

Seasonal and daily variation of honeybee dancing temperature under constant feeding conditions

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Summary — The seasonal and daily variation of the thorax temperature of dancing honeybee foragers, which gathered sucrose solutions from feeding places of constant quality (concentration and distance), was investigated by infrared thermography. Dancing temperature varied significantly between different days of the foraging season and depended on the time of day. In the morning and evening it varied much more than during the rest of the day. Part of this variation was caused by the hive temperature. The degree of cloudiness had no effect. In addition to intra-individual variations, some bees differed in the level of thermoregulation throughout the whole day (= inter-individual variation). Dancing temperature correlated neither with the stores of honey or pollen nor with the number of brood cells or empty cells. Since no correlation was found between the rate of recruited bees and dancing temperature it seems improbable that the dancers' body temperature acts as a predominant signal of food source profitability for the recruited bees.

honeybee / dancing / season and daytime / thermoregulation / thermography

INTRODUCTION

Honeybees foraging from artificial food sources exhibit high variability of dancing temperature: it is increased when the food contains much sugar and when the food source is near the hive (Stabentheiner and Haggmüller, 1991; Stabentheiner et al, 1995; Stabentheiner, 1996). In previous investi-

gations, however, the dancing temperature of individual bees sometimes changed between different experiments or different times of the day though the feeding conditions (ie, sugar concentration and foraging distance) were kept constant, ie, *intra*-individual variability of dancing temperature was observed (Stabentheiner and Haggmüller, 1993; Stabentheiner et al, 1995). Some dancers

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differed in the level of thermoregulation despite the fact that they had been foraging from the same food source at the same time (ie, they showed *inter*-individual variability). Although part of this variation can be attributed to the air temperature in the hive (Stabentheiner et al, 1995) these experiments suggested that time of day, season and other factors might also have an effect. In the present paper, therefore, for the first time the *intra*- and *inter*-individual variability of the thoracic temperature of dancing foragers was investigated by means of the non-invasive method of infrared thermography, which allowed repeated temperature measurements without affecting social or individual behavior.

Lindauer (1948) reported that the dancing threshold (ie, the sucrose concentration at an artificial food source that just elicited dancing) changed within a wide range during a foraging season. Since the threshold was high when much natural food was available (and vice versa) he concluded that it was the relative profitability of the artificial food source in comparison with natural sources which set the threshold concentration for dancing. In order to see to what extent the competition of natural food sources modulates the thermal behavior of dancing honeybees foraging from food sources of constant quality (sucrose concentration and foraging distance) their thorax temperature was measured thermographically throughout a foraging season. The thoracic temperature was compared with the air temperature in the hive, the meteorological conditions at the feeding place and the hive status.

Lindauer (1948), Boch (1956), Bräuninger (1964) and von Frisch (1965) showed that, if the food source is kept constant, the percentage of dancing foragers usually drops temporarily around noon during days with fine weather. A similar drop was observed in the duration of dances (von Frisch, 1965) and in the arrival rate at the

feeding place as a measure of foraging intensity (Schuà, 1952). This effect was called 'midday sluggishness' ('Mittagsträgheit'). The present investigation addressed the question as to whether the foraging intensity correlates with the foragers' dancing temperature as an indirect estimate of their dancing and foraging motivation (Stabentheiner and Haggmüller, 1991).

As the body temperature of dancing bees is modulated by food source quality (sugar content and distance; Stabentheiner and Haggmüller, 1991; Stabentheiner et al, 1995; Stabentheiner, 1996), it was hypothesized that it might provide the dance attendants with information about the quality of a food source (Schmaranzer et al, 1988; Stabentheiner and Haggmüller, 1991). However, attempts to test this working hypothesis with a heated robot bee were not successful (Michelsen, 1993). In the present investigation, the comparison of the dancing temperature with the rate of bees recruited to a feeding place should give further hints as to whether or not dancing temperature might act as a signal of food source profitability for the recruits.

MATERIALS AND METHODS

The experiments were performed in August 1991 and during the whole foraging season in 1992 (24 April to 25 October), with one colony in 1991 and two different colonies in 1992 in a farmland location near Graz, Austria. The bees (*Apis mellifera carnica* Pollm) were housed in four-comb observation hives (two parallel rows of combs). In order to shield the measurement site from solar radiation, which would have disturbed the thermographic measurements, the hive was placed inside a garden house in 1991 and inside a heated blockhouse in 1992. Since the glass pane covering the hive would have absorbed all infrared radiation it was replaced by an infrared transmissive plastic foil, which also reduced heat loss of the hive (Stabentheiner, 1991). Calibrations took into account the foil's attenuating effect on the radiation emitted by the bees.

The air temperature within the hives was measured 1 cm above the dance floor within 5 cm of the dancers' positions by several NiCr/Ni thermocouples (diameter of wires: 0.2 mm) which were clamped beneath the infrared transmissive foil. Temperatures were taken from Technoterm 9400 thermocouple thermometers.

Thoracic surface temperature was measured by means of an AGA 782 SW real-time thermovision system (AGEMA IR-Systems; Schmaranzer, 1983). The infrared radiation emitted by the bees was compared with the radiation of an AGA 1010 reference source, which was precision calibrated against a black body radiator of our own construction (Stabentheiner and Schmaranzer, 1987). Using an emissivity of 0.97 of the honeybee cuticle (Stabentheiner and Schmaranzer, 1987), self-written PC-software allowed calculation of absolute body surface temperatures. This way an absolute measurement accuracy of 0.65 °C could be achieved. Relative (comparative) measurements could be made to the nearest 0.25 °C. The thermographic scenes were stored on videotape and analyzed later in the laboratory.

The experiments were conducted to investigate the effect of season (= seasonal investigation) and daytime (= daytime experiments) on the thorax temperature of foragers upon their returns to the hive. In both experimental setups the bees were marked individually by small dots of shellac color on the abdomen and one side of the thorax. To prevent disturbance of thermographic measurements only one small dot was applied to the left or right side of the thorax. In 1991 the bees were trained to gather a sucrose solution of 0.75 molar concentration from a pneumatic feeding bowl 500 m south of the hive (daytime experiment 1). In 1992 they gathered a 2 molar solution 120 m south of the hive (seasonal investigation and daytime experiment 2). Training of bees to the desired distances was finished at least 1 day before measurement. At the feeding stations, which were protected by a sun shade, meteorological factors (ambient air temperature, relative humidity, degree of cloudiness) and the foragers' arrival rate (bees/30 min) were recorded. Unmarked bees that had been recruited by the dancing foragers were caught immediately after their arrival and counted. They were left free after the experiments. Measurements were restricted to days of little or no wind.

In the seasonal investigation, care was taken to conduct the experiments around midday (1100

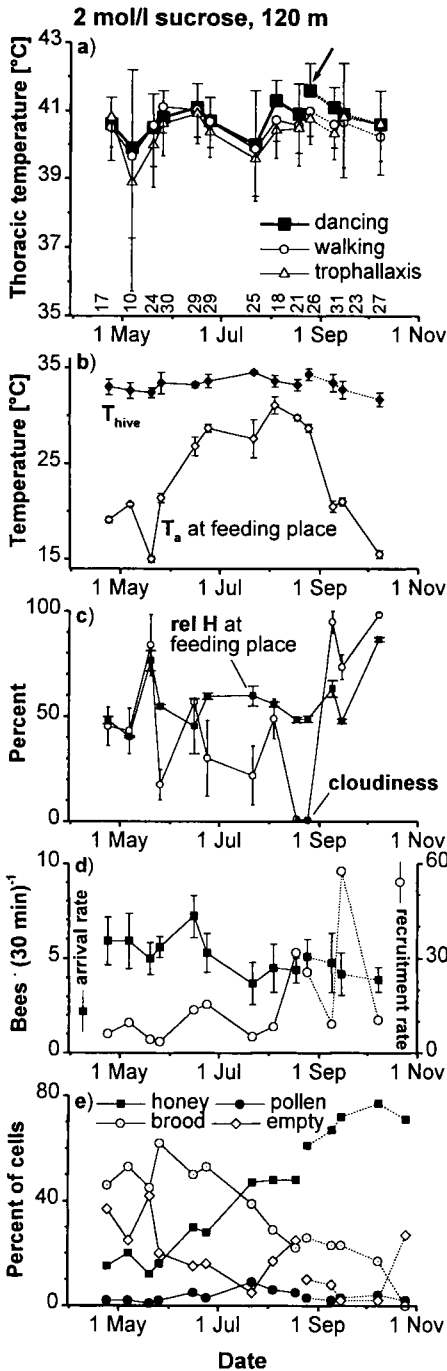
to 1500 hours) to reduce variation of the hive and outside temperature due to diurnal changes, and to avoid daytime effects on dancing temperature. The rate of recruited bees (per 30 min) was recorded at the feeding place. Every day of measurement the hive status was examined after the experiments. For this purpose we opened the hive in the periphery and between the two rows of combs, and estimated the number of cells with honey, pollen or brood and the empty cells separately for each side of the combs. Control countings showed a good agreement with our estimation. Finally, these values were summed up for all eight comb sides. A good estimate of the colony size (number of bees) would only have been possible by removing all bees from the hive and weighing them. Because such a procedure would have disturbed the colonies too much only a rough estimate was possible by appraising the number by eye (in lots of 500).

RESULTS

Seasonal variation

The foragers carried the 2 molar sucrose solution repeatedly into the hive. This high concentration was chosen to ensure that the bees were dancing throughout the whole foraging season (see Lindauer, 1948). Thoracic surface temperature was evaluated during dancing, walking and trophallaxis. For samples of thermographically measured temperature curves see Schmaranzer (1984), Stabentheiner and Haggmüller (1991), Stabentheiner et al (1995) and Stabentheiner (1996). From each of the temperature curves mean temperatures were calculated for the three activities. Statistical analysis was based on mean temperatures. From the mean temperatures average values were calculated for each day of measurement.

The average thorax temperature ranged from 39.9 to 41.6 °C during dancing; during other activities it was at a similar level or lower (39.7 to 41.1 °C during walking and 38.8 to 40.9 °C during trophallaxis; fig 1a). The mean temperatures during dancing and



other activities (walking, trophallaxis) correlated significantly ($P < 0.0001$, table I). Throughout the season the dancing temperature remained rather constant from 24 April to 16 June, decreased significantly between 16 June and 22 July ($P < 0.01$, U test) and increased significantly from 22 July to 4 August ($P < 0.01$; fig 1a). In the second hive the dancing temperature decreased successively from 25 August to 8 October ($P < 0.01$, fig 1a).

The standard deviation of average dancing temperatures varied between 0.56 and 1.53 °C, with the exception of 2.26 °C on 7 May, which was caused by one cool individual with mean temperatures of 35.3 to 35.4 °C (versus 40.3 to 41.6 °C in the other bees).

Table I shows that the dancing temperature correlated positively with the air temperature in the hive and at the feeding place. Between the dancing temperature and the relative humidity at the feeding place a negative trend but no significant correlation was indicated by t -statistics (table I), whereas Spearman's rank correlation test indicated a significant correlation ($P < 0.05$, rank correlation coefficient = -0.119). However, for the seasonal investigation only dances mea-

Fig 1. Seasonal variation of honeybee foragers' thorax temperature upon their return to the hive at constant feeding conditions (2 mol/L sucrose, 120 m feeding place distance, time of measurement 1100–1500 hours), in comparison with hive air temperature (T_{hive}), meteorological conditions at the feeding place (T_a : ambient air temperature, rel H: relative humidity), the foragers' arrival rate at and their recruitment success for the feeding place, and the percentage of different cell types in the four-comb observation hives (solid lines: hive 1, broken lines, hive 2). Vertical bars indicate standard deviation; 8 611 thermograms of 310 dances evaluated. a) Arrow indicates date of daytime experiment 2 (see fig 2), numbers on bottom give number of dances, 5–11 bees measured per day. d) Arrival rate: 5–10 values per mean.

Table I. Correlation of thoracic surface temperature, bioclimatological parameters, behavior (dancers' arrival rate at and the rate of bees recruited to the feeding place), and hive status during seasonal investigation in bees fed 2 mol/L sucrose at 120 m feeding place distance (cf fig 1).

$Y=A+BX$						
Y -axis	X -axis	A	B	N	R	t -Statistics
T_d	T_{hive}	35.96	0.146	310	0.136	*
T_d	T_a	40.25	0.024	310	0.116	*
T_d	rel H	(41.25)	(-0.008)	(310)	(-0.094)	ns ^{ab}
T_d	Cloudiness (%)	(40.85)	(-0.001)	(310)	(-0.029)	ns
T_{hive}	T_a	30.81	0.104	310	0.544	****
rel H	T_a	91.04	-1.410	310	-0.566	*****
T_d	T_w	4.89	0.885	268	0.915	*****
T_d	T_{tr}	8.60	0.797	248	0.876	*****
T_d	Arrival rate	39.82	0.194	310	0.223	****
Recruitment rate	Average T_d	(-405.6)	(10.33)	(13)	(0,323)	ns
Recruitment rate	Average T_d-T_{hive}	(-21.66)	(4.905)	(13)	(0,252)	ns
T_d	Honey cells (%)	(40.44)	(0.008)	(13)	(0,383)	ns
T_d	Pollen cells (%)	(40.84)	(-0.018)	(13)	(-0.085)	ns
T_d	Brood cells (%)	(41.24)	(-0.013)	(13)	(-0.396)	ns
T_d	Empty cells (%)	(40.91)	(-0.008)	(13)	(-0.217)	ns

T_d , T_w , T_{tr} : thoracic surface temperature ($^{\circ}$ C) during dancing, walking, trophallaxis, respectively; T_a , rel H: air temperature ($^{\circ}$ C) and relative humidity (%) at the feeding place, respectively; arrival rate and recruitment rate: bees/30 min. N : number of dances (mean dancing temperatures), R : correlation coefficient, *: $P < 0.05$, ****: $P < 0.0001$, *****: $P < 0.00001$, ns: not significant (^a $0.1 > P > 0.05$). ^b $P < 0.05$ ($R = -0.119$) with Spearman's rank correlation test (cf *Results*).

sured around midday of 25 August (the date of daytime experiment 2, see fig 2 and arrow in fig 1a) were included. When all data from this day are included in the regression analysis, t -statistics also indicates a significant negative correlation ($P < 0.05$).

Dancing temperature correlated positively with the marked foragers' arrival rate (bees/30 min) at the feeding place. The average rate of recruited (unmarked) bees arriving at the feeding place, which was determined for every experimental day, varied between 3.6 and 57.6 foragers per 30 min (fig 1), but did not correlate with dancing temperature (table I). Similarly, neither the supply of the colonies with honey or pollen, nor the amount of brood and empty cells

had an effect on dancing temperature (fig 1e, table I).

Daily variation

To investigate the daily variability of dancing temperature two experiments were conducted. In daytime experiment 1 the bees gathered a 0.75 molar sucrose solution at a pneumatic feeding bowl 500 m south of the hive. The weather was rather cool (fig 3b) with 25 to 100% of the sky covered by clouds (fig 3c). Because of the unsure weather condition, measurements were only possible after 0900 hours. Figure 4 shows two samples of the daily variation of mean

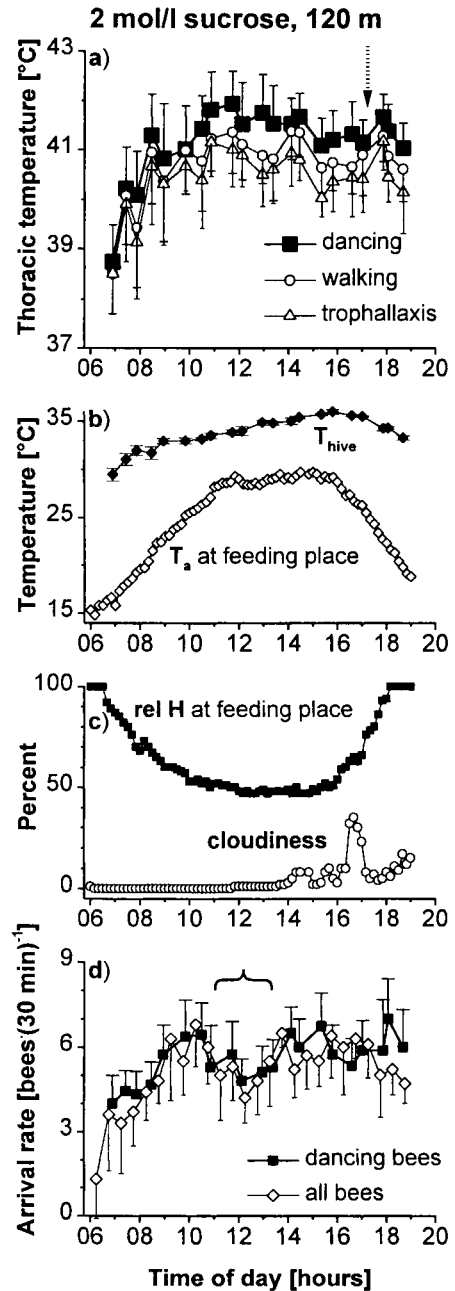
dancing temperature. In general, it varied between 34.1 and 41.1 °C. Most of this variation occurred in the afternoon. Mean dancing temperatures were averaged over intervals of 30 min. These average values fluctuated by about 1.5–2 °C during the main part of the day but decreased by 3.5 °C during the last 1.5 h of foraging (from 39.6 to 36.1 °C, fig 3a). Walking and trophallaxis temperatures were similar to or slightly lower than dancing temperature and followed its changes closely, which is confirmed by the significant correlation between the dancing temperature and the thoracic temperature during walking and trophallaxis, respectively ($P < 0.0001$, table IIa).

Hive temperature varied only slightly on this day. Accordingly, regression analysis indicated a positive trend but no significant correlation between dancing temperature and hive temperature or outside temperature, respectively (table IIa). Dancing temperature correlated negatively with relative humidity and (to a lesser extent) with cloudiness but not with the foragers' arrival rate at the feeding place (table IIa).

In daytime experiment 2 the bees gathered a 2 molar sucrose solution 120 m south

Fig 2. Daily variation of honeybee foragers' thorax temperature upon their return to the hive at constant feeding conditions (2 mol/L sucrose, 120 m feeding place distance), in comparison with hive air temperature (T_{hive}), meteorological conditions at the feeding place (T_{a} : ambient air temperature, rel H: relative humidity) and the foragers' arrival rate at the feeding place. Vertical bars indicate standard deviation. a) Symbols represent 30-min averages of seven foragers with three values per mean for the first average in the morning and 5–12 values for the rest of the day; 5401 thermograms of 169 dances evaluated; dotted arrow marks time of sunset. d) Brace marks significant drop of arrival rate around midday ($P < 0.01$, U test); no comparable drop in dancing temperature was observed. Dancing bees: for number of values see (a), all bees: seven values per mean.

of the hive (fig 2). On this day the weather was fine with only a few clouds in the late afternoon (fig 2b, c). As was expected from



previous experiments (Stabentheiner and Haggmüller, 1991; Stabentheiner et al, 1995) the bees that gathered the 2 molar solution

had higher thoracic temperatures than the foragers gathering the 0.75 molar solution in daytime experiment 1. The level of thermoregulation changed between different times of the day. Mean dancing temperatures (per stay in the hive) increased from 38.0–39.5 °C at dawn to 40.0–43.0 °C before midday. Referring to averages of 30 min this equals an increase by 3.2 °C (38.7–41.9 °C; $P < 0.02$, U test). During the rest of the day, dancing temperatures remained at this high level (fig 2a). In this experiment only a small but significant decrease was examined in the late afternoon (after sunset) before the bees stopped dancing ($P < 0.05$). Thoracic temperatures during walking and trophallactic contact with hive bees were similar to dancing temperature in the morning but 0.2–0.9 and 0.5–1.3 °C lower during the rest of the day, respectively (fig 2a). Dancing temperature correlated significantly with both of them ($P < 0.0001$, table IIb).

Ambient temperature at the feeding place increased from 14.9 °C at dawn to 29.7 °C after midday and decreased again in the late afternoon. Though the blockhouse was heated by a radiator at low ambient temperatures and despite the thermoregulatory efforts of the hive bees the air temperature in the dancing area correlated with outside

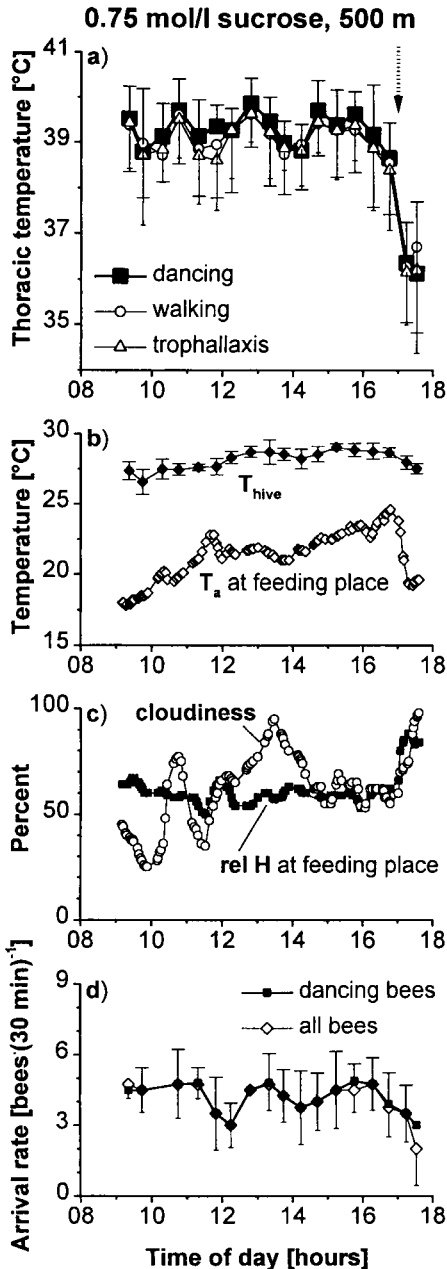


Fig 3. Daily variation of six honeybee foragers' thorax temperature upon their return to the hive at constant feeding conditions (0.75 mol/L sucrose, 500 m feeding place distance), in comparison with hive air temperature (T_{hive}), meteorological conditions at the feeding place (T_{a} : ambient air temperature, rel H: relative humidity) and the foragers' arrival rate at the feeding place. Vertical bars indicate standard deviation. a) Symbols represent 30-min averages of six foragers with 5–9 values per average; 3605 thermograms of 114 dances evaluated; dotted arrow marks time of sunset. d) Dancing bees: 3–7 values per mean, all bees: 6–7 values. For the daily course of two foragers' mean dancing temperature see fig 4.

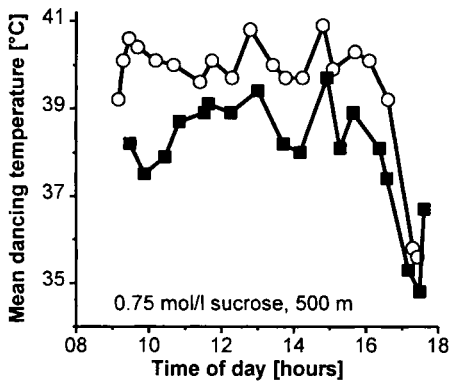


Fig 4. Samples of *inter*-individual differences of two foragers' mean dancing temperatures (per stay in the hive) over 1 day, from the experiment of fig 3.

temperature (table IIb, fig 2b). Accordingly, dancing temperature correlated with both hive and outside air temperature ($P < 0.0001$, table IIb). Because of the stable meteorological conditions the relative humidity at the feeding place changed approximately inversely to ambient temperature (fig 2b, c). Therefore, dancing temperature correlated negatively with relative humidity as in daytime experiment 1. No correlation was found with cloudiness (table IIb).

The arrival rate of the dancing foragers at the feeding place increased in a similar way to dancing temperature in the morning. However, its pronounced drop around mid-day (marked by a brace in fig 2d; $P < 0.01$, U test) was *not* accompanied by a comparable drop of dancing, walking or trophallaxis temperature (fig 2a). Accordingly, no correlation was found between mean dancing temperature and arrival rate (table IIb).

Interindividual differences

In both experiments concerning the daily variability some bees had a higher thoracic temperature than others all day long (fig 4).

Inter-individual variability could be confirmed in both experiments by analysis of variance (experiment 1: $df = 5$, $F = 5.21$, $P < 0.001$; experiment 2: $df = 6$, $F = 14.08$, $P < 0.0001$). Referring to the whole day, in daytime experiment 1 two of the six investigated bees had dancing temperatures that differed significantly from that of one other individual ($P < 0.01$, Scheffe's test). In daytime experiment 2 all of the seven investigated bees showed dancing temperatures that differed significantly at least from one and a maximum of five other individuals ($P < 0.01$).

DISCUSSION

Previous investigations showed that the thermal behavior of honeybee foragers is more variable than expected both inside the hive (Stabentheiner and Haggmüller, 1991; Stabentheiner et al, 1995; Stabentheiner, 1996) and outside during foraging from artificial food sources (Schmaranzer and Stabentheiner, 1988) and plants (Kovac and Schmaranzer, 1996). Since this research showed that quality and foraging distance modulate the foragers' thermal behavior to a remarkable extent, the experiments were performed with a food source of constant quality (ie, sucrose concentration and distance). Because of the high expenditure of time necessary to evaluate real-time thermographic scenes and because of the many variable parameters in field experiments the investigations have to be considered (and were designed) as a first screening of the seasonal and daily variability of honeybee dancing temperature. Together with previous research (Stabentheiner and Haggmüller, 1991; Stabentheiner et al, 1995; Stabentheiner, 1996) the results can give an impression of the possible variation of dancing temperature under constant feeding conditions but are not suited to allow an exact prediction for a certain day or time.

Table II. Correlation of thoracic surface temperature, bioclimatological parameters and behavior (dancers' arrival rate at and the rate of bees recruited to the feeding place) during daytime experiments.**a) Experiment 1:** bees fed 0.75 mol/L sucrose at 500 m feeding place distance (cf fig 3).

$Y=A+BX$						
<i>Y-axis</i>	<i>X-axis</i>	<i>A</i>	<i>B</i>	<i>N</i>	<i>R</i>	<i>t-Statistics</i>
T_d	T_{hive}	(33.60)	(0.192)	(114)	(0.134)	ns
T_d	T_a	(36.62)	(0.112)	(114)	(0.160)	ns ^d
T_d	rel H	45.78	-0.109	114	-0.723	****
T_d	Cloudiness (%)	40.18	-0.019	114	-0.289	*
T_{hive}	T_a	21.31	0.319	114	0.655	*****
rel H	T_a	96.09	-1.601	114	-0.346	**
T_d	T_w	6.94	0.826	111	0.913	*****
T_d	T_{tr}	6.36	0.842	111	0.933	*****
T_d	Arrival rate	(38.25)	(0.175)	(114)	(0.168)	ns ^d

b) Experiment 2: bees fed 2 mol/L sucrose at 120 m feeding place distance (cf fig 2).

$Y=A+BX$						
<i>Y-axis</i>	<i>X-axis</i>	<i>A</i>	<i>B</i>	<i>N</i>	<i>R</i>	<i>t-Statistics</i>
T_d	T_{hive}	34.02	0.213	169	0.374	*****
T_d	T_a	38.67	0.101	169	0.451	*****
T_d	rel H	42.14	-0.014	169	-0.278	***
T_d	Cloudiness (%)	(41.24)	(0.0007)	(169)	(-0.007)	ns
T_{hive}	T_a	25.99	0.315	169	0.797	*****
rel H	T_a	155.23	-3.6369	169	0.834	*****
T_d	T_w	4.28	0.905	142	0.924	*****
T_d	T_{tr}	6.48	0.858	141	0.866	*****
T_d	Arrival rate	(41.21)	(0.005)	(169)	(0.007)	ns

T_d , T_w , T_{tr} : thoracic surface temperature (°C) during dancing, walking, trophallaxis, respectively; T_a , rel H: air temperature (°C) and relative humidity (%) at the feeding place, respectively; arrival rate: bees/30 min. *N*: number of dances (mean dancing temperatures). *R*: correlation coefficient. *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ****, $P < 0.0001$; *****, $P < 0.0001$; ns: not significant (^d $0.1 > P > 0.05$).

During a foraging season significant variations in dancing temperature may occur (fig 1). Maximum differences between daily averages of dancing temperatures amounted to 1.7 °C. However, temperatures were higher and variation was much lower than observed in bees communicating the location of natural nectar and pollen sources to other bees (Stabentheiner, 1995). This can be explained by the high dancing (and foraging) motivation caused by the high profitability of the 2 molar sucrose solution, which was offered at a feeder with continuous and

unlimited flow at close proximity to the hive (Stabentheiner and Hagmüller, 1991; Stabentheiner et al, 1995; Stabentheiner, 1996). For many natural nectar sources a lower foraging and thus dancing motivation has to be expected because it is more time consuming to gather many small nectar portions from different flowers than sucking from a continuous-flow source with unlimited reward (compare Pflumm, 1977; Balderrama et al, 1992; Moffat and Núñez, 1997). This is supported by the observation of Kovac and Schmaranzer (1996) that bees

foraging on flowers in summer had much lower thorax temperatures, and thus a reduced energetic investment, than bees gathering a 0.5 molar sucrose solution on artificial food sources with unlimited flow (Schmaranzer and Stabentheiner, 1988).

The experiments on daily variability showed that dancing temperature may change to a considerable extent in the morning or evening. During the rest of the day it is more constant (figs 2–4), which is supported by previous, independent experiments with 0.5 molar (1010–1435 hours), 1 molar (1050–1550 hours), 1.5 molar (1025–1430 hours) and 2 molar concentrations (1230–1420 hours) (Stabentheiner et al, 1995). Thermobiological investigations in dancing honeybees, therefore, should be avoided in the early morning or late afternoon except, for instance, for the purpose of demonstrating this variability.

In the morning or late afternoon dancing temperature changed within a few hours to a comparable extent as during a whole foraging season (compare figs 2 and 3 with fig 1). However, a colony's reserves of honey or pollen, or the amount of brood ordinarily do not change within a few hours to the extent found during the season. Because of the sometimes remarkable daily variability of dancing temperature, therefore, a direct influence of the number of honey, pollen, brood or empty cells on dancing temperature seems improbable from theoretical considerations. Therefore, it is not surprising that in the seasonal investigation no significant correlation could be detected between dancing temperature and the supply of the colonies with honey and pollen or with the amount of brood and empty cells.

Regression analysis indicated a significant positive correlation between dancing temperature and the estimated colony size. However, this significance resulted exclusively from a parallel decrease in dancing temperature and colony size in colony 2 ($P < 0.01$) which, in early autumn, was

developing more and more toward a winter colony and accordingly decreasing in size (compare Ruttner, 1992). In colony 1, which was investigated for the greater part of the foraging season, no relation was visible ($P = 0.561$). Taking into account that the colony size could be estimated only roughly it is obvious that investigations designed especially for this question would be needed.

In addition to daily changes in dancing temperature (= *intra*-individual variability) differences between bees (= *inter*-individual variability) contributed significantly to the total variability (fig 4), which was supported by analysis of variance in both daytime experiments. At present, however, the factors responsible for the differences between bees are not yet understood. Schweiger (1958) observed that the dance tempo (reversals/15 s) decreases with experience of foraging at a feeding place. Since there exists a positive correlation between dance tempo and thoracic temperature (Kirchner and Stabentheiner, unpublished data), further investigations will have to consider the foragers' experience of foraging and/or their age as possible contributors to the variability of dancing temperature.

In the seasonal investigation (fig 1), dancing temperature correlated with foraging intensity (measured as arrival rate at the feeding place). However, it is doubtful that there exists a direct relation between these two factors because no significant correlation was observed in the experiments concerning daily variability (table II), though even in these experiments, for part of the daytime, both parameters changed in the same direction (figs 2 and 3). The lack of a direct relation is demonstrated unequivocally by the experiment wherein the weather was constantly fine all the day: while the dancing foragers exhibited the classical drop in arrival rate around midday on days with fine weather (see brace in fig 2d; compare Schuà, 1952; von Frisch, 1965), no comparable drop in dancing temperature was

measured. If we accept dancing temperature as a rough estimate of the foragers' dancing and foraging motivation (Schmaranzer and Stabentheiner, 1988; Stabentheiner and Hagmüller, 1991) this means that the midday drop was probably not a result of a reduced foraging motivation. Since around midday an increased flight activity of the hive bees was observed (not quantified), it would be worth investigating the relation between dancing temperature and the following parameters: intensity of flight activity and 'playing about' (von Frisch, 1965) of hive bees in front of the hive entrance, foraging activity, and temporal patterns of interactions between hive and forager bees.

Among the factors modulating the thermal behavior of dancing honeybees ambient air temperature is very important (Esch, 1960; Stabentheiner et al, 1995). In two out of three investigations this could be confirmed for both hive and outside temperature (table I, table IIb). The lack of a significant relation between dancing and hive temperature in the daytime experiment 1 (table IIa) is assumed to be a result of the smaller variation in the hive temperature in this experiment (fig 3b). When the hive temperature varies in a broader range, the effect is highly significant (tables I, IIb; Stabentheiner et al, 1995). Despite the thermoregulatory efforts of the hive bees and the setting of a lower temperature limit by heating the blockhouse in the seasonal investigation and daytime experiment 2, the air temperature on the dance floor was always significantly correlated with the outside air temperature at the feeding place (tables I and II). Therefore, it cannot be decided conclusively whether dancing temperature was influenced directly by the hive temperature or indirectly by the outside temperature, or both. Because of the great heat loss small-sized animals such as honeybees have to cope with (Esch, 1960), the hive temperature is supposed to have a more direct effect, which in turn is influenced by the outside temperature.

According to the inverse relation between air temperature and relative humidity outside the hive correlation analysis indicated a negative relation of dancing temperature and relative humidity (tables I and II). The effect is an indirect one via the coupling of outside temperature with relative humidity and hive temperature.

In the investigation of seasonal variability and in experiment 2 concerning the daily variability, regression analysis did not indicate a relation between dancing temperature and cloudiness (tables I and IIb). Therefore it is suggested that the weak correlation found in the first investigation of daily variability (table Ia) results from a part coincidence of cloudiness with other meteorological factors (eg, ambient temperature) and does not indicate a direct relationship.

From theoretical considerations about the communication process between dancers and followers it seems probable that the number of dances and dance circuits per dance are important parameters to match a colony's foraging activity with the quality of a food source (Seeley and Towne, 1992). Schmaranzer et al (1988) and Stabentheiner and Hagmüller (1991) presented the working hypothesis that the dancers' body temperature might provide a signal of food source profitability for follower bees which receive the information about the location of a food source. If this was the case, the rate of bees recruited to a feeding place should correlate with dancing temperature. Table I shows that this was neither the case for the absolute values of dancing temperature nor for the differences between dancing and hive temperature. Therefore, the present investigation does not support the hypothesis of the dancers' thorax temperature as a direct signal of food source profitability. On the other hand, keeping in mind that the dancing temperature increases with food quality and proximity to the hive (Stabentheiner and Hagmüller, 1991; Stabentheiner et al, 1995; Stabentheiner,

1996), some participation of the thorax temperature in the recruitment process cannot be completely excluded at present. The increased rate of attacks against a heated robot bee (in comparison with a cold one) as was reported by Michelsen (1993) suggests that the hive bees and dance attendants notice a dancer's body temperature. Therefore, if body temperature has a meaning in dancing communication at all, it might play a role in the basic acceptance of the foragers by the attendants and/or hive bees. However, further investigations are needed to elucidate this question.

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Résumé — Variations saisonnières et journalières de la température thoracique des butineuses qui dansent dans des conditions constantes de nourrissage.

On a disposé une solution sucrée de qualité constante (concentration et éloignement par rapport à la ruche) à des stations de nourrissage et on a étudié, à l'aide d'une méthode de thermographie infrarouge ne perturbant pas la colonie, les fluctuations saisonnières et journalières de la température thoracique des butineuses qui dansent dans la ruche. Au cours de la période de végétation la température des danseuses a varié significativement, bien que les butineuses aient toujours récolté du sirop de concentration constante (2 mol/L) à la même station de nourrissage (120 m au sud de la ruche d'observation) et à la même période de la journée (11–15 h) (fig 1). Alors que du 24 avril au 16 juin on n'a mesuré aucune

variation significative (moyenne journalière 39,9–41,1 °C), la température des danseuses est tombée à 40,0 °C jusqu'au 22 juillet puis est remontée à 41,3 °C jusqu'au 4 août. Dans une seconde colonie la température a chuté de 41,6 °C le 25 août à 40,6 °C le 8 octobre. Chez des groupes d'abeilles qui ont récolté toute la journée du sirop à la même station de nourrissage (0,75 mol/L à 500 m et 2 mol/L à 120 m) les variations les plus fortes ont été observées le matin et le soir (figs 2 et 3). Une partie de ces variations saisonnières et journalières était due aux fluctuations de la température de l'aire de danse (tableaux I et II). Le niveau de population de la ruche n'a eu aucun effet décelable. Outre des variations intra-individuelles (journalières) on a mis en évidence des variations interindividuelles significatives qui se maintenaient souvent toute la journée (fig 4). La cause de telles différences n'a pu être élucidée. La température des danseuses n'était corrélée ni avec la quantité de miel ou de pollen emmagasiné, ni avec la quantité de couvain ou le nombre de cellules vides (fig 1, tableau I). Puisqu'aucune corrélation n'a pu être mise en évidence entre le taux de recrutement (nombre de novices recrutées/30 min) et la température thoracique des danseuses (tableau I), il semble improbable que la température corporelle des danseuses serve aux nouvelles recrues de signal primaire concernant la qualité de la source de nourriture.

thermorégulation / thermographie / danse / variation journalière / variation saisonnière

Zusammenfassung — Jahres- und tageszeitliche Variation der Thoraxtemperatur tanzender Honigbienen unter konstanten Fütterungsbedingungen. Die jahres- und tageszeitlichen Schwankungen der Thoraxtemperatur tanzender Honigbienen, die Rohrzuckerlösung von Futterplätzen konstanter Qualität sammelten (Konzentra-

tion und Entfernung vom Stock), wurden beim Aufenthalt der Bienen im Nest mit Hilfe der berührungslosen Infrarothermografie ohne Störung des Sozialverhaltens untersucht. Im Laufe einer Vegetationsperiode schwankte die Tanztemperatur signifikant, obwohl die Sammlerinnen immer Zuckerwasser gleicher Konzentration (2 mol/L) am selben Futterplatz (120 m südlich des Beobachtungsstockes) und zur gleichen Tageszeit (1100–1500 Uhr) sammelten (Abb 1): Während vom 24. April bis 16. Juni keine signifikanten Schwankungen gemessen wurden (Tagesmittelwerte: 39,9–41,1 °C), sank die Tanztemperatur anschließend (bis 22. Juli) signifikant auf 40,0 °C ab, um dann bis 4. August wieder signifikant auf 41,3 °C anzusteigen. In einem zweiten Volk sank die Tanztemperatur sukzessive von 41,6 °C am 25. August auf 40,6 °C am 8. Oktober. Bienengruppen, die einen Tag lang Zuckerwasser vom selben Futterplatz sammelten (0,75 mol/L bei 500 m bzw 2 mol/L bei 120 m) zeigten die größten Schwankungen der Tanztemperatur am Morgen bzw Abend; während der restlichen Zeit waren die Schwankungen viel geringer (Abb 2, Abb 3). Ein Teil der jahres- und tageszeitlichen Schwankungen war durch unterschiedliche Lufttemperatur am Tanzboden bedingt (Tabelle I, Tabelle II). Der Bewölkungsgrad hatte keinen nachweisbaren Einfluß. Neben diesen *intra*-individuellen (tageszeitlichen) Schwankungen wurden auch signifikante *inter*-individuelle Unterschiede zwischen Bienen festgestellt, die oft den ganzen Tag über bestehen blieben (Abb 4). Die Ursache solcher Unterschiede konnte nicht festgestellt werden. Die Tanztemperatur korrelierte weder mit der Menge an eingelagertem Honig oder Pollen, noch mit der Brutmenge oder Zahl leerer Zellen (Abb 1, Tabelle I). Da keine Korrelation zwischen dem Rekrutierungsfolg der Sammlerinnen (angeworbene Neulinge/30 min) und der Tanztemperatur feststellbar war (Tabelle I), scheint es unwahrscheinlich, daß die Kör-

pertemperatur der Tänzerinnen den angeworbenen Bienen als primäres Signal für die Qualität eines Futterplatzes dient.

Honigbiene / Tanz / Jahres- und Tageszeit / Thermoregulation / Thermografie

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