Thermographic Determination of Body Temperatures in Honey Bees and Hornets: Calibration and Applications

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•This study presents calibrations allowing absolute thermographic temperature measurements in honey bees and hornets. The band emissivity (~ $3.5-5.6 \mu$ m) of a heated honey bee thorax (mesosoma) is limited to a range of 0.955-0.990.

The development of thoracic heat production was investigated in young honey bees (Apis mellifera carnica). Five-hour-old bees did not actively produce heat in their thoraces, whereas 1- and 2-day-old bees did.

We made continuous thermographic temperature recordings of adult honey bees during stops at a nearby feeding bowl containing 1-M sucrose solution. At ambient temperatures of 23.8-26.2C, thoracic surface temperatures were increased up to 45C, with mean values of 41.4C (41.1 - 43.7C) after landing and 43.5C before taking off.

Similarly, hornets ($Vespa\ crabro$) actively regulated their body temperatures when fed with honey in front of their nest. Thoraces reached a mean minimum temperature of 32.7C and 37.4 - 36.8C before taking off (ambient temperature 18-18.6C). Head (~29.2C) and abdomen (~25.2C) always remained cooler than the thorax.

The behavior and the physiologic functions of many insects are strongly related to ambient temperature. Some species are capable of endothermic heat production by activation of their thoracic flight muscles.^{1,2} Honey bees (Apis mellifera L.) and hornets (Vespa crabro L.), common social insects, have highly specific social and individual thermoregulatory capacities. In summer, honey bees maintain their brood nest temperature at 34-36C.³ In winter, they keep the temperature in the center of their "winter clusters" around 28C, even when outside temperatures are -30C.⁴ These regulatory abilities are made possible by their antennal thermal sense, which is sensitive to temperature differences of at least 0.2C.⁵ Hornets, too, regulate their brood nest temperature: at about 30C

Early investigators (e.g., Himmer⁴) were able to measure brood-nest and winter-cluster temperatures accurately by means of thermocouples. Determination of body temperatures of individual insects was initially difficult because of the low heat capacity of an insect's body (e.g., approximately 2.4 x 10^{-2} cal/ deg for the honey-bee thorax). Only the use of very fine thermocouples (wire diameter 50 µm or less) led to reliable body temperature recordings.⁷ However, with thermocouples, exact measurements are possible at only one point and only for a short time, because thermocouples are inserted into the body with "thermoneedles"⁸ or are hung in prepared cuticular holes.⁷ Longer-lasting measurements are possible only if the animals remain connected with the thermocouple wires. Their mobility is constrained, and possible injury effects cannot be excluded.

Cena and Clarc⁹ were, as far as we know, the first to introduce thermography to the study of insect thermoregulation. Despite the advantages of thermographic temperature recording over conventional thermometry, the full possibilities were not recognized by other investigators, and thermocouple techniques remained the standard method until now.⁸

In 1981, Schmaranzer began to use thermography for the study of honey bees.^{10,11} The calibrations carried out allowed really quantitative measurements with an accuracy of at least ± 0.8 C.^{12,13} Temperature recordings in free-moving, undisturbed bees were possible during stops at a feeding place and even during their communicatory "dances".¹⁴

Recently, thermograms of a winter-flying moth *(Eupsilia morrisoni)* were published,⁸ but because no calibrations or emissivity-determinations were carried out or cited, important questions were left unanswered.

Because thermography is now beginning to be more widely used by entomologists, we are presenting extensive calibration procedures that would enable other investigators to take the step from qualitative to quantitative thermography.

First, we used thermography to show the development of heat production capacity in individual young honey bees. Later, we investigated the thermal behavior of honey-bee workers and hornets foraging at feeding places near their hives. These measurements should help us understand the insects' energy balance and the energetic costs of foraging.

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Materials and Methods

All thermographic measurements were carried out using an AGA 782 SW Thermovision system, with Discon for converting the black-and-white images to 10-step colored thermograms. The images were stored on videotape, allowing precise analysis after the experiments.

REFERENCE SOURCE CALIBRATION: To get absolute temperatures of appropriate accuracy with the AGA 782 SW system, we used an AGA 1010 reference source (Figure 1), which was especially well suited for field applications because of its robustness, simple handling, and fast heating or cooling-down to desired temperature levels. Nevertheless, as the calibration of the source by AGEMA Inc. (Sweden) guaranteed an accuracy of only ± 0.2 C, the making of our own calibration in our measurement range of 15-45C was indispensable.

For this purpose, we designed a black body, as shown in Figure 1. A brass cylinder 18 cm long, 3 cm in diameter, 1-mm wall thickness, projected horizontally into a temperature-controlled, stirred, and insulated water bath. The inner surface of the cylinder was covered by Nextel Velvet Coating 2010 black (3M), which has a high emissivity (ϵ) of about 0.95 throughout the main sensitivity range of the infrared (IR) camera (3.5-5.6 µm). To allow precise definition of the cylinder temperature by measuring the



Figure 1. Experimental set-up during the calibration of the AGA 1010 reference source. BC: brass cylinder; StC: Styrofoam cover (the big dotted arrow symbolizes its removal). The calibration steps are numbered consecutively (cf. text). The 12-mm extension ring (d = 18 cm) described in the text is also shown.

water-bath temperature, the cylinder opening was tightly insulated before the measurements were taken. The temperature of the water bath was measured by a mercury thermometer with 0.02C scaling. It was precision gauged in steps of 2.5C between 20 and 40C by the Bundesamt für Eich- und Vermessungswesen (Vienna, Austria). The maximum error observed was 0.013C. Therefore, we are certain to have controlled the water-bath temperature to within ± 0.025 C. On the basis of the described physical conditions, the emissivity of the black body was considered to be $\epsilon \geq 0.99$.¹⁵⁻¹⁷

For the calibration procedure (Figure 1) the black body was heated to the same temperature as indicated on the temperature setting of the AGA 1010 reference source and the IR camera was focused on the opening of the black body.¹⁸ After some time, the insulation was removed. The first view of the opening was analyzed from the videotape and was compared to the radiation of the reference source.

The calibration showed that our reference source indicated temperatures up to 1.5C too high, probably as a result of the age of the source, not general instability. The source remained stable for 2 years after initial calibration. For computing the corrections, we assumed $\varepsilon = 0.99$ for the black body, but this value could have been a bit too low (or too high). However, because we used the same reference source for the determination of the emissivity of a honey-bee thorax and for the temperature measurements, this could not affect our temperature measurements.

EFFECT OF CLOSE-UP INSTRUMENTATION ON CAMERA SENSITIVITY: For measurements in honey bees and hornets, which are small insects, close-up instrumentation (12-mm or 21-mm extension rings, inserted between the IR camera and 20° lens) had to be used. Because the calibration of the system had been performed by the manufacturer with a 20° lens at a 50-cm focal distance, we had to check whether the use of extension rings changed the sensitivity and whether the calibration curves were still valid.

For this purpose the radiation emanating from the AGA 1010 reference source was measured with and without the extension rings at different referencesource temperature settings. The focal distances with the 20° lens and the 12-mm and 21-mm extension rings were 50 cm, 18 cm and 15 cm, respectively. Using stops, care was taken that the reference source always had the same size in the IR image.

The emissivity of the reference source when viewed with the 20° lens was assumed to be 1. Computing of fictitious emissivity values with the AGA calibration formulas (see Discussion) resulted in ϵ'

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= 1.001 (SD = 0.003; N = 39) for the 12-mm and ε' = 1.0002 (SD = 0.004; N = 37) for the 21-mm extension ring at reference source temperatures between 28 and 47C (ambient temperature = 20.5-22.7C). Hence no significant change of the IRcamera sensitivity was observed with the close-up instrumentation; the AGA calibration curves were applicable with sufficient accuracy.

CALIBRATIONS REFERRED TO HONEY-BEE THORACES: For thermographic temperature measurements, the emissivity of a viewed object should be known. Otherwise, separate calibration curves must be obtained for every measurement situation. Honey-bee cuticle emissivity is not obtainable from literature. Some papers gave only rough estimations without measurements.¹⁹ Schmaranzer¹⁰ reported that $\varepsilon = 0.95$, but because he had not been able to check the reference source (AGA 1010) used in his study, more precise calibrations had to be carried out. Certainly the accuracy of the determination of absolute surface temperatures had to be less than ± 0.8C.¹⁰ Because honey bees produce the majority of their heat in their thoraces (see Figure 5), we restricted our calibrations to thoraces.

Dead bees The thoraces of killed bees were heated ventrally by a slightly inserted Peltier element (Fig. 2). Dorsally (at the notum) a NiCr/NiCu-thermocouple (50-µm diameter wires) was fixed on the surface with a very small droplet of a wax-colophony mixture. The thermocouple was insulated by plastic lacquer near the tip and by thin Teflon[®] tubes in its other parts. Its readout was registered by a Beckman Dynograph-Recorder (R511 A). The IR camera was also used to measure the emitted radiation. The arrangement was protected against air currents and uncontrolled ambient radiation by a box and a cloth (Figure 2). The thorax was heated to the calibrated temperature values of the reference source (32.5,



Figure 2. Experimental set-up for the calibrations using artificially heated thoraxes of dead bees.

34.6, 39.0, and 41.0C). When the thoracic temperature had reached one of these plateaus, three readings were made and averaged to one measurement value. Afterward, the camera was turned to the reference source, which was covered by a 4-mm-diameter stop of size similar to a thorax cross-section. Every measurement value was converted into a theoretical emissivity value (ϵ'), using the AGA calibration formulas (see Discussion).

Living bees were fixed on cork in calm air and in a dark room by needles crossed above their petioli. After we removed the needles, the insects began to activate their flight muscles, heating up their thoraces. Fixed insects usually did not heat up their thoraces. Surface temperature and IR radiation of a thorax were measured simultaneously and evaluated as described above.

Thoracic hairs In the course of calibrations, a question arose about whether the thermographic studies were influenced by thoracic hairs. To explore this question, the measurement arrangement was the same as described above for dead bees, but, for better fixation, the thermocouple was only slightly inserted into the insect's thorax. In the first measurement, the temperature and IR radiation of very hairy bees were recorded parallel during heating and cooling down. Before the second measurement, the hairs were completely removed from the part of the thorax where the radiation was registered.

Internal thoracic temperatures To predict internal thoracic temperatures from surface temperatures, experiments were carried out with an arrangement like that for dead bees, but with the thermocouple inserted into the thorax just beneath the cuticle. The thorax was heated up to 39-41C. In comparison with data obtained from dead bees, the temperature difference between the surface and the tissues just beneath the cuticle could be determined.

YOUNG HONEY BEES: Young bees were hatched in their brood comb in a thermostat in August 1985. At the ages of 5 hours, 1 day, and 2 days, they were allowed to find their preferred temperatures⁵ in l-m long, U-shaped aluminum rails (inclined 40°) within a temperature gradient of 50-25C. The rails were covered with IR-transmissive plastic foils. Attenuation of the IR radiation by the foils was corrected for. In each trial, five bees were placed in one rail and thermographed from the dorsal view. Adult bees produce a lot of heat in their thoraces, but not in their abdomens. Knowing this, we could make relative comparisons with greater accuracy, and temperature differences between thorax and abdomen were used to define phases of heat production. FORAGING HONEY BEES: By the end of June 1986, we had trained 30 adult bees to fly from their 2-comb observation hive¹⁴ to a pneumatic feeding bowl 2 m from their hive. The foragers drank 1-M sucrose solution from this glass bowl and repeatedly carried food into their hive. The feeding bowl was protected from wind and direct solar radiation by a box that was open on one side; the whole feeding place was protected by a wind guard and a sun shade. During a bee's entire visit at the bowl (landing, drinking, cleaning, and flying off) thermography was performed from the dorsal view. In this way, continuous body temperature curves and the associated activity patterns were obtained for undisturbed foragers.

FORAGING HORNETS: Twenty cm from their artificially covered housing, adult hornets were fed with unlimited honey and thermographed in the same way as described for foraging bees. The hornets could reach or leave the honey by crawling or flying. Again, the feeding place was protected from air movements and uncontrolled ambient radiation.

Results

CALIBRATIONS REFERRED TO THE HONEY-BEE THORAX: Figure 3 shows the calibration values determined for artificially heated dead bees at the four measurement temperatures. The mean was calculated as $\epsilon'(H) = 0.994$ (SD = 0.028, 28 measurements with 8 bees; H means artificially heated). This calibration value was used for temperature determinations in connection with our equipment.

A typical calibration curve for a living honey bee is shown in Figure 4. The mean calculated emissivity $[\epsilon'(L)]$ was 1.007 (SD = 0.047, 190 measurements with 4 bees; L means living), which is well within 1 SD



Figure 3. Emissivity values, $\varepsilon'(H)$, of the thoraces of 8 artificially heated honey bees, measured at different thoracic surface temperatures. Ambient temperature = 23.2-24.3C. Vertical bars = standard deviations.



Figure 4. Calibration values from the thoracic surface of a living honey bee with medium hair density. IU = instrument-specific isotherm units (see text). Ambient temperature = 22.4C.

of $\varepsilon'(H)$, and thus confirms the calibrations with the artificially heated bees.

Slightly less radiation was registered from a completely depilated thorax than from the hairy thorax, probably because the hairs extend outward from the thorax and therefore have lower tip temperatures. Conversion of the radiation difference into a temperature difference indicated ~0.2C lower temperatures were indicated for the hairy bees. However, because our calibrations on dead bees (see above) included the effect of the natural variation in hair density, this correction was omitted.

Temperatures within the thoraxes, just beneath the cuticle of a thorax heated to 39-41C (ambient temperature 20-23C), are about 1C higher than on the surface.

MEASUREMENT ACCURACY: The calibrations with living bees clearly confirmed those from artificially heated thoraces. Because experimental conditions could be more accurately controlled in the latter case, the standard deviation of $\varepsilon'(H)$ was used to estimate the measurement accuracy for absolute determinations of thoracic surface temperatures. In calm air and without direct solar radiation, absolute surface temperatures were measured with an accuracy of approximately ± 0.45 C. Relative measurements were made with an accuracy of about ± 0.25 C.

MEASUREMENTS IN HORNETS: Because hornets are anatomically and biochemically related to honey bees, the above calibrations are thought to be a sufficient basis for thermographic temperature recordings in hornets.



Figure 5. A: A young honey bee sitting motionless on the temperature gradient of an aluminium rail, viewed through a foil. Head (top), thorax, and abdomen have the same surface temperature (35.6°C). Five of her 6 legs are visible. Air temperature near the bee is ~35.C (21-mm extension ring); the honeybee's length is ~1.5 cm. With respect to the bee, each color represents a difference of about 0.22C; white indicates the hottest and black the coolest parts of the scale. B: A young bee (viewed through a foil) walking on the rail has actively warmed her thorax (head with the two violet antennae). Part of the warmth produced in the thorax has reached the bee's head. Surface temperature of her head (blue) is about 25.8C; thorax (orange), 27.6C; abdomen (green), ~25.2C. Air temperature near her is ~25.0C. 21-mm extension ring. With respect to the bee, each color represents a difference of approximately 0.60C, with white indicating the highest temperature. The central color disc on her thorax was taken for exact measurements (the same was done for the head and abdomen), mainly because the thorax is spherical and most radiation reaches the IR detector from the central disk. The outer rings show wrong, cooler values.

YOUNG HONEY BEES: The five bees either sat motionless on the rail at their preferred temperature (rail temperature about 41.5C) or walked up and down. If an insect that did not actively heat up herself walked to the warmer parts of the rail, she was passively warmed. After she had run back to cooler regions, her head, thorax, and abdomen were still warm and gradudlly (nearly synchronously) cooled down to the new ambient temperature.

In walking and resting 5-hour-old bees, heads, thoraces, and abdomens were always at the same temperature (Figure 5A. Figure 6). One-day-old bees that were walking around had a mean thoracic temperature 1.8C (SD = 1.12) warmer than their abdominal temperature. In the 2-day-old bees, the difference between thoracic and abdominal temperatures was 3.9C (SD = 2.29), with a maximum value of 7.1C (Figure 5B, Figure 6). The thorax of resting bees was only slightly warmer than the abdomen at the ages of 1 and 2 days, although in 1-day-old bees the highest difference was 1.8C and in 2-day-old bees it was 2.6C (Figure 6).

FORAGING HONEY BEES: During their visits, the foragers stayed at the feeding bowl for 46.4 sec (SD = 8.82; n = 42). The mean ambient temperature (t_a) was 25.2C (Table 1; see Figure 9); the temperature of the sucrose solution was about 26C.

Figure 7 shows a thermogram of two foraging bees. Thoracic temperature curves for eight honey bees are presented in Figure 8, A and B. Heated by flight, the foragers landed with a mean thoracic surface temperature (t_{Th}) of 41.1C (Table 1; Figure 9). Afterward, they showed distinct warming-up and smaller cooling-down phases. During the total stay, thoraces were heated up to a mean maximum value of 43.7C (highest observed temperature 45.4C) without wing strokes.

In 72% of the visits, the insects reached the highest $t_{Th}s$ during drinking, cleaning, and going, and in 28% of the stops before taking off. The lowest $t_{Th}s$ were observed (in 53% of the visits) immediately



Figure 6. Temperature elevation of the thorax as compared to the abdomen of young bees of different ages. Filled boxes are sitting bees; open boxes, walking bees, means with SDs; the total numbers of bees in each group are written below the boxes; filled circles, sitting bees; open circles, walking bees—maximum values; t_{Th} : thoracic surface temperature, t_{Abd} : abdominal surface temperature.

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Table 1. Thoracic Surface temperatures (t_{Th}) of Honey Bees Foraging at a Feeding Place 2 m from the Hive and Fed a 1-M Sucrose Solution at ~26°C. t_a = Ambient Temperature

Temperatures	Mean (°C)	SD	Ν	Range (°C)
Landing t _{Th}	41.4	0.86	48	39.4-42.9
Minimum t _{Th}	41.1	0.97	51	38.9-43.0
Maximum t _{Th}	43.7	0.92	73	41.8-45.4
Take-off t _{Th}	43.5	0.91	56	41.8-45.4
t _a	25.2	0.93	83	23.8-26.2

after landing, during drinking, cleaning, and going (in 43%), and before taking off (in only 4% of the visits).

Five individuals warmed their thoracic surfaces to 45C (!) and remained at this high level for up to 30 seconds (Figure 8, A & B). Of special interest are the enormous heat production rates. One bee, for example, increased her t_{Th} by 4C within 8 seconds, and by 5C within 18 seconds, beginning at the very high baseline value of 40.2C (Figure 8 A, continuous curve at $t_a = 26.0$ C).

Heads and abdomens were always significantly cooler than thoraces and, therefore, invisible in the IR image when registered with the measurement ranges of 5 and 10C per full scale (Figure 7). However, some infrared pictures showed head temperatures of about 31.5C and abdominal temperatures of \sim 29C (Figure 9).



Figure 7. Thermogram of two foragers at a feeding place 2 m from their hive, drinking 1-M sucrose solution. The bee on the right has one leg on the thorax of the bee on the left. Therefore, it is impossible to obtain precise measurements of the thoracic temperature of the bee on the left. The thoracic surface temperature of the right forager is 45.IC (central, yellow disc). Her head and abdomen are cooler and not detectable with the range used. Each color represents an interval of 0.7C, with white being the hottest. Ambient temperature is 26.0C. A 21-mm extension ring was used.



Figure 8. A: Thoracic surface temperatures of 4 foragers during their visit to a feeding place 2 m from their hive. Full arrows symbolize landing (at 0 sec) and taking off. c = cleaning; d = drinking; g = going; $t_a =$ ambient temperature. Vertical lines separate different activities. **B:** Further surface temperature curves of the thorax of the 4 foragers during their visit to the feeding place. Symbols as in Fig. 8A.

Some inscets could be thermographed in free flight just before landing. Their thoracic surface temperatures were similar to the temperatures measured after landing.

FORAGING HORNETS: Figure 10 is a thermogram of a hornet sitting in front of its nest. Its thorax is warmer than its head and abdomen.

The 11 observed female hornets remained at their feeding place 100-280 sec when the ambient tem-



Figure 9. Mean thoracic surface temperatures of foragers during their visit to the feeding place. Open boxes = means with SDs; max = mean maximum thoracic surface temperature; min = mean minimum thoracic surface temperature; thick black arrow directed downward = mean landing, and thick black arrow directed upward = mean take-off thoracic surface temperatures; small horizontal arrows = sample temperatures of head (Ca), thorax (Th), and abdomen (Ab) on one bee; t_a = ambient temperature. Temperature of the 1-M sugar water = ~26C.

perature was 18 - 18.6C. The surface temperature curves of head, thorax, and abdomen of one hornet that went from the nest entrance to the honey and stayed there for 4.25 min are shown in Figure 11A. Her thoracic temperature is clearly elevated (29.8-38.2C), warming-up phases without visible wing movements were seen during drinking and departure. Her head reached about 28C, and her abdomen reached nearly 24C, indicating heat flux from her thorax to her head and abdomen. Surface tempera-



Figure 10. A hornet in front of its housing before she went to her feeding place. Her antennae (right), head, thorax, legs, wings and abdomen are clearly visible. Surface temperature of head (full red) = ca. 22.8C; thorax (orange) = 24.2C; abdomen (red) = ca. 22.1C. Ambient temperature = 18.6. 12-mm extension ring, the hornet's length is ca. 3 cm. Each color represents an interval of ca. 1.3C with white being the hottest. See Fig. 5B too.

tures and activities of another three hornets are given in Fig. 11B.

Mean values were calculated from the individual temperature curves during the visit. Because of the high fluctuations in t_{Th} , as in honey bees, the highest and lowest values and the temperatures just before taking off were averaged separately (Fig. 12). The highest t_{Th} measured in a walking hornet was 41.6C, which was 23C above the ambient temperature of 18.6C.

Discussion

True Emissivity of Honey-Bee Thorax: Theoretically, emissivity should not vary significantly within a temperature range of l0C, as it does in our calibrations However, Figure 3 shows that $\varepsilon'(H)$ was higher at higher thoracic surface temperatures. For the present calibration set-up, the following errors are possible.

Ambient temperature ε' had been calculated by means of the calculator programs supplied by AGEMA. The main formulas were:

$$\varepsilon_{o} = \frac{\Delta i_{or} + \tau_{r} \varepsilon_{r} (I_{r} - I_{a})}{\tau_{o} (I_{o} - I_{a})} \text{ and}$$
$$I = \frac{A}{C \cdot e^{\frac{B}{T}} - 1}$$

where: I = calibrated thermal value, referring to the instrument's calibration function (in instrument-specific "isotherm units," IU); A, B, C = instrument-



Figure 11. A: Body-surface-temperature curves for one hornet during a visit to the feeding place. Open horizontal arrow = the hornet went to the honey; t_a = ambient temperature; other symbols as described in Fig. 8A. **B:** Body-surface-temperature curves for 3 hornets fed with honey at the feeding place. f = fanning; other symbols as described in Fig. 8A and Fig. 11A. t_a = ambient temperature (range).

specific calibration constants; ϵ' = emissivity; Δi_{or} = measured relative thermal value, referring to the difference between object and reference source measurements (IU); τ = atmospheric correction factor; subscripts a, o, r refer to "ambient", "object", "reference source"; T = absolute temperature (°K).

These equations are valid when the ambient temperature and the distance from the scanner are the same for object and reference source. Since these conditions were fulfilled, correction for ambient radiation by inserting the ambient temperature into the above equations was possible. Without correction, the values in Figure 3 would have been expected to be higher at lower thoracic temperatures; because the



Figure 12. Mean surface temperatures of head, thorax, and abdomen of 11 hornets (female imagines). $t_a = ambient$ temperature (range = 18.0-18.6C). For other symbols, see Fig. 9.

reverse was the case, possible errors were corrected by the calculator program with sufficient accuracy.

Cuticular temperature gradient Our calibrations have demonstrated that, in calm air, the temperature beneath the cuticle of a heated thorax is about 1C higher than on the surface. If the cuticle were partly transparent to IR radiation, the scanner could have detected additional radiation from the underlying cuticular layers and tissues. This could have caused the higher ε' -values at higher temperatures in Figure 3. Similar effects were reported for human skin.²⁰⁻²² We know of no reports on cuticular IR transparency

in honey bees, so this problem can only be resolved in so far as ε' is not influenced if the cuticle is opaque and slightly elevated ε' -values have to be expected if there is some transparency.^{21,22} Until this question is solved, all calibrations and ε -values presented in this paper are fully valid only for the intact, heated thorax.

Surface-temperature recording by thermocouples During calibration, the thoracic surface temperature was measured by thermocouples of low heat capacity (wire diameter 50 μ m). Nevertheless, one has to take into account that slightly-too-low surface temperatures would have been recorded in any case. With higher thoracic temperatures (greater difference from the ambient temperature) greater measurement errors should be expected. Therefore, corresponding to the AGEMA formulas, ε' seems to be (more) overestimated at higher thoracic temperatures (cf. Figure 3).

Conclusions

From the above discussion, it appears that the values of ε' presented are most likely a bit too high. Therefore, the lower parts of the standard deviations in Figure 3 are considered more valid than the upper ones. In addition, the ε' values at 32.5 and 31.6C are probably less influenced by possible measurement errors than those at 39 and 41C. So the band emissivity (~3.5-5.6 µm) of the honey bee thorax with intact and heated underlying tissues is supposed to lie within the following limits

 ϵ (3.5-5.6 μ m) ~ 0.955 - 0.990

where ε refers to the radiation emitted normal to the surface of the thorax.^{23,24} The emissivity of honeybee thoracic cuticle therefore is as close to the emissivity of a black body as that of the human skin.^{21,24}

YOUNG HONEY BEES: Five-hour-old bees did not actively heat up their thoraces.²⁵ Confirming Himmer's finding,⁴ it was demonstrated that l-day-old bees are already able to produce heat in their thoraces. The thermogenic capacity of 2-day-old bees seems not to be so well developed as that of adult honey bees.

FORAGING HONEY BEES: Five very hot foragers, who kept their thoracic surface temperatures at about 45C for up to 30 sec (at an ambient temperature of 25C) are most remarkable. Taking into account that 41C was registered beneath the cuticle at a surface temperature of 40C ($t_a = 20-23C$, see calibrations), we expect near 47C in the innermost part of the thorax at 45C surface temperature. Similarly high thoracic temperatures of 50C were measured with inserted thermocouples by Heinrich²⁶ and Cooper et al.,¹⁹ but only at much higher ambient temperatures (> 40C). According to Esch and Bastian,²⁷ the heat is produced by activation of the indirect flight muscles. Whether honey bees are capable of biochemical thermogenesis, as discussed by Surholt and Greive for bumblebees (personal communication), is unknown.

Until now the following facts were known on the temperature behaviour of foragers at feeding sources:

Esch⁷ fed a 2-M sucrose solution to honey bees (A. *m. mellifera*) at feeding places at various distances from their hive. A microthermocouple was hung in a prepared cuticular hole in a bee's thorax after landing. He observed that the thoracic temperature

depended on t_a and feeding place distance. At a t_a of about 25C (as in our experiments), the average thoracic temperatures after landing were found between 34-36C.

Heinrich²⁶ caught worker bees (*A. m. adansonii*) from flowering plants and inserted a thermoneedle tip into them. With higher t_a their thoracic temperatures increased. At a t_a of 25C in shade the insects had 37C (mean) thoracic temperatures.

Schmaranzer^{10,13} trained bees (*A. m. carnica*) to visit a feeding place 90 meters from their hive where 1-M sucrose solution was offered. Their body temperatures were registered by means of thermography. The foragers showed distinct warming-up and cooling-down phases at different activities between landing and taking off. The average t_{Th} (surface) was 40.4C ($t_a = 20.8C$), and the mean abdominal temperature was 27.8C.

Stabentheiner and Schmaranzer²⁸ thermographically investigated bees (A. m. carnica) foraging 335 m from their hive. At $t_a = 25C$, foragers drinking 0.25-M sucrose solution reached mean maximum $t_{Th}s$ of 38.7C; those fed with 0.5 M solution reached 40.1C. Bees drinking sweeter sugar-water of 0.5-M were warmer and showed less temperature fluctuations than bees drinking 0.25-M solution. At test time (September), not much natural food was available. The higher molarity might have led to an elevation of food attractivity combined with more motivation for the animals to store the sugared water. In the present study, the bees drank 1-M solution, reaching an average maximum t_{Th} of 43.7C (Figure 9). These results, together with the data of Schmaranzer^{10,13} support our preliminary model that an increased motivation to gather food can probably increase the thoracic temperature. Because they used different experimental conditions and different bee races, comparisons with the works of Esch and Heinrich are difficult. Body temperatures in our study were measured at artificial feeding places, they should not be directly extrapolated to free-flying bees foraging on plants.

Present knowledge about temperature behavior as it relates to activity patterns at feeding places allows a better starting place for estimating energy balance in bees. During stops at food sources, neither the respiratory capacity nor carbohydrate metabolism of freemoving individuals is known. Therefore, body temperature is a valuable physiologic parameter.²⁹ The unexpectedly high $t_{Th}s$ at relatively low t_as should revise some speculative energy balance calculations for foraging honey bees.

FORAGING HORNETS: Like adult honey bees, hornets actively regulated their body temperature at their

feeding place. Ours reached a thoracic temperature excess of up to 23C over t_a . Head and abdomen temperatures stayed below t_{Th} . They surely have obtained a great amount of their warmth by hemolymph circulation from the thorax; we suspect that the heat production, as in honey bees, effected by activation of the indirect flight muscles.

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