar radiation, the linear regressions being significantly different from 0 ($P < 0.0001$, Table 2). The gradient between T_{th} and T_a increased in *Vespula* from 2.6 to 5.9 °C (4.0 °C per $\text{kW}^{-1} \text{m}^{-2}$), in *Polistes* from 2.2 to 5.5 °C (4.0 °C per $\text{kW}^{-1} \text{m}^{-2}$) and in dead *Vespula* from 1.0 to 10.0 °C (10.7 °C per $\text{kW}^{-1} \text{m}^{-2}$) as solar radiation increased from 68 to 907 Wm^{-2} (T_a : 30–40 °C). We could not conduct measurements on dead *Polistes* in

this range of T_a . Comparing the four linear regressions with an ANOVA revealed no differences between the slopes of living *Vespula* and *Polistes*, but significant differences were observed for all other slopes and intercepts ($P < 0.00001$, statistics in Table 3).

3.3. Endothermic temperature elevation

Fig. 6 gives an overview of the endothermic temperature elevation of *Vespula* and *Polistes* at the two ranges of T_a . The thorax temperature excess ($T_{th} - T_a$) of the dead wasps reveals the heat gain of the insects from solar radiation. The difference of the regression lines of the thorax temperature excess in Fig. 5 between living and dead wasps therefore yields an indirect measure of the endothermic heat production of the wasps. At moderate T_a , *Vespula* exhibited a distinct active heat production even at high solar radiation (Fig. 6A). The *Polistes*, by contrast, were only weakly endothermic (Fig. 6B). The difference of the thorax temperature

Table 2

Equations of regressions, coefficients of regressions (R), number of measurements (N) and probabilities (P) for the thorax temperature excess ($T_{th} - T_a$) of *Vespula* and *Polistes* during water foraging, and of dead wasps in dependence on solar radiation (SolRad) at two different levels of ambient temperatures (Fig. 5A: 20–30 °C, Fig. 5B: 30–40 °C).

T_a (°C)		Equations	R	N	P
20–30	<i>Vespula</i>	$T_{th} - T_a = 10.5374 + 0.00191 * \text{SolRad}$	0.31775	520	< 0.0001
	<i>Polistes</i>	$T_{th} - T_a = 3.41373 + 0.00420 * \text{SolRad}$	0.69657	30	< 0.0001
	Dead <i>Vespula</i>	$T_{th} - T_a = 2.82083 + 0.00610 * \text{SolRad}$	0.79317	366	< 0.0001
	Dead <i>Polistes</i>	$T_{th} - T_a = 1.54654 + 0.00584 * \text{SolRad}$	0.75599	501	< 0.0001
30–40	<i>Vespula</i>	$T_{th} - T_a = 2.38616 + 0.00385 * \text{SolRad}$	0.56460	515	< 0.0001
	<i>Polistes</i>	$T_{th} - T_a = 1.91603 + 0.00390 * \text{SolRad}$	0.61785	442	< 0.0001
	Dead <i>Vespula</i>	$T_{th} - T_a = 0.46817 + 0.01045 * \text{SolRad}$	0.94036	110	< 0.0001

Table 3

Comparison of the linear regressions of Table 2 with an ANOVA. For curves see Fig. 5. Right upper parts of the table parts represent F-ratios (P -values) of the regressions' slopes, and left lower parts F-ratios (P -values) of the regressions' intercepts.

20–30 °C	<i>Vespula</i>	<i>Polistes</i>	Dead <i>Vespula</i>	Dead <i>Polistes</i>
<i>Vespula</i>		7.24 ($P < 0.0073$)	145.99 ($P < 0.00001$)	
<i>Polistes</i>	241.25 ($P < 0.00001$)			6.10 ($P < 0.0139$)
Dead <i>Vespula</i>	1858.85 ($P < 0.00001$)			1.95 ($P = 0.1624$)
Dead <i>Polistes</i>		14.55 ($P < 0.0002$)	234.78 ($P < 0.00001$)	
30–40 °C				
<i>Vespula</i>		0.10 ($P = 0.7511$)	123.37 ($P < 0.00001$)	
<i>Polistes</i>	18.62 ($P < 0.00001$)			32.87 ($P < 0.00001$)
Dead <i>Vespula</i>	236.14 ($P < 0.00001$)			111.65 ($P < 0.00001$)
Dead <i>Polistes</i>		80.71 ($P < 0.00001$)	237.43 ($P < 0.00001$)	

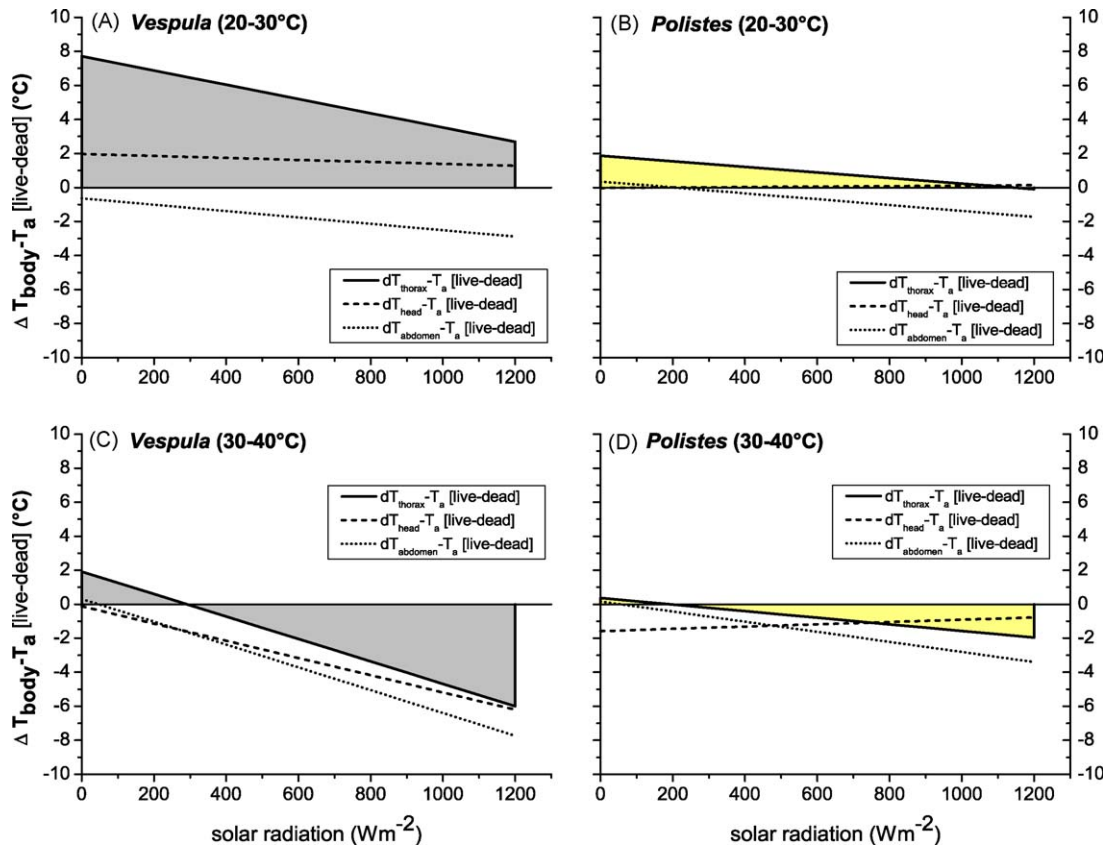


Fig. 6. Difference of the gradient between head, thorax, abdomen and ambient temperature ($T_{\text{body}} - T_a$) of living *Vespula* and *Polistes* during water foraging, and dead wasps, in dependence on solar radiation at two levels of ambient temperature (A and B: 20–30 °C, C and D: 30–40 °C).

excess decreased in both species with increasing solar radiation. In *Vespula* the active heat production of the thoracic muscles had an effect on the head temperature excess (which was positive), but in *Polistes* the head temperature excess was not elevated above zero. However, the difference of the abdomen temperature excess was negative for both wasps. The reliability of the data of the head and the abdomen is not as good as that of the thorax because their temperature depends more on the angle of incidence of the solar radiation.

As already observed at moderate T_a , at high T_a the differences of the thorax temperature excesses decreased with increasing solar radiation (Fig. 6C and D). For *Vespula*, a positive gradient ($T_{\text{th}} - T_a$ live $>$ $T_{\text{th}} - T_a$ dead) was only detectable at solar radiation less than about 300 Wm^{-2} . In *Polistes* it soon decreased below zero, but not as quickly as in *Vespula*. This means that *Vespula* exhibited a stronger cooling effort in the thorax. The curves of the head and the abdomen were always negative, and their slope followed that of the thorax, except for the head of *Polistes* (Fig. 6C and D).

4. Discussion

4.1. Body temperature and ambient temperature

In water and nectar foraging wasps (exception *Polistes* on rhubarb in the shade) an obvious positive correlation between body temperature and ambient air temperature was detected (Fig. 3, Table 1). This result is in good accordance with thoracic temperature measurements of foraging *Dolichovespula maculata* and *V. vulgaris* (Heinrich, 1984) and of *Vespula germanica* and *Vespula maculifrons* returning to their nest (Coelho and Ross, 1996). Comparing the body temperature measurements of these authors in the same ambient temperature range (T_a : 20–30 °C) with ours, the range of the thorax temperature of *Vespula* was quite similar ($T_{\text{th}} = 30$ –40 °C). Also in this range was the T_{th} of *Paravespula vulgaris* foragers gathering sucrose solution on an artificial feeding bowl, with an average T_{th} of about 35.3–39.1 °C (Kovac and Stabentheiner, 1999). Water collecting honeybees foraging in the

shade had similar T_{th} values, but no obvious dependence on T_a was detected (Schmaranzer, 2000). In our measurements *D. saxonica* (in the shade) and *P. dominulus* foraging nectar or water exhibited similar body temperature patterns, but they were noticeably cooler than *V. vulgaris*. At very warm conditions (T_a : 30–40 °C) the T_{th} of the *Vespula* and *Polistes* was nearly the same and again in good accordance with measurements of *Vespula* of Coelho and Ross (1996). As the T_{th} is important for the ability to take off (flight temperature minimum; Esch, 1976; Coelho and Ross, 1996), and in general the activity is strongly affected by the body temperature (Stabentheiner et al., 2003), thermoregulatory capability likely has some importance for the fitness and foraging success of the insects.

The measurements at moderate ambient temperatures revealed the better thermoregulatory capability of *Vespula* in comparison to *Polistes* through the higher elevation of all body parts above T_a and the weaker dependence of the T_{th} on T_a . With increasing T_a the necessity for an active thermoregulation via thoracic heat production was reduced. The elevation of body temperature above T_a decreased and the gradients between thorax and head and abdomen temperature became smaller. This relationship was also observed by Heinrich (1984) and Coelho and Ross (1996) in other wasp species. However, in contrast to *Vespula* the *Polistes* exhibited a nearly parallel increase of all body parts with increasing T_a , which means a weaker (or nearly absent) endothermic response to ambience. At high T_a , when the endothermic heat production became less important, the differences between *Vespula* and *Polistes* nearly disappeared (Fig. 3).

Sucrose foraging wasps exhibited higher thorax temperatures at departure (Kovac and Stabentheiner, 1999) than at arrival, probably to compensate for the loaded weight. This fact was not detected in the water foraging wasps. Obviously it was not necessary for them to compensate for the loaded water with a higher T_{th} (and thus flight muscle temperature) for proper departure. At high T_a both species even cooled down between landing and take off (Fig. 4). We suggest this to be the result of the reduced endothermic activity and the cooling via the ingested water. At this high T_a the high T_{th} after flight made cooling indispensable in both species. Water foraging wasps prefer wet spots (wood, moss, algae, etc.) rather than open water surfaces. These spots differed in their local temperature (see Fig. 1A). Fig. 3 shows that the correlation of local water temperature was flatter at high T_a (Table 1) and considerably below T_a . From this observation we suggest that the wasps actively selected cooler spots for the purpose of cooling.

4.2. Thorax temperature excess and operative temperature

The thorax temperature excess (difference between T_{th} and T_a) allows an assessment of the thermoregulatory performance of insects and a comparison of different species. Digby (1955) investigated the factors affecting the temperature excess of insects in artificial sunlight under laboratory conditions and found the temperature excess to vary directly with the radiation strength. Our measurements with foraging wasps under natural conditions at moderate and high ambient temperatures confirm this result (Fig. 5, Table 2). The gradient between T_{th} and T_a increased with increasing solar radiation in dead and living wasps. Cena and Clark (1972) and Underwood (1991) described this positive correlation between excess temperature (thorax and abdomen) and solar radiation for honeybees at the hive entrance and upon arrival at a feeder.

In Fig. 6 the differing thermoregulatory behaviour of *Vespula* and *Polistes* is expressed by using the operative temperature (T_e thermometer; Bakken, 1992) in connection with the thorax temperature excess. We used this parameter (T_e) in addition to quantify the insects' thermoregulatory performance, as the T_a is often an inaccurate measure of the thermal environment

experienced by the insects, which is additionally influenced by solar radiation and convective effects of the wind. The positive parts of the curves in Fig. 6 represent correlates of the amount of endothermic heat production by the wasps.

At moderate T_a the thorax temperature excess of *Vespula* in dependence on solar radiation was clearly above that of dead wasps and of living *Polistes* (Fig. 5, Table 2), which indicates their good capability of endothermic heat production with the thoracic muscles and their active thermoregulation. However, the temperature gradient of the dead and living *Polistes* did not differ, which means no or only a weak degree of endothermy (for statistics see Table 3). The values of nectar and sap foraging *Polistes* (Fig. 3) in the shade confirm this result. At very warm conditions the thermoregulation of *Vespula* and *Polistes* became similar, because *Vespula* reduced endothermic activity, which obviously was not necessary. The dead wasps, both *Vespula* and *Polistes*, exhibited a steeper slope of the temperature gradient with dependence on radiation. The fact that they were heated stronger than the living wasps means that the living wasps exhibited active cooling (negative parts of the curves in Fig. 6C and D). The difference between the dead individuals of the two wasp species may result from varying colouration of the body parts, differences in shape or body orientation, or different micro-environmental temperature and convection conditions. This is also valid for the living wasps and remains to be investigated in detail. The body of the living water collecting wasps was probably cooled via the ingested water. Active cooling of the body in wasps by means of water droplets was reported by Coelho and Ross (1996). In addition, cooling via respiration has to be taken into consideration. Fig. 6C and D indicate that the cooling efforts were smaller in *Polistes* though their body temperatures were below that of *Vespula* (Fig. 3). We cannot exclude the possibility that at least part of this difference originated from remaining partial endothermic heat production of *Vespula* even at high T_a .

4.3. Endothermy

Though *Vespula* and *Polistes* are similar in size they displayed striking differences in endothermic capability. However, in other insects a positive relationship between thermoregulatory capability and body size (or mass) was observed, e.g. in moths (Bartholomew and Heinrich, 1973), beetles (Bartholomew and Heinrich, 1978), 18 species of Alaskan bees (Bishop and Armbruster, 1999), and also in wasps by Heinrich (1984). In general, small bees initiate flight at lower thoracic temperatures than larger ones. For bees smaller than 15 mg dry mass (<~40 mg living weight), Bishop and Armbruster (1999) detected no appreciable ability to regulate T_{th} , and their results are largely in agreement with other studies (e.g. Stone, 1993a, b; Stone and Willmer, 1989a, b). Their results also indicate that bees display continuous variation in the degree of endothermy with weight, even in the smallest solitary bees (Bishop and Armbruster, 1999). However, Dyer and Seeley (1987) detected deviations from the expected size-related patterns in foragers of three Asian and the European honeybee species. The smallest species, *Apis florea*, showed the smallest temperature excess ($T_{th}-T_a$), but the intermediate-sized *A. cerana* and *A. mellifera* both showed a consistently higher temperature excess than the largest species, *A. dorsata*. Our two investigated wasp species also seem to be an exception from the rule of the relationship between thermoregulatory capability and size. Although they have a similar body size and mass (*Vespula* ~57–97 mg and *Polistes* ~83–111 mg) they nevertheless showed a quite different thermoregulatory performance.

It seems that *Polistes* reach a comparable success in individual and colony survival without the high energetic investment of *Vespula* to generate thermal power for a highly elevated T_{th} . Future experiments are needed to investigate the question of the benefit

of the high energetic investment of the Vespine wasps. Possibly it enables them to collect higher quantities of water in a shorter time, while allowing them to maintain the necessary high body temperature for a safe and quick take off (Esch, 1976; Coelho, 1991). A comparison of the thermoregulatory behaviour of these two wasps species shows that survival of similarly sized insects in the same habitat may be ensured by different physiological strategies.

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