Thermochimica Acta, 151 (1989) 13-21
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

MICROCALORIMETRIC INVESTIGATIONS OF THE ENERGY METABOLISM OF HONEYBEE WORKERS, *Apis mellifera carnica*

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SUMMARY

Heat production measurements were performed for individual workers of different age and for worker groups of the honeybee *Apis mellifera carnica* by means of a 100-ml-Calvet-calorimeter. Individual worker bees show a strong positive correlation of the weight specific heat production rate with age. Increasing numbers of workers together in a group reduce the heat production drastically, so that a group of 12 bees dissipate less heat than one isolated animal. Addition of a queen or of bee brood to a group of 6 workers lowers the heat output, too. These effects could be described as socially conditioned by the use of an endoscope or a microphone incorporated into the calorimetric vessel. Endoscopic observations have been performed in the visible and the infrared region of the spectrum.

INTRODUCTION

Thermoregulation in biological systems is known on an individual scale in higher, "homoiothermic" animals (ref. 1) and on a population scale in socially living insects such as honeybees, wasps, bumblebees and hornets (refs. 2, 3). These "poikilothermic" animals follow the environmental temperature individually but establish a fairly constant temperature in the brood areas of the nest, comb or hive (ref. 5) or in the center of the cluster of overwintering bees (ref. 6). Honeybees possess several possibilities to stabilize the hive temperature by heating during cold periods and by cooling during hot days (ref. 7). The latter is performed by shedding water in the entrance of the hive and by fanning to obtain an intensive evaporation. In this paper the effect of active heat production by non-locomotive shivering of the flight muscular system, by locomotor activities and by metabolic heat dissipation shall be considered only.

004-6031/89/$03.50

Most of the numerous investigations on the metabolism of honeybees were performed by manometric techniques, determination of sugar consumption or by calculation from the thorax temperature. Only very few true calorimetric experiments are described in the literature (ref. 8). The aim of this paper was to investigate directly the heat output of worker bees of different age, in varying groups and under changing social conditions. Results of further experiments concerning the three castes of a bee colony (queen, workers, drones), the bee brood and of temperature influences will be published elsewhere (ref. 9).

METHOD AND MATERIAL

A hive of honeybees (*Apis mellifera carnica*) was kept in the laboratory a few meters away from the calorimeter so that the bees could be transferred to the calorimetric vessel directly after catching and weighing. After hatching in an incubator the bees were marked at the thorax and added to the colony. A mechanical balance (type 414; SAUTER/Ebingen) served for obtaining the wet weight of the animals. Table 1 compiles the wet weights and the occupations of the workers at different ages.

TABLE 1

Age, weight and social occupation of worker bees

Age / days	Weight / mg	Occupation
1	110	freshly hatched
3	115	cleaning cells
6	126	feeding brood
12	125	shaping combs
21	99	foraging

All experiments were performed at 30°C with a Calvet calorimeter (MS70; SETARAM/Lyon) with four vessels of 100 ml. Its sensitivity was ~57.8 mV/W. The electrical signals were fed to a multichannel recorder (BD5 + BA5; Kipp & Zonen/Delft). An endoscope (rigid Boroskop; Storz/Tuttlingen; length 570 mm; outer diameter 6.5 mm; aperture 67°) for visual observation of the animals was incorporated into the vessel support (ref. 10). Additionally, a wavelength range from 780 to 960 nm could be selected by means of infrared (IR) filters. The bee-eye is insensitive to this range (ref. 11) as well as the human eye. Therefore, the activities of the animals were monitored by an IR sensitive night viewing system (NFP18; AEG/Hamburg) connected to the endoscope. The additional heat input due to the endoscopic illumination amounted to 0.57 mW under acceptable observation conditions while a mean heat production by the bees figured to 15 mW. It was proofed that the bees did not respond to the IR illumination neither by eye nor by heat sensation.

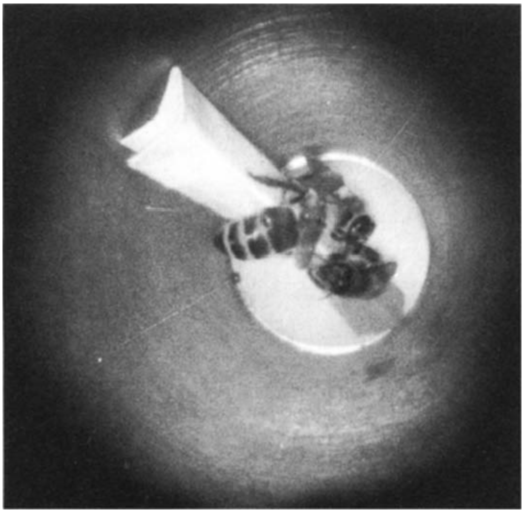

Fig. 1 Endoscopic view of three bees in the calorimetric vessel together with the climbing stick.

The calorimetric vessels were equipped with a little container for sugar so that the bees could feed *ad libitum* and with a wooden stick for sitting and climbing. Fig. 1 shows an endoscopic pfoto of three bees and the stick in the calorimetric vessel.

Additionally to the endoscope a microphone was incorporated into the vessel to follow acoustically the various locomotor activities of the bees. A schematic picture of the whole instrumental setup is presented in Fig. 2.

No groups larger than 18 workers were investigated since the handling of larger numbers introduced to much rumor into the group whereas the limited space in the vessel played no role. After calming down the bees were sitting in a cluster around the sugar container so that the largest part of the vessel remained empty.

On the other hand, the inner diameter of the vessel was so large that bees could spread their wings and perform flight simulations.

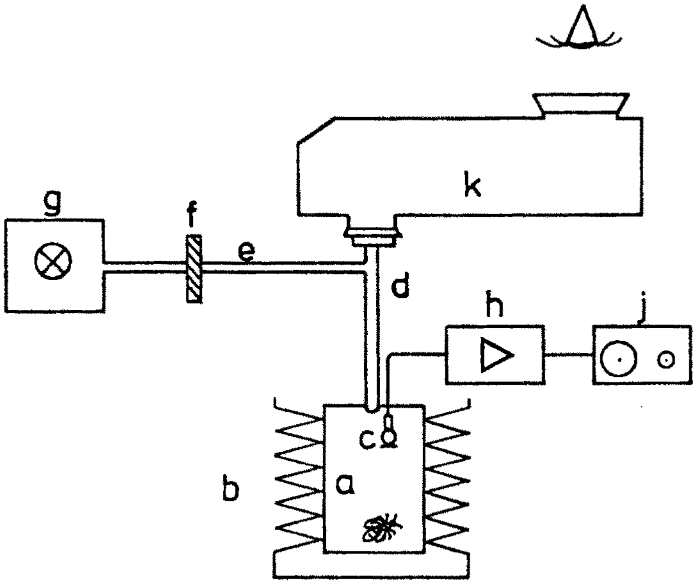

Fig. 2 Schematic drawing of the experimental setup. a: bee in the calorimetric vessel; b: heat flux meter; c: microphone; d: endoscope; e: flexible light guide; f: optical filters; g: light source; h: amplifier; j: recorder; k: night viewing system.

To compare the literature data of indirect calorimetry (manometry, food consumption) with our results, values of oxygen or food consumption were transformed to heat units. It is known that metabolism in bees proceeds with a respiratory quotient of RQ = 1.00 (ref. 12). Therefore, 1 ml oxygen consumed corresponds to a heat production of 21.13 J and 1 mg of sugar to 15.78 J. All experiments described here were performed at 30°C during daytime between 8:00 and 18:00.

RESULTS AND DISCUSSION

Fig. 3 shows typical power-time curves of isolated workers of different ages. Two informations can be drawn from the pictures. (i) The level of the mean rate of weight specific heat production increases significantly with age (see also Fig. 4). (ii) There are by far more structure in the curves of the 6 day old bee than in the smooth curves of the 1 day or 21 day old bee. The reason for these structures will be discussed later.

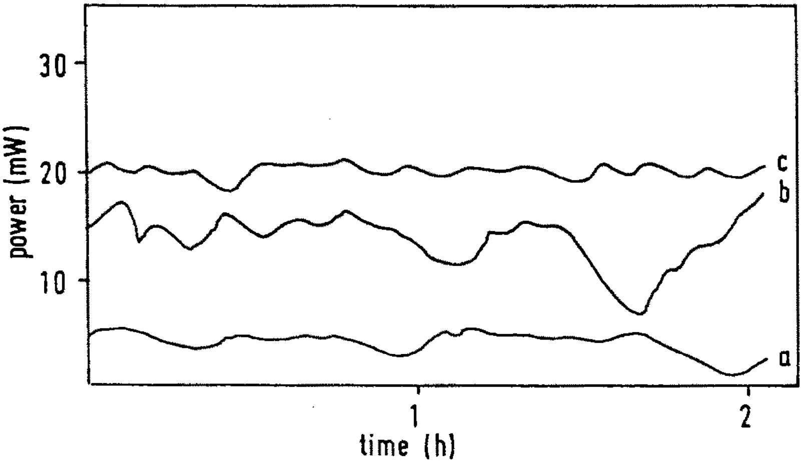

Fig. 3 Typical power-time curves of three workers of different age. (a) 1 day old bee; (b) 6 days old nurse bee; (c) 21 days old forager bee.

Fig. 4 represents the age dependence of the specific heat production rate during the life span of a bee which amounts to 40 to 50 days in the summer period. No occupational and physiological changes appear after the 20 th day. The figure shows that the heat production rate of the freshly hatched bee starts at a very low level from where it rises by more than a factor 6 till to the end of the development of the bee.

Correspondingly, Allen (ref. 13) found 5.9 mW/g for freshly hatched bees and 21 mW/g for 30 days old ones at 32°C. As the cited rates are weight specific the increase is not due to the growth of the animal which is shown in Fig. 4, too. Thus the larger rate must be due to higher metabolic turnovers and to stronger locomotor activities. The values given in Fig. 4 are very large as they are determined for isolated, normally restless individuals. Such results are in agreement with those under similar conditions by other authors. They showed large differences between active and resting bees (99.9 versus 5.6 mW/g at 25°C (ref. 14)) or between day and night (143.2 versus

11.7 mW/g at 20°C (ref. 15). Free flight of bees resulted in 351 mW/g, rest in 18.3 mW/g (ref. 16).

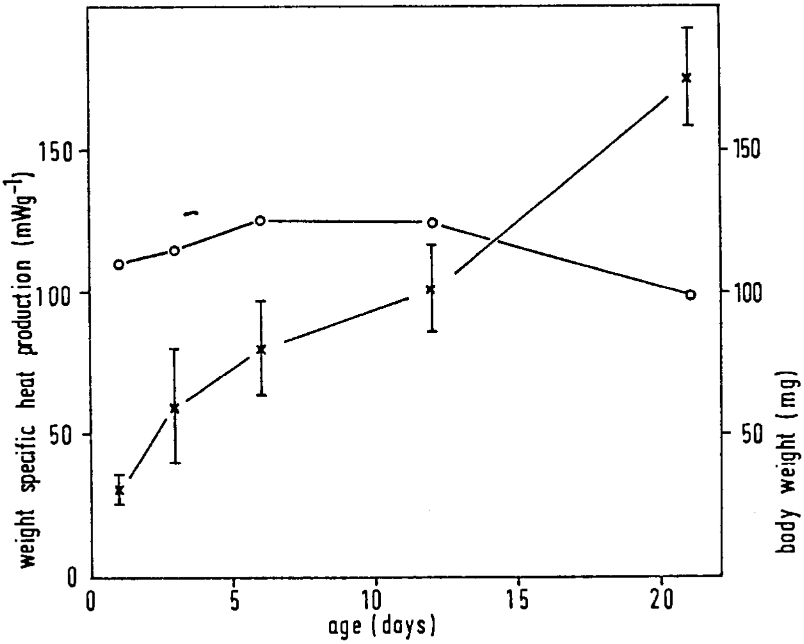

Fig. 4 Body weight m (o) and weight specific heat production rate p (x) of isolated worker bees as a function of their age.

As bees are socially living insects they are used to stay together in groups and become "nervous" when they are isolated. This can be seen from the slope in Fig. 5 for worker groups of different numbers. The weight specific rate of heat production drops from a value of 175 mW/g for an isolated bee to a value of 12 mW/g (or to 7% of the initial value) for groups of 15 or more bees. This value represents the minimum heat production as a consequence of the basal metabolism. Presenting the same data as total heat flux from the groups one observes a broad minimum for groups of 10 to 20 animals and the same heat flux for a group of 30 bees as for 3 isolated workers.

This drastic decrease and the structures in the power-time curves of groups (Fig. 6) can be explained by means of the endoscopic and acoustic observations of the animals. When several bees are introduced into the calorimetric vessel they sit quietly together forming a little cluster and show by far less locomotor activities than the isolated ones. They are occupied with cleaning cells or feeding one another.

Only these caloric figures obtained for larger groups can be compared with those measured for whole colonies by indirect methods. Ritter determined 11.0 mW/g for an intact colony at 24°C (ref. 12), Heinrich (ref. 2) 8.8 mW/g at 28°C and 22.9 mW/g at 35°C. At 20°C differences of 25.7 versus 10.1 mW/g were seen for day and night (ref. 17, 18). These values are in reasonable good agreement with our results if considering the large standard deviations connected with such measurements.

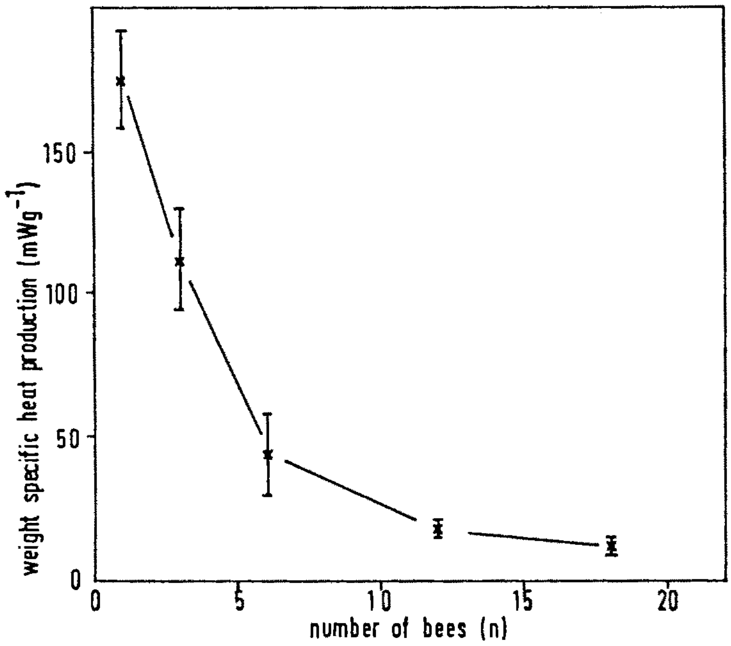

Fig. 5 Weight specific rate of heat production p as a function of the number n of bees forming a group.

In the same manner, as larger groups of bees show a reduced heat production, the presence of a queen or of bee brood appeases the activities within a smaller worker group.

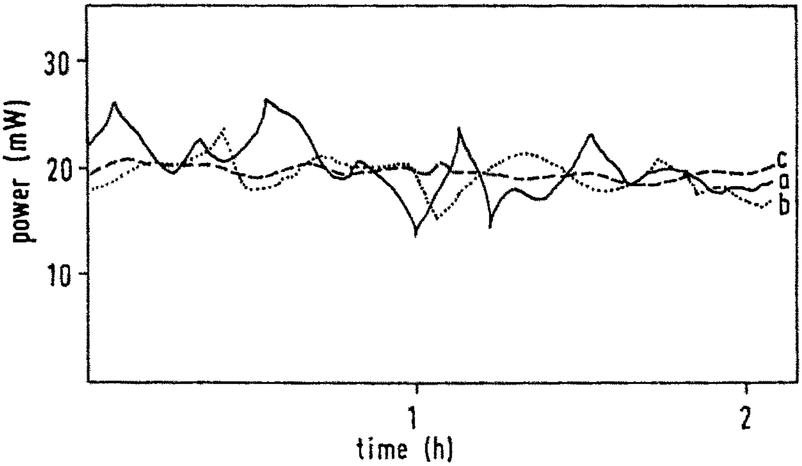

Fig. 6 Typical power-time curves of worker groups of different numbers. (a,——) 3 bees; (b,•••) 6 bees; (c,---) 18 bees.

TABLE 2

Influence of introducing a queen or bee brood on the rate of heat production (+ standard deviation)of a group of 6 adult workers.

workers alone	44 + 14 mWg^{-1}
workers + queen	25 + 3 mWg^{-1}
workers + brood	25 + 3 mWg^{-1}

Endoscopic observations indicate that the bees gather around the queen, feed her and perform social contacts. Similar behaviour is stimulated by the addition of bee brood in a small piece of wax combs. Table 2 compares the heat production rates of a worker group of 6 animals under three different conditions. The reduction due to a queen or to brood comes up to 57%. Investigations at 20 and 25°C demonstrate that the presence of a queen is more effective than that of brood. Experiments with larger groups are not useful as such groups already operate near the minimum heat production of the basal metabolism.

REFERENCES

1 M. Kleiber, The fire of life. An introduction to animal energetics, Wiley, New York (1961).

2 B. Heinrich, Energetics of honeybee swarm thermoregulation, Science, 212 (1981) 565-566.
B. Heinrich, Insect Thermoregulation, Wiley, New York (1981).

3 F. Kronenberg and H.C. Heller, Colonial thermoregulation in honey bees (*Apis mellifera*), J. Comp. Physiol., 148 (1982) 65-76.

5 J. Simpson, Nest climate regulation in honey bee colonies, Science, 133 (1961) 1327-1333.

6 J.B. Free and J. Simpson, The respiratory metabolism of honey-bee colonies at low temperatures, Ent. exp. & appl., 6 (1963) 234-238.

7 M. Lindauer, Die Temperaturregulierung der Bienen bei Stocküberhitzung, Naturwissenschaften, 38 (1951) 308-309.

8 M. Roth, Adaptation de la thermogenese a la temperature ambiante et effet d'economie thermique du groupe chez l'abeille (*Apis mellifica* L.), C.R. Acad. Sc. Paris, 258 (1964) 5534-5537.

8 M. Roth, La production de chaleur chez *Apis mellifera* L., Ann. Abeille, 8(1) (1965) 5-77.

9 L. Fahrenholz, B. Schricker and I. Lamprecht, Thermal investigations of a honey bee colony. Thermoregulation of the hive during summer and winter and heat production of members of different bee castes, J. Comp. Physiol., submitted.

10 I. Lamprecht and W.Becker, Combination of calorimetry and endoscopy for monitoring locomotor activities of small animals, Thermochimica Acta, 130 (1988) 87-93.

11 A. Kühn, Über den Farbensinn der Bienen, Z.vergl.Physiol., 5 (1927) 762-800.

12 W. Ritter, Experimenteller Beitrag zur Thermoregulation des Bienenvolkes (*Apis mellifera* L.), Apidologie, 13 (1982) 169-195.

13 M.D. Allen, Respiration rates of worker honeybees of different ages and at different temperatures, J. exp. Biol., 36 (1959) 92-101.

14 T.H. Stussi, L'heterothermie de l'abeille, Arch. Sci. Physiol., 26 (1972) 131-159.

15 A. Heusner and M.Roth, C. rend. hebd. Acad. Sci., 256 (1963) 284-285.

16 B. Hocking, The intrinsic range and speed of flight of insects, Trans. R. Ent. Soc. London, 104 (1953) 218-234.

17 E.E. Southwick, Metabolic energy of intact honey bee colonies, Comp. Biochem. Physiol., 71A (1982) 277-281.

18 E.E. Southwick and J. Mugaas, A hypothetical homeotherm: The honeybee hive, Comp. Biochem. Physiol., 40A (1971) 935-944.