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Thermal investigations of a honey bee colony: thermoregulation of the hive during summer and winter and heat production of members of different bee castes

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Summary. The temperature at the centre, the periphery and the entrance of a honey bee colony (*Apis mellifera carnica*) was continuously determined during the summer season and the broodless time in winter. During the summer season the temperature in the brood nest averages 35.5 °C with brief excursions up to 37.0 °C and down to 33.8 °C. Increasing environmental temperatures resulted in linear increases in the temperature of the hive entrance, its periphery and its centre. The temperature in the centre of an overwintering cluster is maintained at an average value of 21.3 °C (min 12.0 °C, max 33.5 °C). With rising ambient temperatures the central temperature of a winter cluster drops whereas the peripheral temperature increases slightly. With decreasing external temperatures the peripheral temperature is lowered by a small amount while the cluster's centre temperature is raised. Linear relationships are observed between the central and the ambient temperature and between the central temperature and the temperature difference of the peripheral and the ambient temperatures. The slopes point to two minimum threshold values for the central (15 °C) and the peripheral temperature (5 °C) which should not be transgressed in an overwintering cluster. Microcalorimetric determinations of the heat production were performed on the three castes of the honey bee: workers, drones and queens of different ages. Among these groups single adult workers showed the highest heat production rates (209 $\mathrm{mW \cdot g^{-1}}$) with only neglectible fluctuations in the heat production rate. Juvenile workers exhibited a mean heat production rate of 142 $\mathrm{mW \cdot g^{-1}}$. The rate of heat production of adult workers is strongly dependent upon the number of bees together in a group. With more than 10 individuals weight-specific heat dissipation remains constant with increasing group sizes at a level approximately 1/17 that of an isolated bee. Differences are seen between the rates of virgin (117 $\mathrm{mW \cdot g^{-1}}$) and laying (102 $\mathrm{mW \cdot g^{-1}}$) queens. Laying queens showed less thermal fluctuations than virgin queens. High fluctuations in heat production rates are observed for drones. In both groups (fertile, juvenile) phases of high and extremely low activity succeed one another. The heat production of juvenile drones was 68 $\mathrm{mW \cdot g^{-1}}$, that of fertile drones 184 $\mathrm{mW \cdot g^{-1}}$ due to stronger locomotory activities.

Key words: Bees – Calorimetry – Heat production – Temperature – Thermoregulation

Introduction

One of the conditions necessary for development from a solitary mode of life to a life in an eusocial community is a shortening of the period required for individual development. Brood care, by providing energy through intensive feeding and warming, leads to a shortening of the time required for complete embryonic development. In addition to the individual requirement (i.e., the individual metabolic balance), heat production occurs which also benefits the adult members of the community. The investigations presented here are an analysis of the dynamics of thermoregulation in bee clusters with and without brood, and of the contributions of isolated members and small groups to the energy balance of the colony (workers with hive duties, foragers, juvenile and fertile drones, virgin and laying queens).

Biological reactions generally involve a significant heat production. Life is a continuous struggle against entropy which must be dissipated in the form of heat to the environment in order to maintain a state of low entropy characteristic of living organisms. Therefore, heat flow from biological systems can be used to monitor metabolic and locomotor activities without interfering with the system. Modern isoperibolic heat flow calorimeters (Calvet and Prat 1956; Hemminger and Höhne 1984) serve this purpose. They can be used in two ways: as instruments for quantitative evaluation of heat production rates as a function of time ($p-t$-curves), or as analytical tools to monitor activity patterns of the investigated animals (Lamprecht 1983). In this paper both methods have been used and reveal significant differences in heat production rates, as well as in activity patterns, between queens, workers and drones.

Most data in the literature on heat production of individuals or groups of bees have been obtained by indirect calorimetry, i.e., calculated from oxygen consumption and carbon dioxide production using a RQ of 1.0 and a factor of 21.13 $\mathrm{J \cdot ml\ CO_2^{-1}}$ produced (Ritter 1982). Direct calorimetric experiments are rare (Roth 1964, 1965), so that the values obtained here have to be compared with those of indirect calorimetry.

Until now most calorimetric experiments on social insects were run with single individuals, sometimes with several in one batch-calorimeter (Roth 1964, 1965). Such results provide information about the heat production of an isolated member of the stock but not about their interactions in terms of thermoregulation. A combination of calorimetry and thermometry for establishing energy balances has not yet been applied to bee populations, but may be compared with that for an ant hill (Coenen-Stass et al. 1980; Bachem et al. 1980; Bachem and Lamprecht 1983). Such investigations determine the contributions to the total energy balance of the stock by external climatic factors, behavioural heat production, metabolic heat production of the social insects and their different states, and finally by microbial populations on the construction material of the colony.

Materials and methods

Measurement of hive-temperature. The hive temperature of a bee colony (*Apis mellifera carnica*) was determined continuously during the spring and summer season of 1985 and during the winter season 1985/86. During summer the specially prepared hive was placed in a flight room. However, the bees were able to forage in the open. During winter the hive was placed in the open.

Temperature was measured with thermocouple wires (Cr/Ni) attached to a multiple channel-printer (Linseis 7005). Measurements were taken of the ambient temperature at the periphery and centre of the hive (in the broodnest between the combs) as well as at the hive entrance. The thermocouples remained in their position throughout the entire period of observation. The external temperature and the temperature of the flight room was monitored hourly by means of a digital thermometer. During winter temperature was monitored at the periphery and in the centre (between the combs) of an overwintering cluster as well as at the hive entrance.

The special hive of five combs was furnished with 12 small plastic tubes inserted into holes drilled in the combs. The thermocouples were adjustable in these plastic tubes. In this way the temperature of every point in the hive could be monitored. Visual control of the broodnest or the cluster position was possible by means of windows in the walls and the cover sheet.

During summer the colony consisted of approximately 20000 bees and brood at all developmental stages. The mass of the combs amounted to 2000 g.

Calorimetry. Calorimetric experiments were performed in a batch calorimeter of the Calvet type (Setaram/Lyon) with 4 vessels of 100 ml each. The sensitivity of the instrument was 53 $\mathrm{V \cdot mW^{-1}}$, with a time constant of approximately 8 min. The mean heat production rate of workers at 25 °C was 20 mW, so that the usual setting of the recorder (Kipp and Zonen/Delft, BD5+BA5) was 5 mV full deflection and a paper speed of 12 $\mathrm{cm \cdot h^{-1}}$. The power-time curves obtained were evaluated for maximum and minimum rates of heat production, the mean heat production over several hours, and for temporal structures, and thus activity patterns, in the heat output of the animals under investigation.

The mean heat production was determined by integrating the heat flow over several hours by means of a mechanical (Ott/Kempen) or electronic planimeter (Digikon; Kontron/München) and dividing by time. By this procedure individual periods of activity are eliminated and an energetic level near to mean metabolism is obtained. Because the time constant of the calorimeter is relatively long compared with the activity patterns the maximum heat flows are flattened.

Keeping of the experimental bees. Shortly before testing the bees were caught at the hive entrance (or in the hive) and transferred individually to the test vial (100 ml) containing some honey for feeding ad libitum and a paper strip for resting purposes. The measurements were made in summer (1985) from 9 am to 5 pm and they lasted 4 hours for drones and workers, and 2 hours for queens.

The bees were divided in six groups of young (3–6 days old) and adult (over 18 days old) workers, juvenile and fertile drones, as well as virgin and laying queens. Before and after the calorimetric measurement the bees were weighed to the nearest 0.1 mg (Sauter balance 414/13). The weight of the bees did not differ significantly before and after the experiments.

Results

Measurements of temperature in the colony

Over a period of 10 months (June 1985–March 1986) the measurements of temperature were made with reference to seasonal ambient temperatures and brood production. During the summer season the temperature in the brood nest averaged 35.5 °C

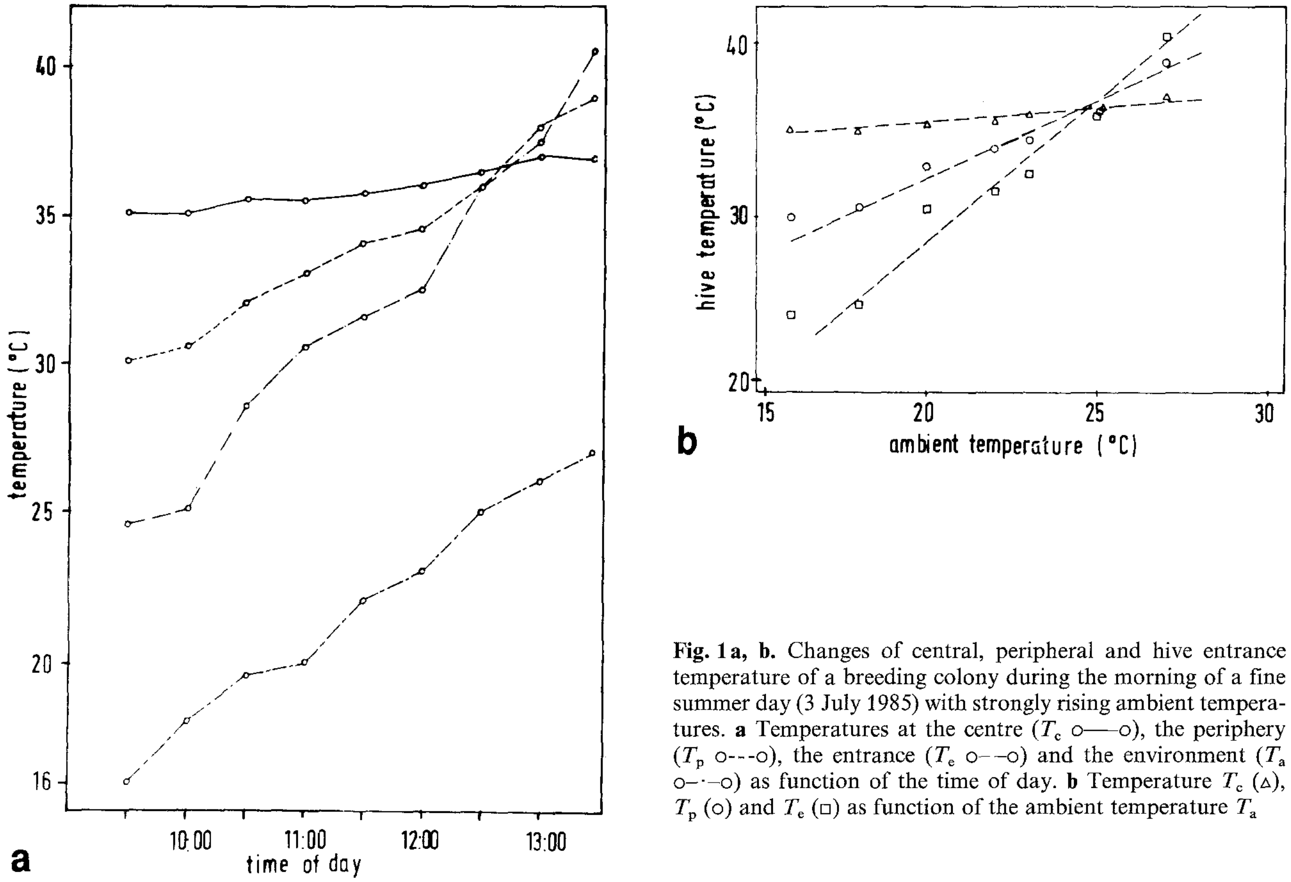

Fig. 1a, b. Changes of central, peripheral and hive entrance temperature of a breeding colony during the morning of a fine summer day (3 July 1985) with strongly rising ambient temperatures. **a** Temperatures at the centre (T_c o——o), the periphery (T_p o---o), the entrance (T_e o–-o) and the environment (T_a o–·–o) as function of the time of day. **b** Temperature T_c (△), T_p (o) and T_e (□) as function of the ambient temperature T_a

with some short excursions up to 37.0 °C and down to 33.8 °C, while the ambient temperature changed between 15 °C and 39 °C. The temperature variations at the peripheral areas amounted to 17 °C and at the hive entrance to 25 °C, about 10 times larger than in the nest centre.

Overheating and thermoregulation of a breeding colony

It is well known that bees concentrate on maintaining an optimal temperature in the brood nest (in this case 35.8 °C), compensating an increase in temperature by spreading water and fanning (Lindauer 1954; Heinrich 1985, 1979, 1980). Figure 1 shows the results of increasing ambient temperatures T_a on hive temperature. While the core temperature T_c rises only slightly (from 35.0 to 37 °C) in response to an outside increase of 11 °C, the temperature T_p at the periphery increases by 9.0 °C and at the entrance (T_e) by 16.5 °C, becoming slightly above that of the periphery. This might be due to the additional fanning activities of the bees for thermoregulation. Above 18 °C all three temperatures show a strong linear dependence upon the ambient temperature T_a. These relationships can be described by the following regressions: centre, $T_c = 0.222 \cdot T_a + 31.0$ ($r = 0.994$, $s = 0.041$); periphery, $T_p = 0.907 \cdot T_a + 14.2$ ($r = 0.991$, $s = 0.210$); entrance, $T_e = 1.612 \cdot T_a - 3.5$ ($r = 0.985$, $s = 0.483$), where r is the regression coefficient and s the standard deviation. Similar linear relationships can be calculated from data of Ritter (1982) (see discussion).

Broodless colony (cluster) and its thermoregulation

In all hive areas of a broodless colony temperature is lower than in breeding colonies. In the centre of an overwintering cluster it is maintained at an average of 21.3 °C during the period from October to March (1985–1986). Daily fluctuations of ±10 °C appeared with minima of 12.0 °C and maxima of 33.5 °C, while the ambient temperature changed from −12 °C to +10 °C. The temperature T_p at the cluster's periphery averaged 11.0 °C and constantly remained at a lower value than in the centre.

The mode of thermoregulation during falling and rising ambient temperatures in a broodless cluster is clearly demonstrated in Figs. 2a and b. These data can be interpreted in two ways, in terms

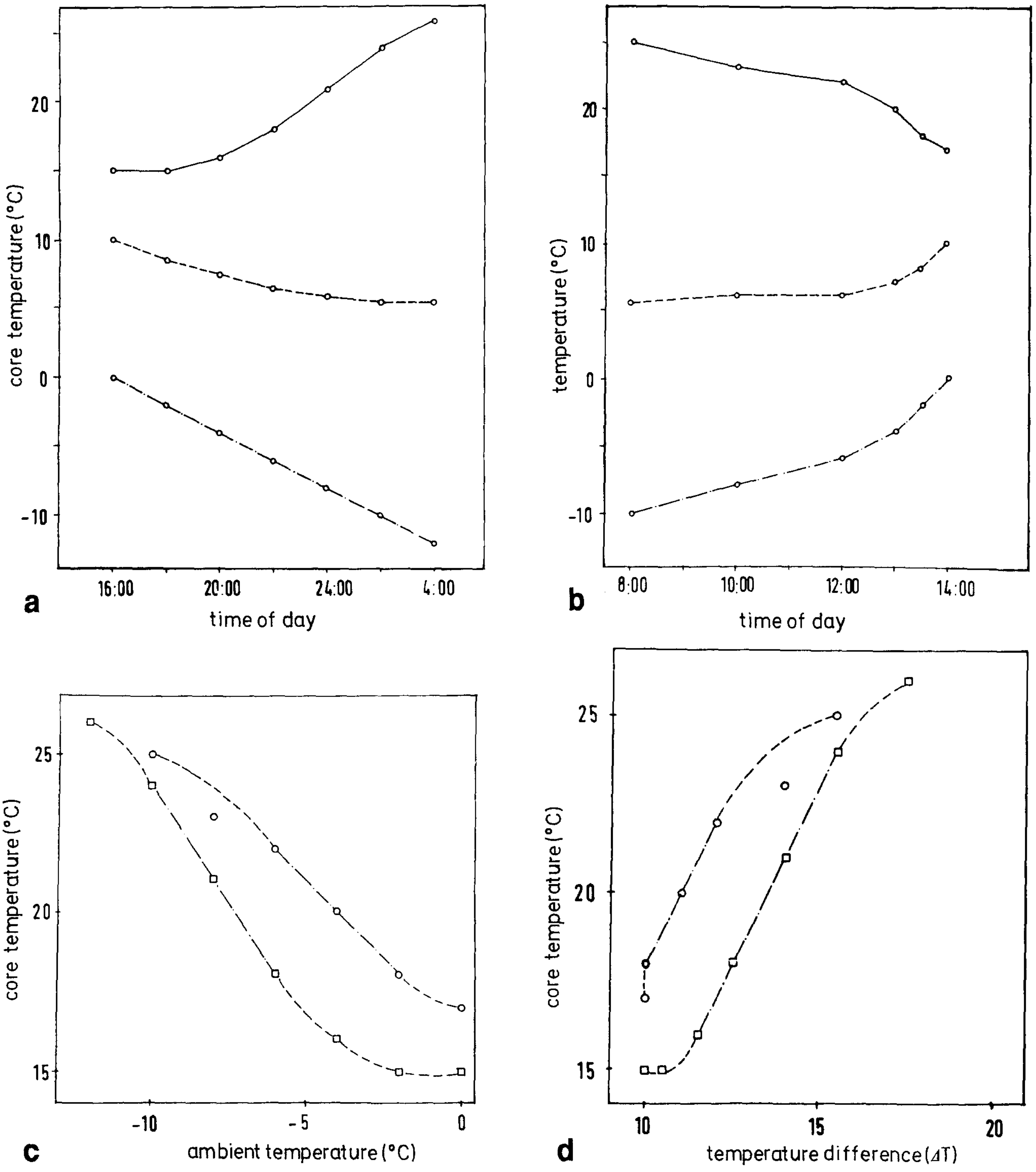

Fig. 2a–d. Changes of the central and peripheral temperature of a broodless cluster during the overwintering period. **a** Influence of rapidly decreasing ambient temperatures in the evening of a winter day (4 February 1986; T_c o——o, T_p o---o, T_a o–·–o). **b** Influence of increasing ambient temperatures in the morning of a winter day (5 February 1986). **c** Temperature in the center of an overwintering broodless cluster as function of the ambient temperature; (o) for rising values, (□) for falling values. The data are taken from Figs. 2a and b. **d** Temperature in the center of an overwintering broodless cluster as function of the temperature difference between the surface and the surroundings. (o) for rising values, (□) for falling values. The data are taken from Figs. 2a and b

of the minimum periphery temperature T_p or energetic balance. One aim of thermoregulation is to keep the peripheral temperature above +5 °C. When the ambient temperature drops in the course of a winter night, the core temperature rises by more than 10 °C and stabilizes the peripheral value at around +6 °C (Fig. 2a). On the other hand, increasing ambient temperatures in a winter morning results in a lowering of the central temperature by 8 °C while the periphery warms up slowly (Fig. 2b). Plotting the temperature T_c of the center versus the ambient temperature T_a gives two straight lines with a slope of +15 °C/−10 °C and −10 °C/+10 °C for falling and rising ambient values, respectively (Fig. 2c).

The heat loss from the cluster is proportional to its momentary surface, the heat conductance through the surface and the temperature difference between the periphery and the surroundings. This loss has to be compensated by the heat production of the bees in the cluster. The reduced heat loss through the surface and the increased heat production in the cluster lead to a temperature rise in the core. Figure 2d shows a linear relationship between the central temperature and the temperature difference between periphery and environment over a wide temperature range (indicated in Fig. 2d by dash-dotted lines). The accumulation of data at $T = 10$ °C again points to the economic aspect of thermoregulation.

Microcalorimetric determinations of the heat production

Calorimetric experiments were performed on workers (total number 40), drones (40) and queens (24) of different ages. Weight-specific heat production rates for all groups are presented in Fig. 3 in a Box-and-Whisker-plot (McNeil 1977; Lorenz 1984) calculated for the cited numbers.

Ignoring the strongly increased energy dissipation in isolated individuals, the Box-and-Whisker-plot clearly shows the high rate of heat production of adult workers (209±21 mW·g^{-1}) compared with isolated individuals of other groups. Similar differences are seen in the rates of virgin and laying queens (117±15 mW·g^{-1} and 102±14 mW·g^{-1}, respectively), and between fertile and young drones (184±37 mW·g^{-1} and 68±19 mW·g^{-1}, respectively), which on average produce only one third of the heat of an adult worker of equal weight. To facilitate a comparison of all groups, maximum, mean and minimum heat production rates are also presented in Table 1.

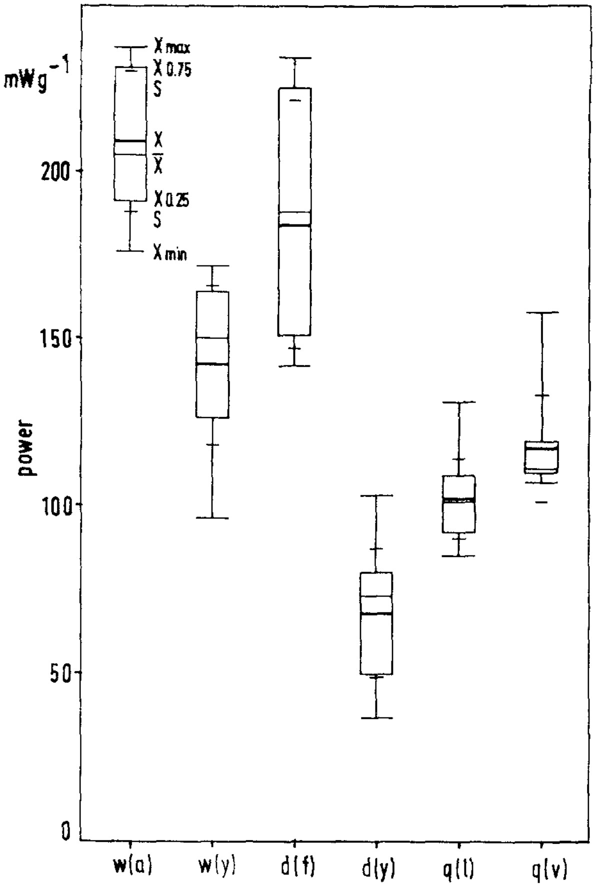

Fig. 3. Comparison of the characteristic figures of heat production rate for the different castes of bees. The weight-specific values are presented in a Box-and-Whisker plot: x, mean; $\tilde{x}$, median; $x_{0.25}$ and $x_{0.75}$, first and third quartile; s, standard deviation; x_{min} and x_{max}, minimum and maximum values observed in all experiments. w(a) adult workers; w(y) young workers; d(f) fertile drones; d(y) young drones; q(l) laying queens; q(v) virgin queens

Table 1. Minimum, maximum and mean rates of weight-specific heat production (mW·g^{-1}) for isolated members of the different castes (SD = standard deviation)

Castes	min	max	mean	SD
Workers				
Adult	176	237	209	21
Young	96	172	142	23
Drones				
Fertile	142	234	184	37
Juvenile	37	103	68	19
Queens				
Laying	85	131	102	12
Virgin	107	158	117	16

Information about the locomotor activities of members of the different groups may be inferred from the patterns in the calorimetric curves of heat production versus time ($p-t$-curves). They are

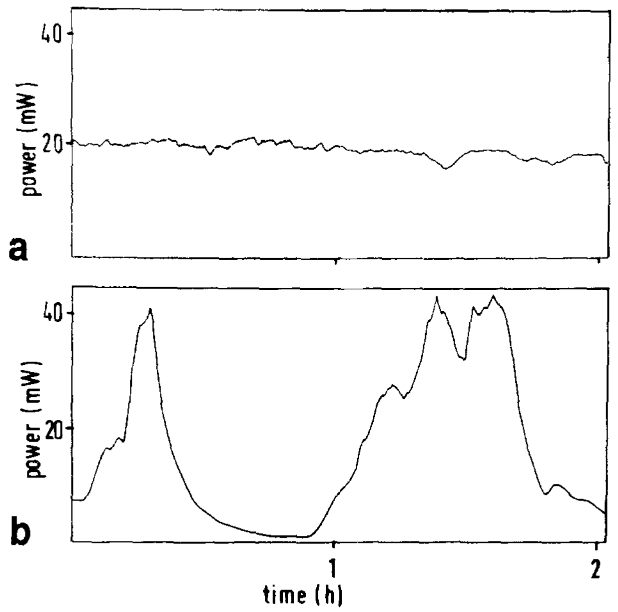

Fig. 4a, b. Typical rates of heat production as a function of time ($p-t$-curves) at 25 °C for isolated individuals. **a** adult worker of 100 mg, 21 days old; **b** fertile drone of 200 mg, 21 days old

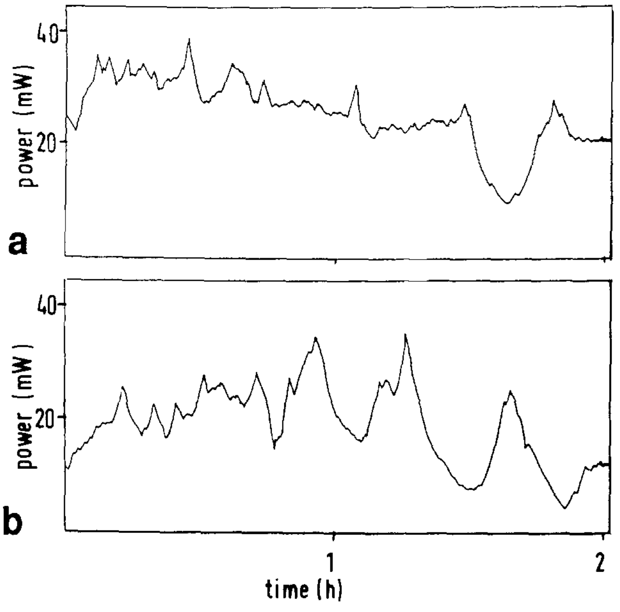

Fig. 5a, b. Typical rates of heat production as a function of time ($p-t$-curves) at 25 °C for isolated individuals. **a** laying queen of 200 mg, 21 days old; **b** virgin queen of 150 mg, 7 days old

shown in a representative manner in Figs. 4 and 5. Adult workers exhibit relatively smooth curves without substantial fluctuations (Fig. 4a) which correspond to a small interval between $x_{\max}$ and $x_{\min}$ in the Box-and-Whisker-plot (Fig. 3). These findings can be interpreted as a continuous locomotor activity of the workers without resting periods, confirmed by direct endoscopic observations of the animals in the calorimetric vessel. Only foragers show a continuous high locomotor activity during the whole experimental time. Young workers and drones (juvenile and fertile) and queens (virgin and laying) exhibit irregular phases of locomotor activities like walking and flying movements (In press). Similar smooth curves of oxygen consumption are reported by Allen (1959) for adult workers. Drones give completely different curves (Fig. 4b). Phases of high and extremely low activity succeed one another. The ratio of maximum and minimum values can rise to more than 100 in special cases and amount to a mean of 35 for fertile, and 46 for young drones, while the corresponding mean ratios for adult and young workers are 1.7 and 2.7, respectively. The location of the median relatively to the mean value and the distances of the standard deviations from the extremes in Fig. 3 emphasise that for drones only a few periods of high activity are responsible for the intensive heat production rate during an extended period of low level activity. Laying queens show less marked fluctuations (ratio 3.9; Fig. 5a) than virgins (ratio 21.1; Fig. 5b) and resemble drones in terms of heat flow patterns.

Since bees are social insects their weight specific rate of metabolism and heat production depends strongly upon the number of animals together in a group (Free and Spencer-Booth 1958; Roth 1964). Figure 6 depicts in a Box-and-Whisker-plot the influence of group size on the heat production rate of workers at 25 °C. Heat production falls rapidly as the number of bees increases but remains relatively stable when there are more than six individuals in the group. The mean reduction amounts to a factor of approximately 17. The minimum, mean and maximum heat production rates are also given in Table 2 for all groups.

Discussion

Measurement of hive temperature

The thermal investigations of an entire bee colony indicate that thermoregulation is related to different activities of the bees. High ambient temperatures, which may result in an overheating of the colony, are compensated mainly in the brood area (Lindauer 1951, 1954; Wohlgemuth 1957). Although the brood-nest temperature is maintained above 33 °C, the temperatures in the broodless areas and at the hive entrance may fluctuate widely.

Heinrich (1981) found that above an ambient temperature T_a of 16 °C the mantle temperature

Table 2. Minimum, mean and maximum weight specific heat production rates ($mW \cdot g^{-1}$) for different groups of worker bees

Number of bees in a group	min	max	mean	SD
1	176	237	209	21
3	72	11	87	11
6	20	40	30	7
12	8	20	13	4
18	7	17	12	3

is not regulated and follows T_a. This is in agreement with our observations (Fig. 1a, b) that above 16 °C T_p follows T_a with a slope near to 1 (0.907) as expected for an inert, thermally neutral system. The slope of 0.222 for T_c as a function of T_a clearly points to the thermoregulatory activity of the bees in the core of the hive. The stronger increase in the T_e slope might be partly due to bees warming up for flight, and above 35 °C to fanning activities for thermoregulation of the core. It should be noted that the three lines meet at one point (+35.5 °C) of preference temperature. Corresponding behavior may be deduced from Fig. 9 (B) of Kronenberg and Heller (1982) for the temperature distribution of brood at different ambient temperatures in the presence of bees.

The linear relationship between the hive and ambient temperatures may be cautiously compared with those of Ritter (1982, his Figs. 5–8), although his temperature values were not obtained in the course of rising ambient temperatures during one morning. Between 9 °C and 24 °C in the environment the temperature in the outer passages of the hive with brood increased linearly with a slope of 0.63 °C per degree ambient, while the slope for the centre was 0.15 °C per degree ambient. For the temperature difference between the hive and the environment Ritter observed a further linear relationship with the ambient temperature, expressed as $\Delta T = T_c - T_a = 24.7 - 0.7\ T_a$, which transforms to our notation as: $T_c = 24.7 + 0.3\ T_a$. The slopes are similar, although higher central temperatures result in our example. Some other observations in the literature point to such linear relationships but they are difficult to evaluate.

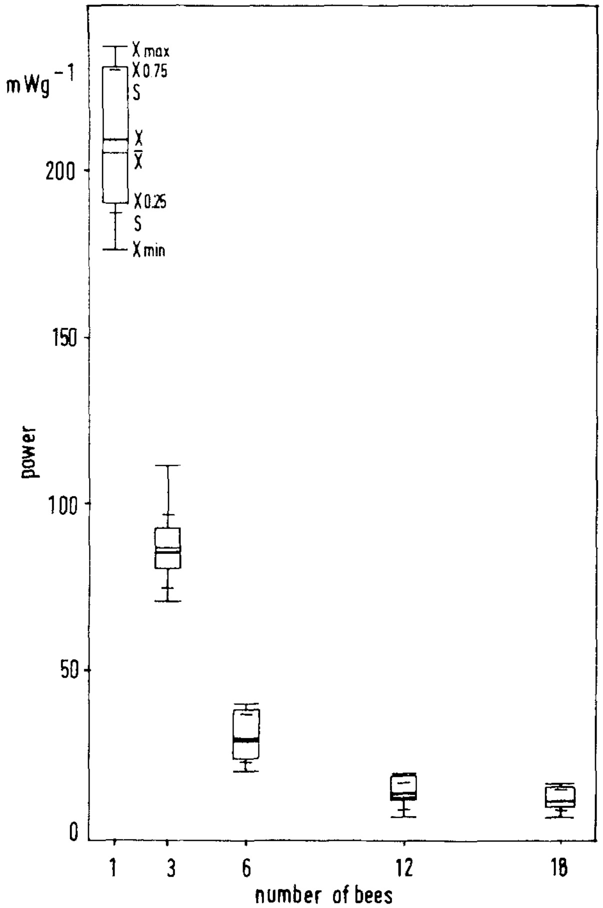

Fig. 6. Box-and-Whisker-plot of the specific heat production rates in groups of workers at 25 °C. n = number of bees in a group

A sudden drop in ambient temperature induces a temperature increase in the core (Fig. 2a, c) which is due to reduced thermal losses at the mantle and to increased metabolic activities. It is known from the literature (e.g., Free and Spencer-Booth 1958, 1959; Simpson 1961; Free and Simpson 1963; Heinrich 1981) that in winter honeybee clusters use two methods to lower their heat loss in the face of falling temperatures. At first the cluster diameter is reduced and a denser packing of the mantle bees results, thus reducing the heat transducing surface and the heat conductance (Free and Spencer-Booth 1958). Since only a limited reduction is possible (Free and Spencer-Booth 1959), further losses have to be compensated by an active heat production. This was demonstrated by an increased metabolic activity at low ambient temperatures (Free and Spencer-Booth 1958, 1959; Southwick 1982; Worswick 1987; Nagy and Stallone 1976; Ritter 1982).

Figure 2c shows how the core temperature T_c follows the decreasing ambient temperature T_a. At values just below zero it remains constant and rises in an inverse fashion with a slope of +15 °C/ −10 °C below −5 °C. At a T_a below −10 °C the core temperature levels off, resulting in an inverse sigmoid curve. Increasing T_a leads to a corresponding change of the centre temperature but with a less steep slope (−10 °C/+10 °C) and in a hysteretic manner. This slope may be interpreted in terms of a delayed sensing of the ambient temperature changes, and as an enhanced response to the dangerously low temperature compared to the more favourable increasing temperature. Further investigations are necessary to develop a cybernetic model (e.g., Ritter 1982) for such behaviour, although similar inverse relationships as indicated in Fig. 2c were postulated or demonstrated by several authors (e.g., Himmer 1932; Free and Spencer-Booth 1958).

The slope of the core temperature in Fig. 2b might be extrapolated to roughly 15 °C for a further increase in the ambient temperature. This indicates that a first set point is essential for thermoregulation: In Fig. 2a and b +15 °C is the lower threshold for the core temperature which has to be guaranteed in an overwintering cluster. This is in agreement with observations of different authors of a minimum core temperature. Simpson (1961) recorded temperatures as low as 15 °C in the center of broodless winter colonies with usual minima around 20 °C. Worswick (1987) found strong fluctuations in the core with minimum temperatures always above 13 °C. These results complement our mean value of 18 °C. As may be deduced from Fig. 2a a temperature of 15 °C is maintained for as long as possible provided there is a sufficient peripheral temperature. If the ambient temperature falls further it rises by some degrees. On the other hand, Fig. 2c clearly demonstrates that the temperature drop in the core ceases when the threshold of 15 °C is reached.

A mantle temperature T_p of +5 °C may be recognized as a second set point for thermal regulation. Reducing the cluster surface and its heat conductivity, as well as increasing metabolic rates, are intended to guarantee the minimum temperature for activity at the surface (Himmer 1932; Free and Spencer-Booth 1959). Southwick and Mugaas (1971) stated that it is more important for a cluster to maintain a correct surface temperature rather than centre temperature. Worswick (1987) observed a value of 6 °C, and Simpson (1961) 4.5 °C, for the mantle temperature, in good agreement with the results presented here.

Southwick and Mugaas (1971) determined temperature variations from 33.2 to 19.4 °C in the core of a winter cluster, and from 31.3 to 15.1 °C for its shell, while the ambient temperature changed between 11.1 and −2.2 °C. Furthermore, their results show that the cluster core temperature depends upon outside air temperature. As air temperature fell, the cluster core temperature generally increased, reaching maximum mean values of 28–30 °C at the lowest ambient temperature (−15 to −17 °C). These data are in good agreement with our findings.

Thus, thermoregulation of an overwintering cluster is not intended to maintain a temperature optimum necessary for successful brood development. It is orientated towards a suitable temperature for survival of those bees which cover the cluster. Both methods of thermoregulation, by changing the surface properties of the cluster and its metabolism with respect to the two set points, ensure energy consumption is minimal while still enabling the successful overwintering of the bee cluster.

Microcalorimetric measurements

Most metabolic and energetic investigations were performed on worker bees, sometimes on drones. Virgin and laying queens are incorporated for the first time in metabolic experiments. The calorimetric results show significant differences between the heat production rates of isolated members of the three castes (Fig. 3, Table 1). Foragers exhibit the highest energy dissipation, followed by young workers, in agreement with indirect calorimetry on new-born bees and 30-days old workers (Allen 1959). The lowest level is occupied by drones with a 30–40% lower energy dissipation than workers of corresponding age. Cahill and Lustick (1976) found that drones had an energy dissipation of only 19.2% compared to workers when both were kept in groups (Table 2). Laying and virgin queens exhibit a heat production in between those of the two other castes. The only other available direct calorimetric data on honeybees are those of Roth (1964, 1965, discussed by Chauvin 1968) who found a value of 160 $\mathrm{mW \cdot g^{-1}}$ for an isolated adult worker at 25 °C which is in good agreement with our results.

Other data have been published on indirect calorimetry obtained by measuring oxygen or sugar consumption, carbon dioxide production, or thorax temperature. These data were transformed to weight-specific heat production rates assuming a RQ = 1.00 and a factor of 21.13 $\mathrm{J \cdot ml}$ $\mathrm{oxygen^{-1}}$ (Ritter 1982) and, if not otherwise stated, a mean bee weight of 100 mg. The data are compiled in Table 3 for isolated animals, groups of bees and intact colonies. There is a considerable difference between the various measurements, ranging from 5.9 $\mathrm{mW \cdot g^{-1}}$ for a new born worker (Allen 1959) to over 100 $\mathrm{mW \cdot g^{-1}}$ for other workers on different occasions. The extremely high value of 372 $\mathrm{mW \cdot g^{-1}}$ (Hermann et al. 1982) could be compared with those of free-flying bees (Hocking 1953; Heinrich 1980). Very high values were also obtained by Scholze et al. (1964) who examined the

Table 3. Heat production of isolated bees, groups of several bees, and of intact colonies calculated from indirect calorimetry

Condition	Temperature (°C)	Heat prod. (mW·g^{-1})	References
a) Isolated animals			
0 days old	32	5.9	Allen 1959
30 days old	32	21.0	
worker, day	20	143.2	Heusner and Roth 1963
night	20	11.7	
mean	20	75.1	
worker, day	25	157.3	Heusner and Stussi 1964
night	25	10.0	
mean	25	75.5	
worker, active	25	99.9	Stussi 1972
at rest	25	5.6	
healthy	21	41.6	Moffett and Lawson 1975
Nosema-infected	21	32.2	
	22	372.0	Herman et al. 1982
	15	57.6	Harrison 1987
flight		351.0	Hocking 1953
rest		18.3	
free flight		467.0	Heinrich 1980
flight		685.0	Scholze et al. 1964
walking		154.0	
weighted		909.0	Heran and Crailsheim 1988
non-weighted		830.0	
b) Groups of bees			
10 bees	25	36.5	Free and Spencer-Booth 1958
100 bees	20	105.0	Heusner and Roth 1963
10 workers	25	117.0	Cahill and Lustick 1976
7 drones	25	22.5	
c) Intact colonies			
	25	55.0	Simpson 1961
	10	3.5	Free and Simpson 1963
day	20	126.5	Kronenberg 1979
night	20	42.5	
	28	8.8	Heinrich 1981
	35	22.9	
day	25	75.0	Kronenberg and Heller 1982
night	25	32.3	
with brood	24	16.3	Ritter 1982
broodless	24	11.0	
day	20	25.7	Southwick 1982
night	20	10.1	
(*A. m. capensis*)	20	7.1	Worswick 1987
(*A. m. adansonii*)	20	9.9	

energy input of walking and flying honeybees. Heran and Crailsheim (1988) also analysed the correlation between body weight and sugar consumption of free flying bees (Table 3).

The high rate of energy dissipation of an individual bee becomes much smaller when bees are investigated in groups (Fig. 6). The greatest reduction is seen when the number of bees is increased from 1 to 3, followed by a less dramatic reduction for groups of up to 6 individuals. If there are more than 10 bees the weight-specific heat production remains approximately constant at a value of 12 mW·g^{-1}. Subtracting this basal level for larger groups from the measured rates of heat production, the resulting slope may be interpolated by an exponential curve with an exponent of -0.435. It shows that extra dissipation is reduced to 1/e for "3.3" bees. From Roth's Fig. 2 (1964), corresponding figures of -0.576 and "2.7" bees may be deduced for 10 °C. His suggestion of a constant heat production independent of the group size leads to a hyperbolic interpolation, an interpretation which is incorrect both for his and our data, and contradicts the necessity for a minimum metabolism for each bee.

Group effects of socially living insects are reported in the literature. For honeybees Free and Spencer-Booth (1958) observed a twofold dependency of sugar syrup consumption on temperature and on group size. At 25 °C, a temperature similar to that in our experiments, there was a decrease of 25% from groups of 10 bees to groups of over 200. Roth (1964) found a reduction of 26% for an increase of from 1 to 2 bees and a reduction of 52% for the mean heat production when group size was increased from 1 to more than 6 bees at 10 °C. This difference became smaller with increasing ambient temperatures. Our results show much higher reductions in heat production which level off for groups larger than 10. Since these figures are weight-specific they must be multiplied by the weight of the animals to give the total heat dissipation of a group. However, assuming the same age and physiologic state of the bees, a weight-specific reduction of 17-fold for an increase from 1 to 6 bees transforms to only a 3-fold reduction for the whole group. This clearly indicates that the group in total uses less energy and acts more economically than an isolated individual.

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