

Allometric relations, metabolism and heat conductance in clusters of honey bees at cool temperatures

Edward E. Southwick*

Fachbereich Biologie, J.W. Goethe-Universität, Institut für Bienenkunde (Polytechnische Gesellschaft), Frankfurt/M, Karl-von-Frisch-Weg 2, D-6370 Oberursel, Federal Republic of Germany

Accepted January 21, 1985

Summary. Clusters of honey bees, *Apis mellifera carnica*, showed a clear dependence of oxygen consumption and heat conductance on bee cluster mass (between 5 g and 1.2 kg) when exposed to a cold temperature (2 °C) overnight. As the bee cluster mass was increased, total cluster metabolism increased. Mass-specific oxygen consumption, \dot{V}_{O_2} , decreased with increasing mass following the relation: $\dot{V}_{O_2} = 22.69 BW^{-0.479}$ (Fig. 1). Larger clusters of bees had lower heat conductance (i.e., better insulation) than the smaller groups (Fig. 4). The mechanisms of adaptation and adjustment to cold temperature in bee clusters are discussed and compared with those of mammals and birds.

Introduction

Almost all insects inhabiting north temperature regions pass through winter in a state of reduced animation or dormancy (diapause), usually at a hardy stage of development such as an egg or a pupa (Jungries 1978). Some insects show large increases in the osmotic content of the hemolymph coupled with a capacity for supercooling (Asahina 1969). Honey bees, *Apis mellifera* L., occupy habitats in most parts of the world, from the tropical savannahs of Africa to the northern parts of Canada and Scandinavia (Ruttner 1978). As solitary individuals, honey bees do not overwinter singly in a hardy diapause stage, and cannot survive temperatures below 6–8 °C (Free and Spencer-Booth

1960). The northern races survive harsh winter climates only when gathered together in large colonies with adequate food stores. Bees seek nest sites with characteristics that increase their chances of surviving the winter (Seeley and Morse 1978). Also, they maintain warm central temperatures within the cluster through increased metabolic heat production (Gates 1914; Phillips and Demuth 1914; Owens 1971; Southwick and Mugaas 1971; Southwick 1982).

Bees possess body hairs rather densely distributed, especially over the thorax which contains the heat-generating flight musculature (Snodgrass 1956; Esch 1964). The hairs are plumose, closely resembling bird down (Southwick 1983), but their insulative properties are unknown and probably cannot be directly determined. Some of the more northern races possess longer and more dense hair than the tropical races (Ruttner 1984), which leads to speculation about the thermal effectiveness of these hairs in winter bee colonies. The hairs are small (0.7–1.1 mm in length), and therefore on individual bees cannot trap the same proportion of air in a poorly conducting boundary layer as the feathers and fur of birds and mammals which are 10^2 – 10^6 times larger. However, when the bees form a winter cluster, their body hairs become interlaced and they theoretically could succeed in trapping similarly large relative volumes of air in an effective insulating coat. Thus, the compound effect of the hairs of many bees packed together especially on the outside could provide a more effective boundary layer thereby reducing heat loss at low ambient temperatures. The reduced heat loss should result in energy savings for the cluster which would be reflected in reduced expenditure of metabolic energy. Therefore, I examined the thermal physiology of intact clusters of bees, varying in mass from 5 g to 1.2 kg, at constant cool and cold temperatures (15 and 2 °C) by measuring

Abbreviations: T_a ambient temperature in environmental cabinet; T_{in} air temperature inside bee chamber but outside bees; T_c core temperature of bee cluster; T_b body temperature; \dot{V}_{O_2} oxygen consumption; C heat conductance; BW body mass or cluster mass; MR metabolic rate

* Offprint requests should be sent to: Department of Biological Sciences, State University of New York, Brockport, New York 14420, USA

oxygen consumption and temperatures within the clusters. I estimated heat conductance through the clusters, and compare the results with those reported for mammals and birds.

Materials and methods

Colonies of honey bees, *Apis mellifera carnica* Pollmann, a race inhabiting central Europe, were maintained through the fall and winter at the Institut für Bienenkunde in Oberursel, Federal Republic of Germany. They were kept outdoors following normal management practices except that the queens were confined to insure broodless conditions. All experiments were carried out between October 1983 and February 1984. Worker bees to be tested were counted and weighed and placed with a queen in a 5-frame nucleus (DWK-Dreiwabenkasten) with screened sides and bottom. They were not narcotized (e.g., with CO₂) as this was found to affect later measurements of metabolism. The queen was usually free to move about but in some tests she was confined in a small screened cage (1 cm diameter × 3 cm). All groups were tested with a queen and without brood as these have been shown to affect metabolic conditions (Ritter and Koeniger 1977; Koeniger 1978). For clusters of 50 g or more, ten bees were weighed individually to the nearest 0.1 mg for estimates of numbers of bees in each of the larger clusters.

Metabolism was determined indirectly by measuring oxygen consumption, \dot{V}_{O_2} . \dot{V}_{O_2} of single bees was measured using the Warburg method. Individual bees were weighed and placed in small cloth-net chambers supported over 20% NaOH inside 13 ml Warburg flasks. The flasks were covered with aluminum foil to darken the chamber as earlier experiments showed that minimum \dot{V}_{O_2} would not be obtained under lighted conditions. The Warburg apparatus containing 3–5 duplicates was placed in a controlled temperature cabinet (Rubarth, 0 to 60 ± 0.5 °C) or a controlled temperature water bath (Haake F3, –10 to 60 ± 0.1 °C), and 30 min allowed for equilibration at each temperature. The \dot{V}_{O_2} was measured over 10 min intervals except at 2 °C when 60 min were required for adequate readings. The methods of Warburg and Krippall (1958, cited in Umbreit 1964) were followed.

Groups of bees were monitored in a flow-through system utilizing an air tight acrylic chamber (26 × 20 × 14 cm) enclosing a screened DWK. The resulting inside air volume was about 4 l. The bees were free to move about within the DWK which contained 2 or 3 comb frames, with 1 or 2 being filled with honey. A thermocouple grid of 12 Fe-Con points spaced 2.0 cm apart in both vertical and horizontal directions was placed between the combs, and thermocouple points were also placed at the inlet and outlet ports. For large groups of up to 14,000 bees, a wooden box (43 × 38 × 24.5 cm) was fitted with ventilated acrylic covers on the top and bottom and made air

tight with silastic caulk. Ten frames of comb were placed in the super with at least three containing honey stores. The resulting air volume was about 17 l. A thermocouple grid of 12 points spaced 1.5 cm apart horizontally was placed between the two central frames about 10 cm from the frame tops. Usually large groups of bees were allowed 3 to 5 days to become accustomed to the box before measurements were begun.

Following the methods described earlier (Southwick 1982), the metabolic chamber containing bees to be tested was placed in the controlled-temperature cabinet at 2 ± 1 °C at 1500 h. \dot{V}_{O_2} was monitored during the next 18–48 h to assure that minimum rates (usually at 0400–0700 h) were obtained. Air flow rates were checked with a soap-film flowmeter (Normal-Precision) and a sample stream was directed through an oxygen analyzer (Applied Electrochemistry S3-A or Hartman and Braun Oxytest-S, accuracy of 0.001 and 0.01 vol% respectively). Both systems were 2-channel systems comparing oxygen contents of the air stream entering and leaving the chamber. The respiratory quotient was determined (RQ = 1.03 ± 0.06, *n* = 100) indicating that the bees were existing on a pure carbohydrate diet during the measurements (honey was available ad libitum throughout the experiments). Heat production was determined from metabolism of sugar. Simultaneous measurements of temperatures within the cluster were made. With these combined data sets, heat conductance through the bees under the experimental conditions could be determined.

Results

Mass dependence of metabolism

Minimum \dot{V}_{O_2} attained by groups of bees held at constant temperature overnight is dependent on the mass of the cluster. With greater masses, metabolism increases but not as rapidly as mass. Minimum values of mass-specific \dot{V}_{O_2} are dependent on cluster mass as illustrated in Fig. 1 where the dependence is especially apparent in the small masses of 5 g to about 100 g where the curve has the steepest slope. As the cluster masses were increased above 200 g (ca. 1600 bees), rates of mass-specific metabolism declined only slightly. The best-fit curves at 2 °C (*n* = 16) and 15 °C (*n* = 7) are:

$$\text{at } 2\text{ }^{\circ}\text{C } \dot{V}_{O_2} = 22.69 BW^{-0.48}, r^2 = 0.96 \quad (1)$$

$$\text{at } 15\text{ }^{\circ}\text{C } \dot{V}_{O_2} = 4.23 BW^{-0.27}, r^2 = 0.89 \quad (2)$$

where \dot{V}_{O_2} is mass-specific oxygen consumption (ml O₂ · g⁻¹ · h⁻¹) and *BW* is cluster mass (g).

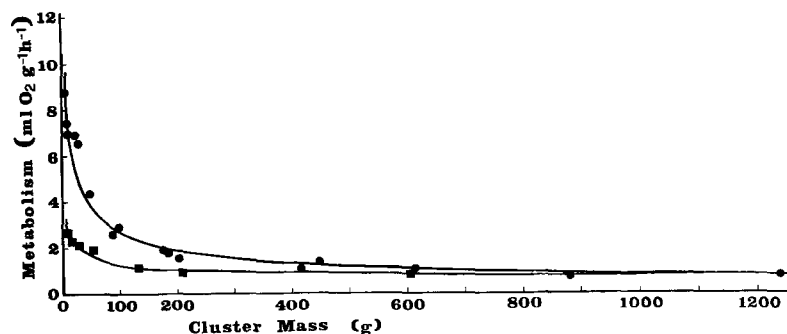


Fig. 1. Minimum mass-specific oxygen consumption maintained by honey bees *Apis mellifera carnica* in groups of various sizes held at 2 °C (●) and 15 °C (■) for 18–48 h

Individuals and groups of bees weighing less than about 5 g, were unable to survive the 2 °C cold temperature overnight. The average value of \dot{V}_{O_2} recorded for 12 individuals held for 1 h in the Warburg apparatus at 2 °C was $(0.12 \pm 0.15 \text{ ml O}_2/\text{g})$. All the individual bees and most of those in the groups of less than 5 g that were exposed to 2 °C overnight, were in fact in a cold-comatose condition but revived at room temperature after the tests. It was difficult to achieve true minimum \dot{V}_{O_2} values in large groups at 15 °C as this is near the critical temperature of cluster formation. At temperatures higher than this, cluster metabolism shows large variation (Southwick 1982). The values reported here for metabolism are the minimum values obtained under rigidly controlled environment conditions. The bee clusters, however, frequently showed wide variation in \dot{V}_{O_2} even at constant environmental temperature. For the clusters tested at 2 °C overnight, the average \dot{V}_{O_2} was 10–15% greater than the minimum values maintained for 20–60 min. A rhythmic variation in \dot{V}_{O_2} and T_c occurred, at least in some of the groups under 300 g. The amplitude was as much as 100% of the minimum value of \dot{V}_{O_2} and the period averaged $1.3 \pm 43 \text{ h}$ ($n=26$). The average temperature amplitude was $1.8 \pm 0.81 \text{ °C}$ ($n=34$).

Temperature profile, cluster geometry and conductance

The thermoregulatory activities of the clusters are dynamic and complex. Figure 2 shows a typical temperature profile through a cluster of 4252 bees (608 g with about 30 cm² of unsealed brood) tested at 2 °C. This profile was essentially the same for 60 min. This reveals an area of steeper slope of temperature gradient (4.3 °C/cm) indicating a better insulating segment between 5 cm from the core and the cluster surface at 9.5 cm from the core. The temperature gradient within 5 cm of the middle of the cluster is smaller (1.9 °C/cm) however in this region where the temperature is high, there may be less stimulus to produce/retain heat. The approximate cluster profile is indicated in the figure with temperature isotherms. When the mass of bees is determined in each segment (i.e., between each known temperature point), and metabolism calculated at the average temperature of the segment from Warburg measurements, the metabolic contribution of each segment could be approximated. Thus, the core of the cluster (to 5 cm from the midpoint where the highest temperature at 34 °C was recorded) constitutes 22% of the mass (assuming the bees are evenly packed) and 25%

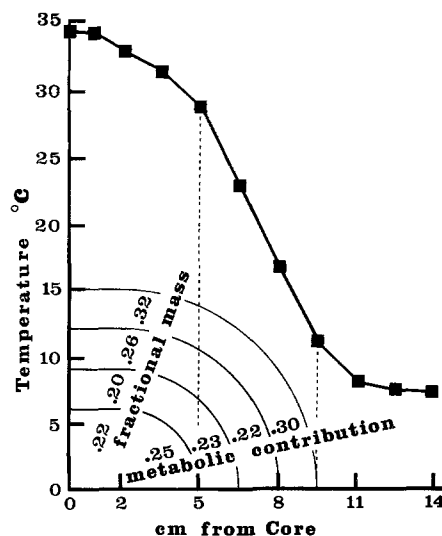


Fig. 2. Temperature profile in a bee cluster of 608 g (ca. 4250 bees) at 2 °C. Partitional masses and metabolism are indicated in the lower left of the figure. The cluster surface is at about 9 °C

of the metabolism. The insulating shell (5–9.5 cm) contains 78% of the mass and has 75% of the metabolism. Summing the metabolism of individual bees determined from the Warburg procedure, however, results in a total metabolism for the 608 g cluster that is about 3 × too high (measured total metabolism was 6.46 ml O₂/min, and totalling individually determined metabolisms yielded 19.62 ml O₂/min).

The entire cluster volume is about 1686 cm³ for this group. The theoretical minimum volume for the 4252 bees packed as tightly as possible in a sphere was calculated from volume measurements (acetone displacement) of individual bees. Single bees averaged $0.145 \pm 0.15 \text{ cm}^3$ ($n=20$) giving an absolute minimum volume for the cluster of 617 cm³ with a minimum spherical diameter of 10.5 cm and minimum surface area of 353 cm². The actual volume was about 2³/₄ times greater than the theoretical minimum. This is due in part to the intrusion of wax combs and the resulting non-spherical shape assumed by the bees (Fig. 3). The bees occupy the spaces inbetween the combs and pack themselves into oval shaped masses 1.5–2 cm in thickness depending on the distance between the combs. The bees do not generally move into the empty individual wax cells but instead form a tight layer above the comb trapping air in each cell. They sometimes move into the cells apparently before becoming comatose in clusters that die in winter, but very few bees were found in this series of experiments within cells in the functioning clusters at cold temperatures. The combs

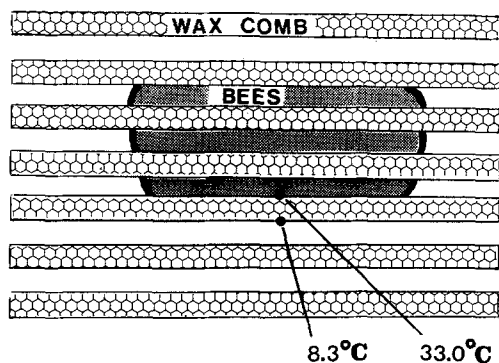


Fig. 3. Bee cluster configuration (shaded area) at 2 °C air temperature with intrusion of wax combs. Temperatures maintained are indicated on two sides of a comb separated by 2 cm

interrupt the cluster, however they also can provide very good insulation. The temperature on one side of an empty comb (i.e., without honey, pollen or brood) adjacent to the bees was maintained at 33.0 °C, while on the other side of the comb where there were no bees (2 cm separation), the temperature was only 8.3 °C (at an air temperature of 2 °C). This yields an average thermal conductivity of only $0.15 \times 10^{-3} \text{ cal} \cdot \text{cm}^{-1} \cdot \text{s}^{-1} \cdot \text{C}^{-1}$ for the comb (calculated from data in Precht et al. 1973, including the wax and still air fractions).

Of the total cluster surface area of 934 cm², 353 cm² were exposed to the cold air inbetween the frames, and an additional 581 cm² were adjacent to the insulating combs on both sides of the cluster (Fig. 3). Although the total surface area was some 2 1/2 times greater than the theoretical minimum, only 32% of the surface (similar to the theoretical minimum; the numbers being exactly the same is coincidence) is actually exposed to the cold air temperatures while the remaining 68% of the surface is adjacent to the insulating combs.

The overall conductance of heat through the bees was calculated from \dot{V}_{O_2} and the temperature

differential maintained between the core and air outside the cluster surface. These values are presented in Fig. 4. The larger masses of bees had lower heat conductance values (i.e., better insulation) than the smaller groups.

Discussion

Apis mellifera carnica shows a strong dependency of heat production, heat retention, and ability to maintain high core temperature on winter cluster size. This is in contrast to mass-independence of metabolism found in broodless swarms of bees reported by Heinrich (1981). The relationship found at 2 °C air temperature (see Eq. 1) is remarkably similar to the relationship found for 52 different species of mammals (at 5 °C T_a) found by Heldmaier (1974). His mass-metabolism equation has both a similar exponent and a similar constant ($\dot{V}_{O_2} = 29.6 BW^{-0.464}$). In Fig. 1 it is apparent that the colder temperature moves the mass-metabolism curve to the right. The exponent for the 15 °C curve (−0.27, see Eq. 2) nearly matches those for basal metabolic rates reported in the literature by many investigators for endothermic vertebrates. These values are tabulated by Gordon (1983, Tables 3–5) and reveal that the bee clusters behave more like birds (with exponents of −0.274 to −0.277) and mammals (−0.24 to −0.266) than reptiles and amphibians (−0.17 to −0.26). When the results are expressed as daily energy expenditure (kcal/day) of the entire cluster at 15 °C, a regression is found that closely resembles Kleiber's (1961) classic mass-metabolism curve for mammals ($MR = 70.0 BW^{0.75}$, Fig. 5). Both the exponent and constant are of similar magnitude. Practically, the data points for bee clusters at 15 °C in the range of 10 to 1000 g are indistinguishable from the regression found for non-passerine birds ($MR = 78.3 BW^{0.723}$; Gordon 1983).

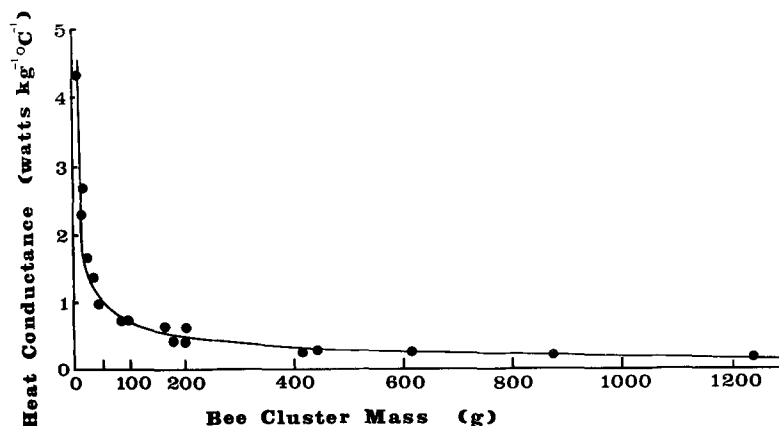


Fig. 4. Heat conductance through clusters of bees held at 2 °C. These values were determined from minimum \dot{V}_{O_2} and temperature difference between the core, T_c , and chamber air temperature outside the cluster, T_{in}

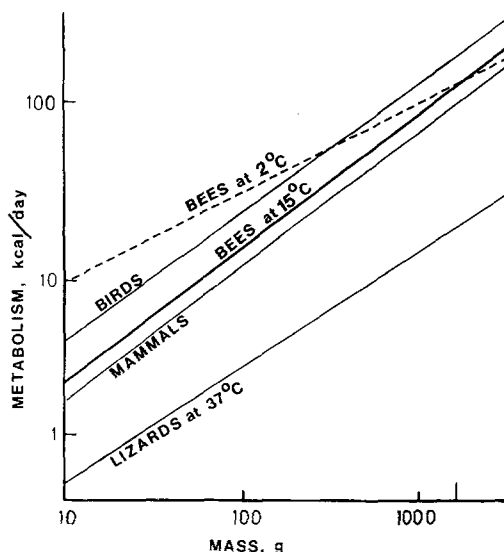


Fig. 5. The relation of standard metabolism to body mass in vertebrates (after Gordon 1983), and bee clusters. The regression are: passerine birds, $129.0 BW^{0.724}$; placental mammals, $70.0 BW^{0.75}$; lizards, $15.4 BW^{0.82}$; bees at 15°C , $88.46 BW^{0.76}$; bees at 2°C , $99.68 BW^{0.52}$.

These results show an evolutionary convergence on basic heat balance in widely diverse living systems. This indicates that there are fundamental physical relationships of heat transfer operating, and metabolic heat production in living organisms may be governed by general principles.

Further, when metabolism of the bee clusters tested at 2°C is plotted in the same figure (Fig. 5), we find that at this colder temperature the regression is rotated clockwise. There is a point where the two bee curves cross at 1665 g mass. This shows that although it costs more metabolically for small clusters to thermoregulate at the colder temperature, clusters of 1.7 kg or larger actually

use less energy at the colder temperature. Therefore it would be advantageous for bees overwintering in the north to maintain colonies in excess of 1.7 kg. This is especially interesting in light of the fact that normal overwintering colonies in West Germany average about 1.6 kg (N. Koeniger, personal communication), and average daily temperature in the coldest month (January) is 1.7°C (mean of 321 measurements 1974–1984 in Frankfurt, Deutscher Wetterdienst). An obvious question that still needs to be answered is what further rotation and/or displacement will occur at lower test temperatures.

The results of this study are particularly intriguing for groups of insects which cannot follow precisely the physiological or morphological mechanism of heat production and heat conservation of intact mammals and birds. In the bees, the metabolic rate per gram or per individual increases as cluster mass decreases. When mass is reduced to one or a few individuals, the bees cannot maintain the high levels of metabolism necessary for temperature regulation and fall into chill coma. The levels of chill coma \dot{V}_{O_2} at 2°C are in the same range as those reported by Allen (1959) for single bees at 7°C and less than a tenth of the minimum values for small groups found in this study.

If the thoracic hairs of an individual bee trapped air in a still boundary layer of about 1 mm depth adjacent to its body, the insulative value would be minor because of the very thin layer combined with the small temperature difference a bee could maintain across the hair layer. However, when the bees are packed together in their winter cluster, the organized structure of the cluster provides for much better insulative protection against heat loss, and thermal conductivity through the

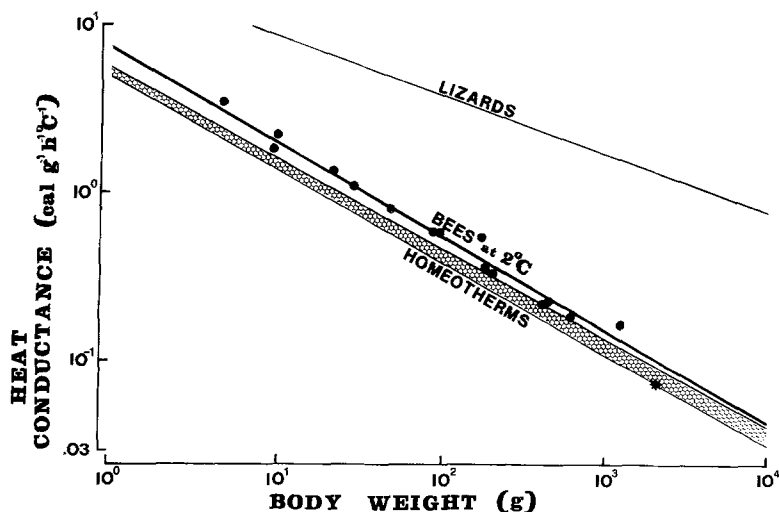


Fig. 6. Comparative heat conductance curves for bees, homeotherms, and a typical poikilotherm. The upper and lower boundaries of the curve for homeotherms are plots of mean conductances reported for mammals and birds, respectively (modified after Herreid and Kessel 1967). The star data point at about 2×10^3 g is a mean value taken from bee clusters at -17 to 11°C T_a (from Southwick and Mugaas 1971).

interlaced hairs could theoretically be as low as that for fur or feathers ($0.06 \times 10^{-3} \text{ cal} \cdot \text{cm}^{-1} \cdot \text{s}^{-1} \cdot ^\circ\text{C}^{-1}$; Precht et al. 1973). The effectiveness of insulative layers of bees is reflected by the slope of the metabolism-temperature curve (Southwick 1983). Heat conductance values for various masses of bee clusters at 2°C are plotted with average conductance data from vertebrates (Herreid and Kessel 1967) in Fig. 6. The data points for the bees lie slightly above the regression for mammals and cannot be said to be different. In a natural setting, conductance would be even lower as the bees' benefit from the nest enclosure.

The cluster of bees is not static, but is dynamic, constantly moving and changing shape with individual bees moving from place to place. Such rhythmic variation in metabolism observed was also noted but not explained by Kronenberg and Heller (1982). It may result from mass movements of many bees in the clusters, reflecting all-at-once changing of position by the bees. Although this could not usually be detected in the larger clusters, it may have occurred and been masked by the larger overall metabolism. Further evidence of this mass movement was seen in large clusters in which the surface of the clusters moved back and forth across fixed thermocouple points. This was detected by the rapid changes in recorded temperatures (i.e., warm-cold-warm again). For example, over a period of 11 h, one bee cluster moved back and forth across a thermocouple point located 7 cm from the center of the cluster. This was indicated by a rapid rise in temperature averaging $1.7^\circ\text{C}/\text{min}$ from 4 to 23°C (means). The rapid increases occurred four times and were followed by much slower declines averaging $-0.33^\circ\text{C}/\text{min}$.

Many different morphological, behavioral and physiological correlates have evolved in the modes of adaptation to low temperature (Scholander 1955). Bees capitalize on at least three mechanisms of adjustment to cold temperature that are similar to those of mammals and birds. (1) Physical mechanisms: As the temperature falls, the cluster heat loss decreases via decreases in the surface area for heat exchange by compaction of the bees into ever smaller cluster sizes (down to about 0°C where a minimum size is reached). This has the same result as changes in posture in mammals and birds. The effectiveness of the insulating layers of bees is enhanced by precise positioning of their bodies with interlacing hairs and closing of ventilating passages through the cluster. The role of mantle bees in controlling heat loss was also reported in swarms by Heinrich (1981). This is quantitatively similar to seasonal increases in insulation under

endocrine control and short-term shifts in cardiovascular patterns in birds and mammals. (2) Chemical mechanisms: As in endotherms, bee clusters augment metabolic heat production as the ambient temperature is reduced. (3) Heterothermy: The outer portions of the bee cluster cool to temperatures of 9°C . Before the cold outer bees become comatose and fall from the surface, there is mass shifting of bees with cooler bees moving into the warm central area. This may be an effective method of sequestering metabolic heat within the core of the cluster and is in some ways similar to countercurrent heat exchange and peripheral heterothermy of vertebrates.

Acknowledgements. I am especially grateful to the Alexander von Humboldt Foundation for support of this research program. I thank Prof. Dr. N. Koeniger for his encouragement and criticism throughout the course of the research and for free use of the facilities at the Institut für Bienenkunde which he directs.

References

- Allen MD (1959) Respiration rates of worker honey bees of different ages and at different temperatures. *J Exp Biol* 36:92–101
- Asahina E (1969) Frost resistance in insects. *Adv Insect Physiol* 6:1–49
- Esch H (1964) Über den Zusammenhang zwischen Temperatur, Aktionspotentialen und Thoraxbewegungen bei der Honigbiene (*Apis mellifica* L.). *Z Vergl Physiol* 48:547–551
- Free JB, Spencer-Booth HY (1960) Chill-coma and cold death temperatures of *Apis mellifica*. *Entomol Exp Appl* 3:222–230
- Gates BN (1914) The temperature of the bee colony. *Bull USDA* No 96:1–29
- Gordon MS (1983) *Animal physiology: principles and adaptations*. 4th edn, Macmillan, New York
- Heldmaier G (1972) Cold-adaptive changes of heat production in mammals. In: *Proc Int Symp Environ Physiol: Bioenergetics*. Fed Am Soc Exp Biol, Bethesda, MD (pp 79–82)
- Heinrich B (1981) The mechanisms and energetics of honeybee swarm temperature regulation. *J Exp Biol* 91:25–55
- Herreid CF II, Kessel B (1967) Thermal conductance in birds and mammals. *Comp Biochem Physiol* 21:405–414
- Jungries AM (1978) Insect dormancy. In: Culter ME (ed) *Dormancy and developmental arrest: experimental analysis in animals and plants*. Academic Press, New York, pp 47–112
- Kleiber M (1961) *The fire of life*. Wiley, New York London
- Koeniger N (1978) Das Wärmen der Brut bei der Honigbiene (*Apis mellifera* L.). *Apidologia* 9:305–320
- Kronenberg F, Heller HC (1982) Colonial thermoregulation in honey bees (*Apis mellifera*). *J Comp Physiol* 148:65–76
- Owens CD (1971) The thermology of wintering honey bee colonies. *USDA Tech Bull* No 1429:1–32
- Phillips EF, Demuth GS (1914) The temperature of the honey bee cluster in winter. *Bull USDA*, No 93:1–16
- Precht H, Christophersen J, Hensel H, Larcher W (1973) *Temperature and life*. Springer, Berlin Heidelberg New York

- Ritter W, Koeniger N (1977) Influence of the brood on the thermoregulation of honey bee colonies. Proc VIII Congr IUSSI, Wageningen, pp 283–284
- Ruttner F (1978) Races of bees. In: Dadant and Sons (eds) The hive and the honey bee. Dadant, Hamilton, Illinois, pp 19–38
- Ruttner F (1984) Über die Anwendbarkeit einiger Regeln der Tiergeographie auf die Geographische Variabilität der Honigbiene. Arbeitsgemeinschaft Institute Bienenforsch, Hohenheim, March 1984. Apidologie 15:235
- Scholander PF (1955) Evolution of climatic adaptation in homeotherms. Evolution 9:15–26
- Seeley TD, Morse RA (1978) Nest site selection by the honey bee *Apis mellifera* L. Insectes. Soc 23:495–512
- Southwick EE (1982) Metabolic energy of intact honey bee colonies. Comp Biochem Physiol 71A:277–281
- Southwick EE (1983) The honey bee cluster as a homeothermic superorganism. Comp Biochem Physiol 75A:641–645
- Southwick EE, Mugaas JN (1971) A hypothetical homeotherm: the honey bee hive. Comp Biochem Physiol 40A:935–944
- Snodgrass RE (1956) Anatomy of the honey bee. Cornell University Press, Ithaca, New York
- Umbreit WW (1964) Manometric techniques. Burgess, Minneapolis