

## Upper thermal limits of honeybee (*Apis mellifera*) and yellowjacket (*Vespula vulgaris*) foragers

Helmut Käfer, Helmut Kovac & Anton Stabentheiner

Karl Franzens University of Graz, Institute for Zoology

**Abstract:** Der Temperaturbereich, in dem Honigbienen (*Apis mellifera*, Hymenoptera, Apidae) und Gemeine Wespen (*Vespula vulgaris*, Hymenoptera, Vespidae) aktiv und überlebensfähig sind, unterscheidet sich beträchtlich. Die Fähigkeit der Bienen, räubernde Wespen einzuballen und „totzuheizen“ ist nur ein Beispiel am oberen Ende der Temperaturskala. Wir untersuchten, ob die unterschiedlichen Vorzugs- und Aktivitätstemperaturbereiche mit unterschiedlichen oberen Thermolimits beziehungsweise kritischen thermischen Maxima einhergehen.

Unter Anwendung eines standardisierten Verfahrens der Thermolimitrespirometrie zur Ermittlung des kritischen thermischen Maximums wurden Sammlerinnen von Honigbienen und Wespen einer Temperaturrampe von 25 °C bis 55 °C bei einer Temperaturänderung von 0,25 °C min<sup>-1</sup> ausgesetzt. Als kritisches thermisches Maximum CT<sub>max</sub> wurde das Aussetzen von optisch erkennbarer Körperbewegung, sowie das Ende von zyklischer CO<sub>2</sub> Abgabe festgelegt. Die Honigbienen (CT<sub>max</sub> = 49,1 °C, SD = 2,6 °C, n = 11) unterschieden sich dabei signifikant von den Wespen (CT<sub>max</sub> = 44,9 °C, SD = 1,3 °C, n = 10; p < 0,001, t-test). Weiters registrierten wir Unterschiede im Atemmuster (CO<sub>2</sub> Produktion) am oberen Ende des für die Tiere lebensfähigen Temperaturbereichs.

Unsere Resultate zeigen, dass der Tod einer eingeballten Wespe durch ein Versagen der Atmung bei niedrigeren Temperaturen (CT<sub>max</sub>) als bei Bienen begründet ist. Die unterschiedlichen Vorzugs- und Aktivitätstemperaturbereiche von Honigbienen und Wespen (wobei die der Wespen offensichtlich einige Grad Celsius auf der Skala nach unten verschoben sind) stimmen mit unterschiedlichen kritischen thermischen Maxima überein.

**Key Words:** critical thermal maximum, upper thermal limit, *Apis mellifera*, *Vespula vulgaris*, thermolimit respirometry, metabolism

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

Honeybees and yellowjackets have substantial different viable temperature ranges. Wasps turn up earlier in the day (= at lower ambient temperatures) at feeding places than bees, while bees forage even in midday heat in the middle of summer. The honeybees' upper thermal limit differs fairly from that of a yellowjacket. The successful killing of predating wasps by bees via heat-balling is a well-known consequence of this fact (ONO & al. 1995, STABENTHEINER & al. 2002, STABENTHEINER & al. 2007) and an example for this difference at the higher end of the temperature scale.

We investigated whether the insects' differing operational temperature ranges coincide with different upper thermal limits (critical thermal maxima, CT<sub>max</sub>). Furthermore we recorded deviations in CO<sub>2</sub> production pattern at the upper edge of the insects' viable temperature range.

### Material and Methods

Following a standardized procedure (LIGHTON & TURNER 2004; see Fig. 1), we ran a temperature ramp from 25 °C up to 53 °C at a rate of 0.25 °C min<sup>-1</sup> for honeybee (*Apis mellifera carnica*, LINNAEUS 1758; N = 11) and yellowjacket (*Vespula vulgaris* (LINNAEUS 1758), N = 10) foragers. The animals were caught in

August 2010 on an artificial feeding place provided with sucrose solution. CO<sub>2</sub> production was measured differentially by an infrared photometer (Advance Optima URAS14, ABB) via flow through respirometry. An infrared camera (ThermaCam SC2000, FLIR Systems) provided not only information on the insects' bodily activity, but also on their metabolic and energetic state (endothermic or ectothermic). For in-depth review of the methodology see KOVAC & al. (2007). CT<sub>max</sub> of the individuals was defined as the temperature where visually observable activity ceased and cyclic CO<sub>2</sub> production stopped (KLOK & al. 2004, STEVENS & al. 2010).

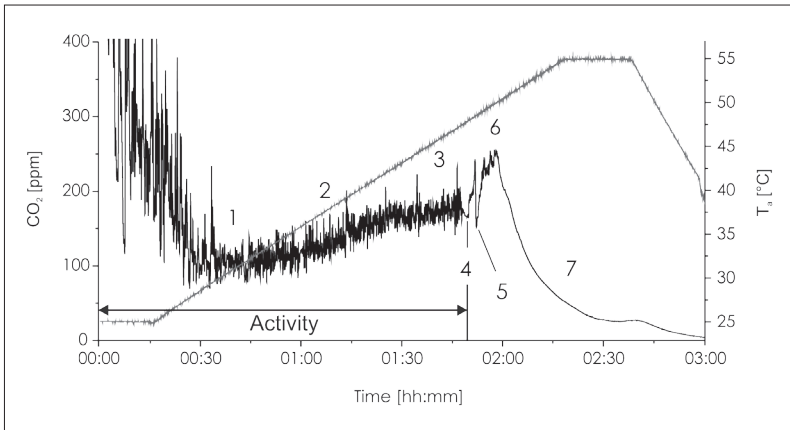


Fig. 1: Thermolimit respirometry on a yellowjacket *Vespula vulgaris*. Visible in the CO<sub>2</sub> recording are the seven typical stages of response to increasing ambient temperature:

- 1 equilibrium, 2 ramping, 3 premortal plateau, 4 mortal fall (= CT<sub>max</sub>), 5 postmortal valley, 6 postmortal peak, 7 exponential decay (LIGHTON & TURNER 2004).
- Although bodily activity (walking, gnawing, self-grooming) ceases with mortal fall, abdominal respiration movements can be observed until around the postmortal peak!

**Results**

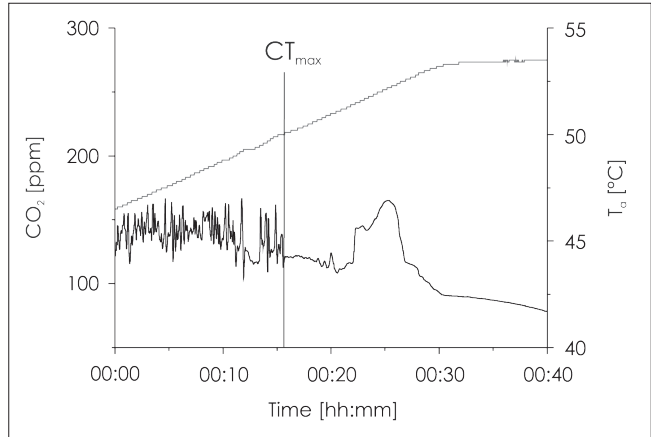
The honeybees' CT<sub>max</sub> deviated significantly from that of the yellowjackets (Tab. 1). Furthermore we recorded differences in the pattern of CO<sub>2</sub> production at the upper end of the insects' viable temperature range. The wasps' output was not only at a higher level altogether (compare CO<sub>2</sub> trace of premortal plateau to postmortal peak in Figs 2 and 3), the CO<sub>2</sub> release was much more pronounced after CT<sub>max</sub> before the postmortal valley (Fig. 3, greyed part of CO<sub>2</sub> trace) and in some cases reached the level of the postmortal peak.

**Tab. 1:** Mean CT<sub>max</sub> of wasps and bees. N = number of individuals, respective mean CT<sub>max</sub> with standard deviation. The wasps' CT<sub>max</sub> differs significantly (p < 0.001) from the bee's.

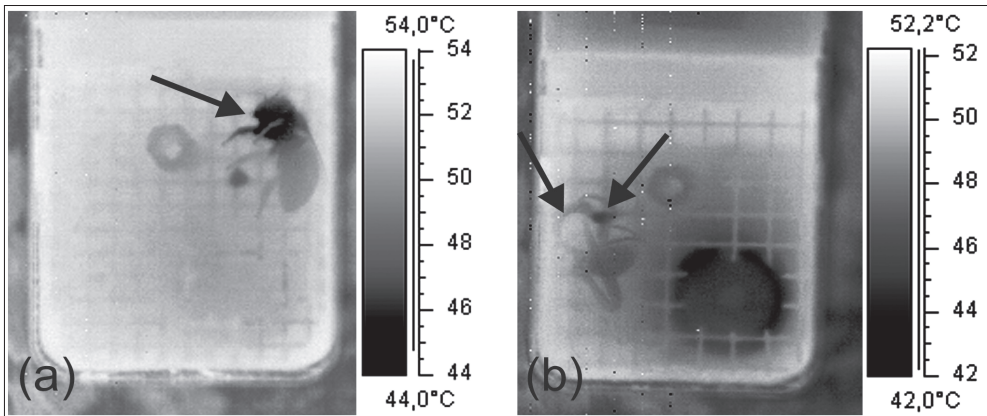
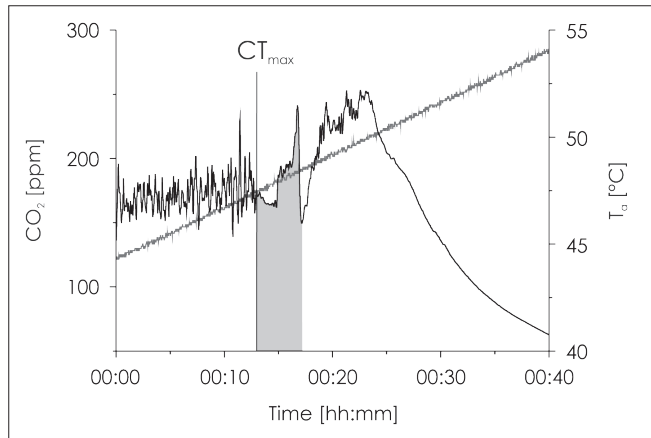
	CTmax [°C]	SD [°C]	n	t-Test
<i>Vespula vulgaris</i>	44.9	1.3	10	p < 0.001
<i>Apis mellifera</i>	49.1	2.6	11	

Figures 2 and 3 show representative recordings of CO<sub>2</sub> release during the last phase (pre-mortal plateau to exponential decay, see Fig. 1) of a thermolimit experiment. CT<sub>max</sub> differed significantly (see Tab. 1) and showed simultaneously in the breathing curve as the stop of cyclic CO<sub>2</sub> production, as well as in the IR recordings as the cease of coordinated motoric activity (see Fig. 4).

**Fig. 2:** Representative CO<sub>2</sub> production curve of *Apis mellifera* during the last part of a thermolimit experiment (CT<sub>max</sub> = 49.1 °C). CO<sub>2</sub> trace shows a typical appearance from premortal plateau to exponential decay (see Fig. 1).



**Fig. 3:** Representative CO<sub>2</sub> production curve of *Vespula vulgaris* during the last part of a thermolimit experiment (CT<sub>max</sub> = 44.9 °C). Characteristic CO<sub>2</sub> release pattern before postmortal valley is marked.



**Fig. 4:** (a) IR image of a bee just after CT<sub>max</sub>. The insect lies motionless (heat stupor) except for occasional abdominal respiration movements. Head and thorax appear cool due to foregoing evaporative cooling and liquid spilled uncoordinated at this stage of experiment (arrow). (b) IR image of a yellowjacket, taken in the postmortal peak (see Fig. 1). Mind the wasp’s cool mandibles. (evaporative cooling) and heated thorax (endothermy, arrows)!

## Discussion

Our results revealed that the death of a wasp during heat-balling is caused by a failure of respiration at a lower temperature ( $CT_{max}$ ) than in the bees. The different thermal preferences and operational temperature ranges of honeybees and vespine wasps (with the yellowjackets' one clearly shifted to the lower end of the scale) coincide with differences in their critical thermal maximum. The combination of infrared thermography and gas exchange measurement revealed fundamentally similar responses to heat stress, as well as particular differences (especially in the  $CO_2$  trace) of the two taxa. The yellowjackets' breathing curve shows a characteristic "peak" (see Fig. 3) after  $CT_{max}$  and before the postmortal valley, which lacks in the bees'  $CO_2$  trace. Furthermore, yellowjackets often showed endothermic(!) behaviour by heating of their thoracic musculature well after the postmortal valley. They did this at a point in the experiment where further elevation of body temperature is clearly contradictory for the animal's survival. The failure of control over the insect's thoracic musculature might be a possible explanation for this finding.

## Acknowledgments

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

## References

- KLOK, C.J., SINCLAIR, B.J., CHOWN, S.L., (2004): Upper thermal tolerance and oxygen limitation in terrestrial arthropods. – *Journal of Experimental Biology* **207**: 2361-2370.
- KOVAC, H., STABENTHEINER, A., HETZ, S.K., PETZ, M., CRAILSHEIM, K. (2007): Respiration of resting honeybees. – *Journal of Insect Physiology* **53**: 1250-1261.
- LIGHTON, J.R.B., TURNER, R.J. (2004): Thermolimit respirometry: an objective assessment of critical thermal maxima in two sympatric desert harvester ants, *Pogonomyrmex rugosus* and *P. californicus*. – *Journal of Experimental Biology* **207**: 1903-1913.
- ONO, M., IGARASHI, T., OHNO, E., SASAKI, M. (1995): Unusual thermal defence by a honeybee against mass attack by hornets. – *Nature* **377** (6547): 334-336.
- STABENTHEINER, A., KOVAC, H., SCHMARANZER, S. (2002): Honeybee nestmate recognition: the thermal behaviour of guards and their examinees. – *Journal of Experimental Biology* **205**, 2637–2642.
- STABENTHEINER, A., KOVAC, H., SCHMARANZER, S. (2007): Thermal behaviour of honeybees during aggressive interactions. – *Ethology* **113**: 995-1006.
- STEVENS, M.M., JACKSON, S., BESTER, S.A., TERBLANCHE, J.S., CHOWN, S.L. (2010): Oxygen limitation and thermal tolerance in two terrestrial arthropod species. – *Journal of Experimental Biology* **213**: 2209–2218.