Thermoregulation of foraging honeybees on flowering plants

Helmut Kovac & Anton Stabentheiner

Karl Franzens University of Graz, Institute for Zoology

Abstract: Die Thermoregulation von sammelnden Honigbienen auf blühenden Pflanzen.

Während des Nektar- und Pollensammelns in gemäßigten Klimazonen sind die Honigbienen einem breiten Temperaturbereich ausgesetzt, der ihre thermoregulatorischen Fähigkeiten herausfordert. Ihre Körpertemperatur resultiert dabei aus der endothermen Wärmeproduktion, exogenem Wärmegewinn durch die Sonnenstrahlung und dem Wärmeverlust. Wir untersuchten das thermoregulatorische Verhalten von Sammlerinnen (*Apis mellifera carnica*; Apidae, Hymenoptera) auf 33 verschiedenen blühenden Pflanzen in Abhängigkeit von der Jahreszeit und den Umweltfaktoren.

Die Bienen waren während des Sammelns immer endotherm. Über einen breiten Temperaturbereich (T_a) wurde die mittlere Oberflächentemperatur des Thorax (T_{th}) auf einem hohen und ziemlich konstanten Level geregelt (T_{th} = 33,7 – 35,7°C; T_a = 10 – 27 °C). Bei einer bestimmten Temperatur konnte die T_{th} sehr wohl stark variieren, in Abhängigkeit davon, auf welchen Pflanzen sie sammelnden. Bei wärmeren Bedingungen (T_a=27 – 32°C) stieg die T_{th} nahezu linear mit der T_a auf ein maximales Level von 42,6°C an. Die Temperaturerhöhung des Thorax über die Umgebung reduzierte sich stark mit steigender T_a (T_{th}-T_a = 21,6-3,6°C). Die mittlere Temperatur des Kopfes (24,3 – 37,2°C) war im Kalten stärker über die T_a erhöht als im Warmen. Das Abdomen war der kühlste Körperteil (16,0 – 37,5°C), seine Temperatur lag konstant ~ 5°C über der T_a und stieg linear mit dieser an.

Die Bienen nutzten den Wärmegewinn durch die Sonne, um die Temperatur von Thorax, Kopf und Abdomen zusätzlich zu erhöhen. Das ermöglicht eine bessere Ausnutzung der Nektarquellen durch eine erhöhte Agilität und schnellere Trinkgeschwindigkeit. Jahreszeitliche Variationen konnten entdeckt werden. Die mittlere T_{th} der Bienen, die im Frühling sammelten, war um 4,2°C höher als im Sommer. Wir vermuten, dass die Motivation der Sammlerinnen für die unterschiedliche T_{th} zwischen den verschieden Pflanzen und Jahreszeiten sehr wesentlich verantwortlich ist.

Key words: honeybee, foraging, thermoregulation, flowering plants, thermography

Helmut Kovac, Anton Stabentheiner, Institut für Zoologie der Universität Graz Universitätsplatz 2, 8010 Graz, Austria,
E-Mail: he.kovac@uni-graz.at; anton.stabentheiner@uni-graz.at

Introduction

Honeybees need nectar and pollen to provide for their young bees and brood. Honey is an energy store for heat production to achieve a constant brood temperature and for overwintering in the temperate climate (Stabentheiner & al. 2003, 2010). During foraging bees are mostly highly endothermic. They may exhibit thoracic temperatures higher than 40 °C (e.g. Heinrich 1979, Kovac & Schmaranzer 1996). The body temperature of foraging insects is influenced by several environmental factors like ambient air temperature, solar radiation, convection and reflectance. The energy gain from solar radiation is of importance for the thermoregulation of foraging bees. The bees minimize the thermoregulatory costs during foraging by adapting their thorax temperature in response to the profitability of foraging at a food source and the colony's need for nectar and pollen (Stabentheiner & Schmaranzer 1987, Dyer & Seeley 1987, Waddington 1990; Stabentheiner & Hagmüller 1991, Underwood 1991, Stabentheiner 2001). From these investigations we know the thoracic temperature to vary in a broad range of ~30-44°C. As flowers differ considerably in their profitability, i.e. as they vary in the amount of pollen and concentration and flow of nectar, we expected a considerable variation of the thorax temperature. Therefore, in order to describe accurately the thermoregulation of foraging bees in their temperate living space, we investigated them on many different flowers at different locations during the entire foraging season.

Materials and methods

We investigated honeybees (*Apis mellifera carnica*; Apidae, Hymenoptera) foraging nectar and pollen on 33 different blossoms of flowers, shrubs and trees at the botanical garden in Graz and several orchards and meadows near Graz/Austria, Middle Europe. We covered the entire foraging season and range of ambient temperatures (T_a=~10–30°C) honeybees are exposed to under Middle European climate conditions. The bees were filmed during the foraging stays at the blossoms (if possible from landing until takeoff) with an infrared camera (ThermaCam SC2000 NTS, FLIR) without disturbing them. We simultaneously measured the surface temperature of all body parts during the entire stay at a blossom. The infrared camera was calibrated periodically by slotting in a self-constructed Peltier-driven reference source of known temperature and emissivity (for details of calibration see Stabentheiner & Schmaranzer 1987, Schmaranzer & Stabentheiner 1988). The ambient air temperature and relative humidity were measured near the foraging bees with NTC-sensors or thermocouples. The solar radiation was measured with a miniature global radiation sensor (FLA613-GS mini spezial, AHLBORN) also in the vicinity of the bees. Data were stored every second with ALMEMO data loggers (AHLBORN). The temperature of the three body parts and the blossoms' surface was calculated from the infrared thermograms by means of the AGEMA Research software (FLIR) controlled by a self-written Excel VBA-macro (Microsoft Corporation). 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 & Schmaranzer 1987, Schmaranzer & Stabentheiner 1988). Because the ThermaCam works in the long-wave infrared range (7.5-13 µm) the reflected radiation from the bees' 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 bees at a sensitivity of <0.1°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 bees' endothermic capability. To evaluate the influence of the radiative heat gain on the body temperature, three classes of solar radiation were established: shade, <200 Wm^{-2}, overcast sky, 200–500 Wm^{-2}, and sunshine, >500 Wm^{-2}.

Results and discussion

In order to allow a comparison of the results of flower-visiting bees with water-foraging honeybees (Kovac & al. 2010), the regression lines for the three body parts of the water foraging bees are also displayed in Fig. 1. On average, the thorax surface temperature (T_{th}) of the flower visiting bees was regulated at a high and rather constant level over a broad range of ambient temperatures (T_{th}=33.7–35.7 °C, T_a=10–27 °C). At warmer conditions (T_a=27–32 °C) the T_{th} increased nearly linearly with T_a to a maximal average level of 42.6°C. The thorax temperature excess decreased strongly with increasing T_a (T_{th}-T_a=21.6-3.6°C). The T_{th} of bees on flowers was cooler below T_a~30°C than that of water-foragers. Regulation of the T_{th} at a high level even at low T_a allows the foragers to keep the T_{hd} at a level high enough to guarantee a high suction speed (Kovac & al. 2010). In nectar foragers, however, a high suction speed is not as important as in water foragers (Kovac & al. 2010) because the nectar is not available in an unlimited amount.

The mean temperature of the head (24.3–37.2 °C) was more strongly elevated above T_a in the cold than in the warmth. The abdomen was the coolest body part (16.0–37.5 °C). Its temperature increased linearly with T_a (about 5 °C above T_a). The T_{hd} of the flower-visiting bees was cooler below T_a~26°C than in the water foragers, and the abdomen was mostly cooler than in the water foragers.

Plotting the body temperature in dependence on three levels of solar radiation (<200, 200–500, >500 Wm^{-2}; Fig. 1) revealed that bees foraging in sunshine were always warmer than bees foraging in shade. The temperature difference between radiation classes >500 and <200 Wm^{-2} was smaller at low T_a (T_a=12 °C: difference T_{th}=2.0, T_{hd}=1.7, T_{ab}=3.0°C) and greater at high T_a (T_a=30°C: difference T_{th}=3.3,

T_{hd}=5.0, T_{ab}=4.8°C). The bees used the heat gain from the sun to enhance their body temperature, which enables a quicker exploitation of the flowers because a high body temperature not only increases suction speed but also increases the bee's agility. Bees were always endothermic during foraging. However, at higher ambient temperatures (~30°C) the thoracic temperature excess was reduced to a low level. At these high ambient temperatures the bees foraging in sunshine were able to reach the optimal upper level of T_{th} for force production and takeoff of 38–39°C (Coelho 1991) without much endothermic effort. The prevention of overheating became more important.

The mean T_{th} of bees foraging in spring was 4.2°C higher than in summer. In Middle Europe a significant amount of the brood is reared in spring until beginning of the summer. We presume that in this period foraging bees are better motivated due to the high demand in the hive and therefore they

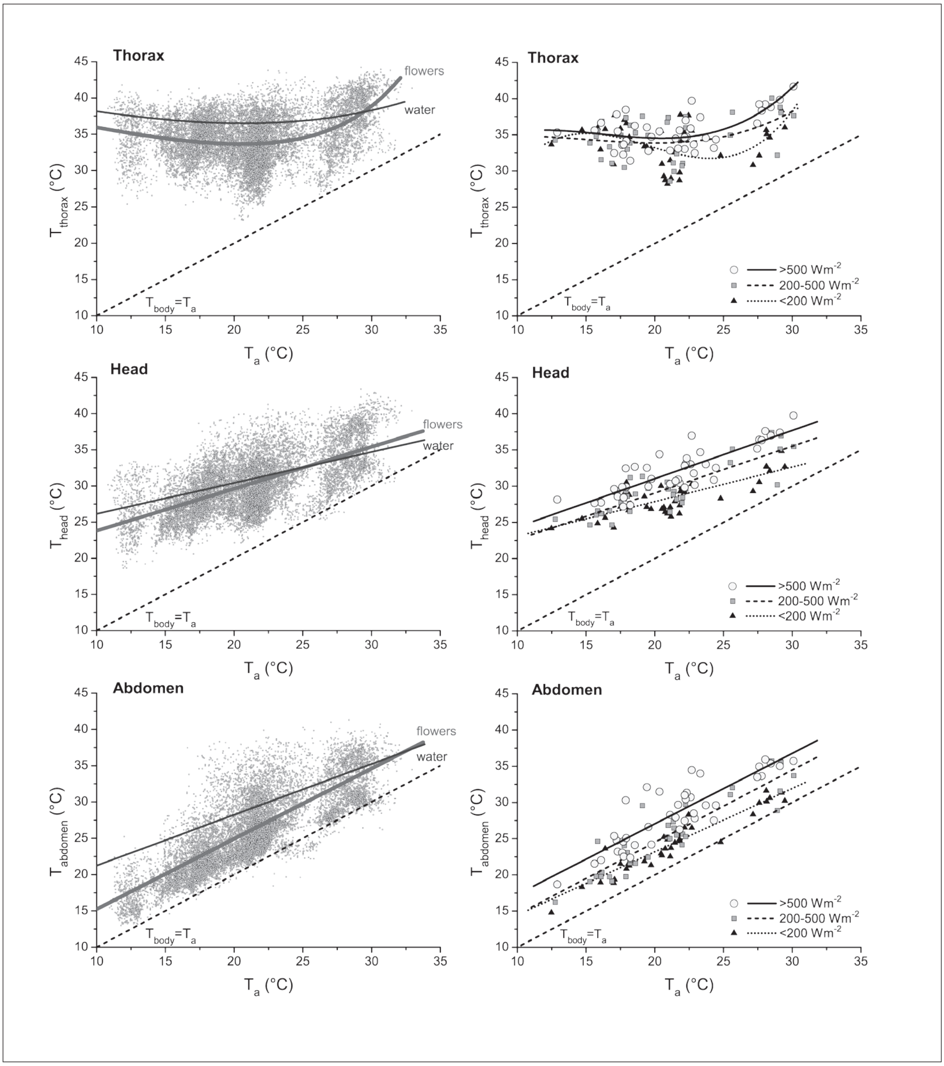

Fig. 1. Surface temperature of thorax, head and abdomen of foraging honeybees in dependence on ambient temperature (T_a). Left: foraging on flowering plants (dots are single values; bold lines are regressions), and foraging water (thin blue lines; from Kovac & al., 2010). Right: Means per flowering plant and day at 3 different classes of solar radiation.

exhibit higher thorax temperatures than bees foraging in summer or autumn.

Acknowledgements

Supported by the Austrian Science Fund (FWF, P16584-B06, P20802-B16).

References

Dyer, C.D. & Seeley, T.D. (1987): Interspecific comparison of endothermy in honey-bees (*Apis*): deviations from the expected size-related patterns. – Journal of Experimental Biology **127**, 1-26.

Coelho, J.R. (1991): The effect of thorax temperature on force production during tethered flight in the honeybee (*Apis mellifera*) drones, workers and queens. – Physiological Zoology **64**, 823-835.

Heinrich, B. (1979): Thermoregulation of African and European honeybees during foraging, attack, and hive exits and returns. – Journal of Experimental Biology **80**, 217-229.

Kovac, H. & Schmaranzer, S. (1996): Thermoregulation of honeybees (*Apis mellifera*) foraging in spring and summer at different plants. – Journal of Insect Physiology **42**, 1071-1076.

Kovac, H., Stabentheiner, A., Schmaranzer, S. (2010): Thermoregulation of water foraging honeybees – Balancing of endothermic activity with radiative heat gain and functional requirements. – Journal of Insect Physiology **56**, 1834-1845.

Schmaranzer, S. & Stabentheiner, A. (1988): Variability of the Thermal Behaviour of Honeybees on a Feeding Place. – Journal of Comparative Physiology B **158**, 135-141.

Stabentheiner, A. & Schmaranzer, S. (1987): Thermographic Determination of Body Temperatures in Honey Bees and Hornets: Calibration and Applications. – Thermology **2**, 563-572.

Stabentheiner, A. & Hagmüller, K. (1991): Sweet Food Means 'Hot Dancing' in Honey Bees –. Naturwissenschaften **78**, 471-473.

Stabentheiner, A. (2001): Thermoregulation of dancing bees: thoracic temperature of pollen and nectar foragers in relation to profitability of foraging and colony need. – Journal of Insect Physiology **47**, 385-392.

Stabentheiner, A., Pressl, H., Papst, T., Hrassnigg, N., Crailsheim, K. (2003): Endothermic heat production in honeybee winter clusters. – Journal of Experimental Biology **206**: 353–358.

Stabentheiner, A., Kovac, H., Brodschneider, R. (2010): Honeybee Colony Thermoregulation – Regulatory Mechanisms and Contribution of Individuals in Dependence on Age, Location and Thermal Stress. – PLoS ONE 5(1): e8967. doi:10.1371/journal.pone.0008967.

Underwood, B. (1991): Thermoregulation and energetic decision-making by the honeybees *Apis cerana*, *Apis dorsata* and *Apis laboriosa*. – Journal of Experimental Biology **157**, 19-34.

Waddington, K.D. (1990): Foraging profits and thoracic temperatures of honey bees (*Apis mellifera*). – Journal of Comparative Physiology B **160**, 325-329.