

## Resting metabolism of vespine wasps (*Vespula* sp.) in comparison with other arthropods

Helmut Käfer, Helmut Kovac & Anton Stabentheiner

Karl Franzens University of Graz, Institute for Zoology

**Abstract:** Wespen (*Vespula* sp., Hymenoptera, Vespidae) sind zu beeindruckenden thermo-regulatorischen Leistungen fähig. Trotzdem sind Informationen über ihre Atmung rar, und über ihren Ruhestoffwechsel ist fast nichts bekannt. Wir untersuchten Atmung und Stoffwechsel von ruhenden Wespen, indem wir die CO<sub>2</sub> Produktion mittels Durchfluss-Respirometrie über Nacht bestimmten. Um sicherzustellen, dass die Tiere unserer Definition nach „ruhig“ waren, wurden etwaige thermoregulatorische Aktivität sowie das Verhalten mittels IR-Thermographie aufgezeichnet.

Die meisten ruhenden Wespen waren ektotherm oder nur schwach endotherm (Temperaturüberschuss Thorax zu Abdomen < 0,6 °C). Bei hohen Temperaturen (> 30 °C) kühlten viele Individuen Kopf und Thorax durch Herauswürgen von Flüssigkeit (Verdunstungskühlung). Im beobachteten Temperaturbereich (T<sub>a</sub> = 2,8 bis 42,4 °C) stieg die CO<sub>2</sub>-Produktion exponentiell (32,6 nl mg<sup>-1</sup> s<sup>-1</sup> bei 2,8 °C, 437,4 nl mg<sup>-1</sup> s<sup>-1</sup> bei 25,0 °C, 2312,5 nl mg<sup>-1</sup> s<sup>-1</sup> bei 42,3 °C) mit der Außentemperatur bis zum Erreichen des kritischen thermischen Maximums bei ~45 °C.

Vergleiche mit anderen Arthropoden zeigen, dass Wespen unter den Arten mit dem höchsten massenspezifischen Ruheumsatz sind. Bei 20 °C ist ihre CO<sub>2</sub> Produktion um 60% höher als die der Honigbiene (*Apis mellifera*): 300,9 nl mg<sup>-1</sup> s<sup>-1</sup> vs. 186 nl mg<sup>-1</sup> s<sup>-1</sup>. *Nowickia* sp., eine Tachinide mit vergleichbarer Masse, hat einen noch niedrigeren Ruhestoffwechsel von nur 38,4 nl mg<sup>-1</sup> s<sup>-1</sup> oder 13% des Umsatzes der Wespe. Ein Vergleich mehrerer Arten anhand von Literaturdaten zeigt, dass der Grundumsatz offensichtlich nicht über Taxongrenzen hinaus mit der Körpermasse korreliert. Sogar relativ nahe verwandte Arten wie Honigbiene und Wespe unterscheiden sich im Ruhestoffwechsel beträchtlich.

**Key Words:** resting metabolism, respirometry, arthropods, infrared thermography

Helmut Käfer, Helmut Kovac & Anton Stabentheiner, Institut für Zoologie der Universität Graz  
Universitätsplatz 2, 8010 Graz, Austria,

E-Mail: [helmut.kaefer@uni-graz.at](mailto:helmut.kaefer@uni-graz.at); [he.kovac@uni-graz.at](mailto:he.kovac@uni-graz.at); [anton.stabentheiner@uni-graz.at](mailto:anton.stabentheiner@uni-graz.at)

### Introduction

Vespine wasps of the genus *Vespula* are capable of very impressive thermoregulatory performance as various investigations brought to light (HEINRICH 1989, COELHO & ROSS 1996). Their resting metabolism as a representation of base metabolism, though, is not yet known.

Although several papers address arthropod resting metabolism, most of them deal with energetic turnover only at one single temperature and few bother to test at a temperature range covering 10 °C to 15 °C (Tab. 1). To compare different taxa, analysis over the organism's whole viable temperature range is a necessity.

With a combination of flow through respirometry and infrared thermography we measured the wasps' gas exchange and body temperature simultaneously over a temperature range from 2.5 °C to 45.0 °C. The chosen setup provided an undisturbed natural behavior of the individuals which was critical for assessment of the resting metabolism.

Comparison of basic metabolism in wasps with honeybees and other arthropods should impart deeper knowledge of the factors promoting or limiting arthropods' distribution as well as their ability to react to environmental changes.

## Material and Methods

Foraging yellowjackets (*Vespula vulgaris* (LINNAEUS 1758), N = 26 and *Vespula germanica* (FABRICIUS 1793), N = 12) were caught at a feeding station provided with sucrose solution in autumn 2008 (September, October, November) and 2009 (October). Individuals were put into a flow through respirometer chamber overnight and provided with food (1.5 M sucrose solution, ad libitum). Ambient temperature ( $T_a$ ) for the wasps was set via a water bath (Julabo F33) from 2.5 °C to 45 °C in steps of 2.5 °C and 5 °C. Individuals brought into the test chamber could accustom to the adjusted  $T_a$  before measurement due to the long-lasting (> 12 hours) duration of the experiments. CO<sub>2</sub> production was measured with a differential IR gas analyzer (Advance Optima URAS14, Hartmann and Braun, ABB) and recorded at 1 second intervals. Gas flow was set to 150 ml min<sup>-1</sup>. The gas analyzer was set to automatic (zero and end point) calibration every 3 hours, using the internal calibration cuvettes.

The chamber's top lid was covered with plastic film, transparent to IR in the range of 3 to 13 μm. Both the wasps' activity and body surface temperature were measured with an IR thermography device (ThermaCam SC2000, FLIR Systems). The insect's temperature was calibrated to 0.7 °C by estimating an IR emissivity of 0.97 of the cuticle and use of a self-constructed Peltier driven reference source of known temperature emissivity (for details see STABENTHEINER & SCHMARANZER 1987; KOVAC & al. 2007). Evaluation was done with AGEMA Research (FLIR Systems) software, controlled by an Excel (Microsoft Corp.) macro. The surface temperatures of head ( $T_{hd}$ ), thorax ( $T_{th}$ ) and abdomen ( $T_{ab}$ ) were evaluated as well as the bodily activity, which let us differentiate between active and resting individuals without impairing the animals' behaviour. Resting individuals had to show 1) ectothermy (no heated thorax) and 2) no or marginal signs of activity (classification according to STABENTHEINER & al. 2003) for at least 10 minutes.

IR video sequences were analysed to assess resting periods. URAS14 data from the same time intervals were used to calculate the mean production rate of CO<sub>2</sub> ( $M_{CO_2}$  and  $V_{CO_2}$ ) using Excel (Microsoft Corp.) and OriginPro (OriginLab).

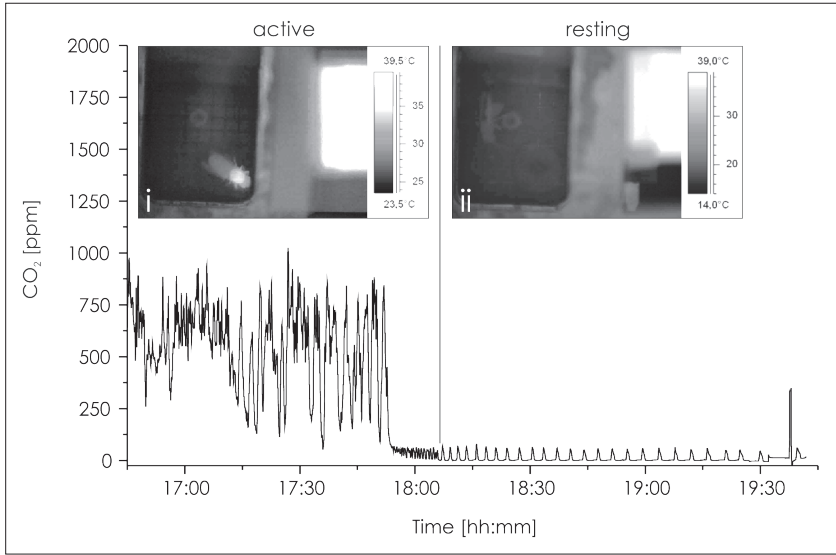
## Results

After insertion into the measurement chamber the wasp was generally agitated and active. At this point the CO<sub>2</sub> production was high, the individual was endothermic (Fig. 1, insert i). After some time the wasp calmed down and was "at rest" with a strongly decreased metabolic rate. This was represented in the breathing pattern as well as in the body temperature (ectothermic, Fig. 1, insert ii). As respiration data from securely identified (CLAPPERTON & al. 1989) *V. vulgaris* and *V. germanica* did not vary significantly, results of all individuals ( $N_{total} = 38$ ) were pooled.

With increasing ambient temperature, CO<sub>2</sub> production rate increased exponentially, reaching 94.3 nl g<sup>-1</sup> s<sup>-1</sup> at 8.3 °C, 308.37 nl g<sup>-1</sup> s<sup>-1</sup> at 20.2 °C, 425.4 nl g<sup>-1</sup> s<sup>-1</sup> at 25 °C (Tab.1), 978.06 nl g<sup>-1</sup> s<sup>-1</sup> at 35.3 °C and 1714.02 nl g<sup>-1</sup> s<sup>-1</sup> at 40 °C (Fig. 4). The equation fitted to the data is as follows:

$$V_{CO_2} = 2934.37752 * e^{Ta/370.70003} + 2934.9629 * e^{Ta/376.5089} + 0.43263 * e^{Ta/5.10183} * -5909.72717$$

where  $V_{CO_2}$  is carbon dioxide production rate [nl g<sup>-1</sup> s<sup>-1</sup>] and  $T_a$  is ambient temperature [°C] in the measurement chamber. Coefficient of determination  $R^2 = 0.96118$ ,  $n = 846$ , 38 individuals. The valid range of the fit curve is 7.7 °C to 39.5 °C. The bold part of the curve in Fig. 2 shows roughly the wasps' operative (activity) temperature range. At high  $T_a > 35$  °C (Fig. 2) CO<sub>2</sub> production increased rapidly until the wasp's upper critical thermal maximum ( $CT_{max}$ ) of 44.9 °C (KÄFER & al. 2011). At the highest temperatures of ≥ 40 °C, individuals showed "rest" according to our definition only for some minutes (Fig. 2, dashed line). These individuals did not survive the experiment.



**Fig. 1:** Representative CO<sub>2</sub> recording of *Vespula* sp. at the initial stage of an experiment. After insertion into the measurement chamber the wasp was agitated and highly endothermic (insert i, “active”). After approx. 1.5 hours the animal calmed down and switched to resting metabolism (~18:07 hours, line) with ectothermy (insert ii, “rest”) and a characteristic discontinuous breathing pattern. The outstanding peak at ~19:38 hours indicates an URAS14 internal end-point calibration.

**Tab.1:** Weight and metabolic rate at  $T_a=25^\circ\text{C}$  of arthropod taxa discussed in this study. \*Animals decapitated; \*\* $T_a = 27.5^\circ\text{C}$

No	Animal	Mass [g]	CO <sub>2</sub> [ml g <sup>-1</sup> s <sup>-1</sup> ]	References	Image © by
1	<i>Vespula</i> sp.	0.0987	425.40	this study	H. Käfer
2	<i>Apis mellifera</i>	0.08	259.48	KOVAC & al. (2007)	E. Dunbar
3	<i>Polistes dominulus</i>	0.106	154.72**	WEINER (2009)	C. Iron
4	<i>Solenopsis invicta</i>	0.003	130.07	VOGT & APPEL (1999)	A. Wild
5	<i>Pogonomyrmex occidentalis</i> *	0.008	179.53	QUINLAN & LIGHTON (1999)	A. Wild
6	<i>Camponotus fulvopilosus</i>	0.0119	61.64	LIGHTON (1989)	BTS Verlag
7	<i>Eupsilia</i> sp.	0.155	199.78	HEINRICH (1987)	H. C. Curtis
8	<i>Nowickia</i> sp.	0.1304	52.27	CHAPPELL & MORGAN (1984)	I. Martínez
9	<i>Centruroides sculpturatus</i>	0.3	31.94	HADLEY & HILL (1969)	H. Käfer
10	<i>Blatta orientalis</i>	0.42	136.11	DAVIS & SLATER (1926)	J. A. Gaspar
		0.15	83.33	SLATER (1927)	
		0.38	72.22	GUNN (1933)	
		0.33	83.33	GUNN (1935)	
11	<i>Achaeta domesticus</i>	0.558	140.0	LACHENICHT & al. (2010)	H. Käfer
12	<i>Periplaneta americana</i>	0.73	144.44	HERREID & FULL (1984)	G. Alpert

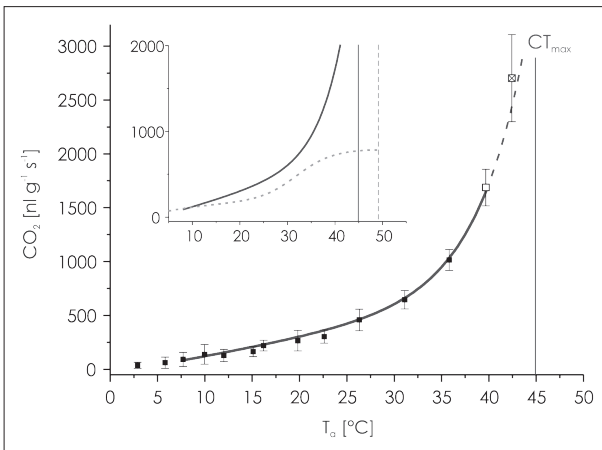
## Discussion

Although the experiments took place overnight, individuals were not at rest for the whole period. All wasps showed certain kinds of activity at some times, be it feeding, self-grooming or just losing grip with one limb and regaining safe foothold. At increasingly higher temperatures ( $T_a \geq 27.6^\circ\text{C}$ ) periods of rest became scarcer in count and length and agitated movement predominated. This as well as the death of all individuals in experiments at  $T_a \geq 40^\circ\text{C}$  (Fig. 2, unfilled squares,  $T_a = 35.8^\circ\text{C}$  for 1 individual)

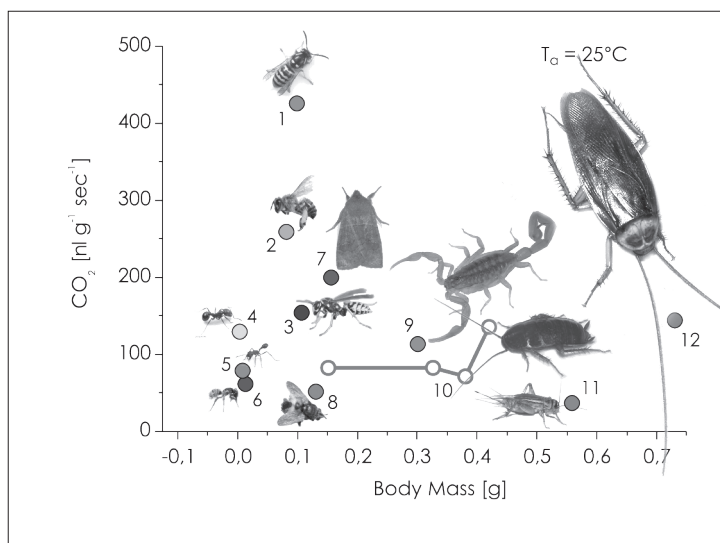
and above are an indication that these temperatures are way out of the wasp’s comfort zone. At  $T_a \geq 40$  °C - towards the upper end of the viable temperature span - individuals still showed periods of “rest” for some minutes. Meticulous examination revealed that this short “resting periods” occurred most often in the so called “deleterious range” (KLOK & al. 2004) or “heat stupor” (FLEURAT-LESSARD & DUPUIS 2010), right after the critical thermal maximum ( $CT_{max} = 44.9$  °C), and were in reality nothing but the beginning of the wasps’ end. At  $T_a = 42.4$  °C all periods evaluated as rest had to be reassessed to be heat stupor (Fig. 2, crossed unfilled square). These temperatures are obviously at the limits of viability. One could reason that either for *Vespula* there is no such thing as rest at ambient temperatures above ~40°C, or that rest at these temperatures is at a very high energetic level. However, as the data fitted the general trend, they were kept but nevertheless marked separately (Fig. 2, dashed line).

Compared to the metabolic rate of bees (KOVAC & al 2007; Fig.2, insert), the wasps’ CO<sub>2</sub> production increased more rapidly at high temperatures until an assumed sudden collapse at the wasps’  $CT_{max}$  of 44.9 °C, without any prior plateau as observed in bees. Generally speaking, the thermal range of wasps as judged from their curve of resting metabolism seems to be lower than that of honeybees, their critical thermal maximum surely is (wasp  $CT_{max} = 44.9$  °C vs. bee  $CT_{max} = 49.1$  °C; KÄFER & al. 2011).

It is common knowledge that with an increase in body mass a decrease in resting metabolism comes along, due to change in the ratio of metabolic active tissue vs. supporting tissue (KLOK & CHOWN 2005). Correlation of basal metabolism and body mass seems valid within same taxa with similar lifestyle, e.g. cockroaches (COELHO & MOORE 1989). Sharing the same basic shape, they weight from 0.055 g to 5.2 g and resting metabolism diminishes with higher body mass. After some inquiry in literature data, though, some doubt occurred that this statement – although fitting by and large – is always true. It seems not to be the case across different taxa, if we compare the tachinid fly *Nowickia* sp. (CHAPELL & MORGAN 1987) and the winter flying cuculinid moth *Eupsilia* sp. (HEINRICH & MOMMSEN 1985, HEINRICH 1987), which weight 0.1304 g and 0.155 g respectively, but differ highly in resting metabolism – and also in way of life (Fig. 3). Even close relatives like bees and wasps show significant differences in their resting metabolism (Fig. 2, insert; Fig 3; compare *Apis mellifera* (KOVAC & al. 2007), *Vespula* sp. and *Polistes dominulus* (WEINER & al. 2009)). This might be based on the differences in thermal preference as well as on diverging overwintering strategies (*Polistes*- and *Vespula*-queen vs. whole *Apis*-colony). It seems that physiological adaptations to life-style and ecological factors play a stronger role in the basal metabolism of arthropods than simple allometric relationships in body size and mass.



**Fig.2:** Metabolic rate of resting wasps in dependence on ambient temperature ( $T_a$ ). Data points are mean values with SD. Unfilled squares represent individuals that did not survive the experiment. Crossed unfilled square represents individuals measured in heat stupor, just after critical thermal maximum ( $CT_{max} = 44.9$  °C, KÄFER & al. 2011). Dashed part of the curve indicates values gathered in heat stupor. Valid range of fit curve is 7.7 - 39.5 °C. Insert shows wasps’ CO<sub>2</sub> production (solid) in comparison with bees’ (dotted, KOVAC & al. 2007) at  $T_a = 5$  to 55 °C.



**Fig. 3:** CO<sub>2</sub> production of several arthropods in dependence of their body mass at T<sub>a</sub> = 25 °C. Even close relatives with similar body mass differ in energy turnover at rest. Numbers near data points correspond with taxa in Tab. 1. Animals are shown roughly in real size ratio to each other.

### Acknowledgments

Supported by the Austrian Science Fund FWF, P 20802-B16

### References

- CHAPPELL, M.A., MORGAN, K.R. (1987): Temperature regulation, endothermy, resting metabolism, and flight energetics of Tachinid flies (*Nowickia* sp.) – *Physiological Zoology* **60**: 550-559
- CLAPPERTON, B.K., LO, P.L., MOLLER, H. SANDLANT, G.R (1989): Variation in colour markings of German wasps *Vespula germanica* (F.) and common wasps *Vespula vulgaris* (L.) (Hymenoptera: Vespidae) in New Zealand. – *New Zealand Journal of Zoology* **16**: 303–313.
- COELHO, J.R., ROSS, A.J. (1996): Body temperature and thermoregulation in two species of yellowjackets, *Vespula germanica* and *V. maculifrons*. – *J. Comp. Physiol. B.* **166**: 68-76
- COELHO, J.R., MOORE, A.J. (1989): Allometry of resting metabolic rate in Cockroaches. – *Comp. Biochem. Physiol.* **94A**: 587-590
- DAVIS J.G., SLATER W.K. (1926): The aerobic and anaerobic metabolism of the common cockroach (*Periplaneta orientalis*), Part I. – *Biochem. J.* **20**: 1167-1172
- FLEURAT-LESSARD, F., Dupuis, S.A. (2010): Comparative analysis of upper thermal tolerance and CO<sub>2</sub> production rate during heat shock in two different European strains of *Sitophilus zeamais* (Coleoptera: Curculionidae). – *Journal of stored Products Research* **46**: 20-27
- GUNN, D.L. (1933): The temperature and humidity relations of the cockroach (*Blatta orientalis*). I. Desiccation. – *J. Exp. Biol.* **10**: 274-285.
- GUNN, D.L. (1935): The temperature and humidity relations of the cockroach. III. A comparison of temperature preference and rates of desiccation and respiration of *Periplaneta americana*, *Blatta orientalis* and *Blattella germanica*. – *J. Exp. Biol.* **12**: 185-190.

- HADLEY, N.F., HILL, R.D. (1969): Oxygen consumption of the scorpion *Centruroides sculpturatus*. – *Comp Biochem Physiol* **29**: 217-226.
- HEINRICH, B., MOMMSEN, T.P. (1985): Flight of winter moths near 0°C. – *Science* **228**: 177-179.
- HEINRICH, B. (1987): Thermoregulation by winter-flying endothermic moths. – *J. Exp. Biol.* **127**: 313
- HEINRICH, B. (1989): Beating the heat in obligate insect endotherms: The nonorganismal problem and the organismal solution. – *Am. Zool.* **29**: 1157-1168.
- HERREID C.F. II, FULL R.J. (1984) Cockroaches on a treadmill: aerobic running. *J. Insect Physiol.* **30**: 395-403.
- KÄFER, H., KOVAC, H., STABENTHEINER, A. (2012): Upper thermal limits of honeybee (*Apis mellifera*) and yellowjacket (*Vespa vulgaris*) foragers. *Mitt. DGaE* **18**: 267-270.
- KLOK, C.J., SINCLAIR, B.J, CHOWN, S.L (2004): Upper thermal tolerance and oxygen limitation in terrestrial arthropods. – *J. Exp. Biol.* **207**: 2361-2370
- KLOK, C.J, CHOWN, S.L. (2005): Temperature- and body mass-related variation in cyclic gas exchange characteristics and metabolic rate of seven weevil species: Broader implications. – *J. Insect Physiol.* **51**: 789–801.
- KOVAC, H., STABENTHEINER, A., HETZ, S.K., PETZ, M., CRAILSHEIM, K. (2007): Respiration of resting honeybees. – *J. Insect Physiol* **53**: 1250-1261
- LACHENICHT, M.W., CLUSELLA-TRULLAS, S., BOARDMAN, L., LE ROUX, C., TERBLANCHE, J.S. (2010) Effects of acclimation temperature on thermal tolerance, locomotion performance and respiratory metabolism in *Acheta domesticus* L. (Orthoptera: Gryllidae) – *J. Insect Physiol.* **56**: 822-830
- LIGHTON, J.R.B (1988): Discontinuous CO<sub>2</sub> emission in a small insect, the formicine ant *Camponotus vicinus*. – *J. Exp. Biol.* **134**: 363-376.
- QUINLAN, M.C., LIGHTON, J.R.B (1999): Respiratory physiology and water relations of three species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). – *PhysEnt* **24**: 293-302
- SLATER W. K. (1927): The aerobic and anaerobic metabolism of the common cockroach (*Periplaneta orientalis*). – *Biochem. J.* **21**: 198-203.
- STABENTHEINER, A., SCHMARANZER, S. (1987): Thermographic determination of body temperatures in honey bees and hornets: calibration and applications. – *Thermology* **2**: 563–572.
- STABENTHEINER, A., VOLLMANN, J. KOVAC, H., CRAILSHEIM, K. (2003): Oxygen consumption and body temperature of active and resting honeybees. – *J. Insect Physiol.* **49**: 881-889
- VOGT, J.T., Appel, A.G. (1999): Standard metabolic rate of the fire ant, *Solenopsis invicta* Buren: effects of temperature, mass, and caste. – *J. Insect Physiol.* **45**: 655-666.
- WEINER, S.A., Upton, C.T., Noble, K., Woods, W.A., Starks, P.T. (2009): Thermoregulation in the primitively eusocial paper wasp, *Polistes dominulus*. – *Insectes Sociaux* **57**: 157-162.