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ENERGY METABOLISM OF EUROPEAN (*APIS MELLIFERA CARNICA*) AND EGYPTIAN (*A. M. LAMARCKII*) HONEYBEES

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Abstract

Two geographical subspecies of the honeybee *Apis mellifera*, the European bee *A. m. carnica* and the Egyptian bee *A. m. lamarckii*, were investigated by direct calorimetry. Maximum, mean and minimum heat production rates were determined for groups of 6 bees as a function of temperature and daytime. Smaller Egyptian subspecies showed significantly higher mass specific metabolic rates than the European one. Maximum and mean heat production rates decreased exponentially with growing temperatures while the minimum values remained constant.

Keywords: *Apis mellifera*, calorimetry, energy metabolism, temperature

Introduction

Twenty-five subspecies of the honeybee *Apis mellifera* are found dispersed in Europe, the Near East and Africa. They are well adapted to their specific habitats and climates and show significant differences in behaviour and size. *A. m. lamarckii* is the original Egyptian honeybee which is used in apiculture for thousands of years. Around the beginning of the twentieth century, the European honeybee *A. m. carnica* was introduced to Lower Egypt because of its higher foraging efficiency and its easier way of handling. Meanwhile, it expels *A. m. lamarckii* from its ancestral foraging sites to areas with scarce forage.

There are considerable differences between the two geographical subspecies: The Egyptian honeybee *A. m. lamarckii* is significantly smaller, slimmer and has shorter wings and legs (Table 1). Its colonies consist of fewer bees (8 000 to 10 000 bees) compared with that of the European subspecies (more than 40 000 honeybees). It neither forms winter clusters nor stores food for overwintering and breed nearly throughout the year. It is regarded as a typical representative of tropical African bees [1]. In

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contrast, the European honeybee *A. m. carnica* faces a less moderate climate with strong temperature fluctuations between day and night, summer and winter [2]. It is forced to form winter clusters and to store food for unfavourable periods. When disturbed or attacked, the Egyptian honeybee shows a more aggressive defence behavior compared with European bees. Larval development time is also shorter for *A. m. lamarckii.*

Until now, only few metabolic and physiological investigations on different geographical bee subspecies are listed in literature, mainly connected with the appearance of Africanised bees in South America [3–5]. Therefore, this paper aimed at comparing the metabolic activities of the Egyptian honeybee, *A. m. lamarckii*, and the European honeybee, *A. m. carnica* at different ambient temperatures. Both, heat dissipation per bee as well as per gram live mass ‘specific heat production’ were determined as a function of ambient temperature between 20 and 40°C. All cited results were obtained by direct calorimetry, a method applied only a few times in bee research [6–8]. They can be transformed to the usual oxygen consumption rates assuming a respiratory quotient of 1.00 and a factor of 5.94 mW (mL oxygen h)$^{-1}$ [9].

Experimental

Honeybees

Isolated bees show discomfort through a strong unrest and a corresponding higher heat production compared with bee groups of increasing number [6, 7, 10]. Therefore, groups of 6 insects were used in this investigation. This number of bees was chosen, because bees in smaller groups are unquiet due to separation from the swarm, and larger groups are more difficult to handle [7].

Investigations were performed on a ‘mixed’ colony comprising an *Apis mellifera lamarckii* queen and approximately 1 000 Egyptian and European worker bees. There are no difficulties keeping such groups of two subspecies ‘queenright’ together in a single beehive. The experiments were conducted in the summer period between April and September 1993. Data were taken daily in four intervals: from 8.00 to 11.00, 11.00 to 14.00, 14.00 to 17.00 and 17.00 to 20.00 to determine possible diurnal rhythms in locomotor activity.

The Egyptian bee *A. m. lamarckii* was imported from Egypt and kept in quarantine in a free-flight room at the Zoological Institute. From this stock colony, a smaller ‘mixed’ one was composed and transferred to a wire-netting cage near the calorimeters. The cage had a rectangular size of 80×80×180 cm^3 and was illuminated from 8.00 to 20.00 h. Containers with sugar solution, water or pollen and a flower bouquet were arranged in the cage at the side opposite to the hive. Relative humidity and room temperature were kept constantly at 50% and 23°C, respectively. The bees had access to food ad libitum in the cage as well as in the calorimetric vessel.

Since worker bees were caught outside the hive in the cage, a homogeneous collective of foragers entered the calorimetric investigations. Before and after each experiment the pooled group of 6 workers was weighed to the nearest 0.1 mg

(Sauter/Ebingen, type 414/13), and the mean live mass was used to calculate the specific heat production rates.

Calorimeters

Two microcalorimeters of the Calvet type (Setaram/Lyon, type MS 70) with vessels of 100 mL open to the air were used for all experiments. The sensitivity amounted to approximately 50 mV W^{-1}. The operating temperature was changed during the investigation period between 20 and 40°C. Lower temperatures were not possible – although desirable – because of experimental reasons.

Six bees of an experimental group were caught in the wire cage and weighed. They were transferred into the calorimetric vessel together with a small container filled with a sugar and pollen mixture (‘bee bread’) and inserted into the calorimeter. The first 30 min of each experiment were discarded because of the calorimetric heat of friction and the increased activity of the bees upon the catch. At the end of the measuring period of 2 h the bees were weighed again and released into the cage. For each temperature and each subspecies, approximately 20 experiments were performed and pooled for statistical analysis. The calorimetric base line was registered for 30 min before and after each experiment. Calorimetric graphs of heat production rate *vs.* time were analysed for the total heat production and rendered the mean heat production rate during the experimental 2 h period.

Heat production rates of bee groups show strong temporal fluctuations which are due to locomotor activities of the insects (Fig. 1). Under the restricted spatial situation in the calorimetric vessel these activities may span from true rest to strong unrest and to intended attempts to fly. To investigate this behaviour in more detail, the total experimental period of 2 h was divided into 10-min intervals for each of which the mean heat production rate was determined. The interval with the highest rate was chosen as maximum value (P_{max}), that with the lowest rate as minimum value (P_{min}) for each experiment. Their difference $P_{loc}=P_{max}-P_{min}$ was taken as the rate of locomotor activity [11]. Bartholomew defined a ‘metabolic scope’ as the difference between the energy turnover in the state of maximum activity and that at rest [12]. P_{loc} differs from this figure because it cannot be guaranteed that the final minimum values of resting metabolism and those of maximum activity were attained during our experiments [7].

Statistical evaluation

As only a limited number of bees was available for the present investigations, the animals were not sacrificed after the experiment but placed back into the cage. Under this experimental conditions it could happen that an individual bee participated several times in the measurements. As the groups were composed of 6 bees the chance to have identical bee groups was negligible. Moreover, life-span of the foraging bees in summer was between 10 and 20 days so that new bees entered the collective continuously. In this way the population was exchanged about 10 times during the investigation period of 5 months. Thus, the experiments may be considered as independent and statistics may be applied to the results.

Standard deviations of the means are given in all values, significance was determined with the Mann–Whitney test. Because of the limited number of experiments, a level of p=0.05 was considered as significant.

Results

Body mass

The body mass of both subspecies was determined in each experiment so that the given means result from 600 bees each. The live mass of both subspecies showed smaller, non-significant fluctuations during the experimental period from April to September. The mean mass of the European bee amounted to 0.120±0.029 g (n=600), that of the Egyptian bee to 0.078±0.013 g (n=600). This shows that the Egyptian bee is much smaller than the European one with only 65% of its mass. Similar results are found for other morphometric characters (Table 1). Thorax masses of both subspecies differ significantly (0.033±0.002 g *vs*. 0.024±0.001 g) although the relative masses in percent are comparable. Similar observations hold good for the wing size as a direct measure and its derived figure wing load.

Table 1 Some morphometric characters of the European honeybee *A. m. carnica* and the Egyptian honeybee *A. m. lamarckii*

Measure	Unit	European bee (1)	Egyptian bee (2)	Ratio ×100 (2)/(1)
Body mass	mg	120±29	78±13	65
Thorax mass	mg	33±2	24±1	73
Thorax/Body	%	28±7	31±6	111
Wing size	mm^2	55±2	45±1	82
Wing load	$N\ m^{-2}$	21±5	17±3	81

The valuse given are means plus standard deviation for 10 bees each, except for body mass with 600 insects. Both masses are given as wet mass

Due to the limited number of Egyptian bees available (see above), the mass specific rates given in the text are related to the total body mass and not to the more appropriate thorax mass [13]. By means of Table 1 and the relationship between thorax and body mass (28% for the European and 31% for the Egyptian bee) the energy values can easily be transformed into the wanted figures.

Heat production rates

Figure 1 presents a typical power–time curve for a group of 6 Egyptian worker bees at 40°C. This graph shows fluctuations around a slowly decreasing mean value of 32 mW in the first and 22 mW in the last 20 min period. They are due to locomotor activities of the bees. A true phase of rest (basal metabolism) does not appear during these 100 min but may be indicated around 90 min approaching a level of 16 mW or 43 mW g^{-1} (2.7 mW/bee). With 6 bees in the calorimetric vessel one would expect a more or less constant level of the heat production rate as individual periods of rest or activity should level out. The distinct fluctuations of the curve indicate that 6 bees act in a some-how co-operative or 'social' manner and that a calming down of the group happens to the end of the period.

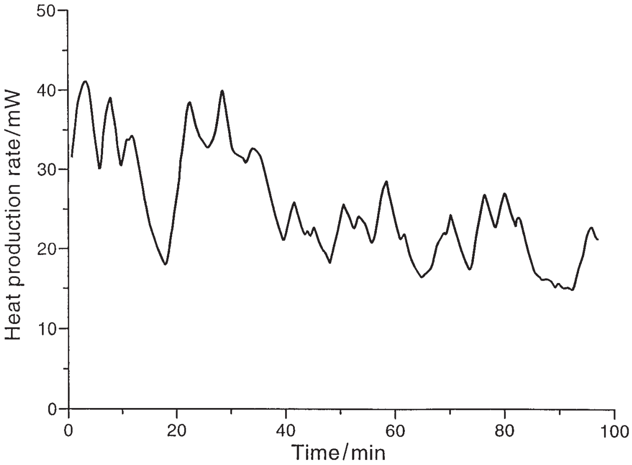

Fig. 1 Heat production rate *vs.* time for a group of 6 Egyptian worker bees (367.8 mg wet mass) at 40°C

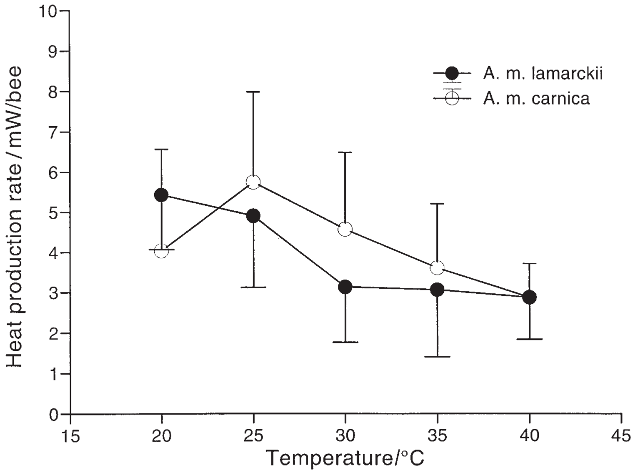

Fig. 2 Mean heat production rate per bee of both subspecies as function of the experimental temperature. Standard deviations are indicated for 20 experiments per point

Under the present experimental conditions and with the aim of this investigation the time constant of the calorimeter and its thermal inertia are not taken into account which results in smoothing of the curve. A 'desmearing' of the power–time curve would be necessary to find the true maximum and minimum values of the heat production rate. From former experiments with the same equipment it is known [11] that short period maxima have to be multiplied by a factor of about 2.5 to render the true size of the metabolic rates. As such desmearing has no influence on the mean values or the long time minima it was not performed routinely for each graph.

Mean heat production rates per bee were determined in the summer period between April and September. They were calculated from power–time curves like that in Fig. 1 for different ambient temperatures (Fig. 2). The mean values varied between 5.8 mW per bee (*A. m. carnica* at 25°C) and 2.9 mW per bee (*A. m. carnica* and *A. m. lamarckii* at 40°C) and showed no significant differences between both subspecies at all temperatures ($p>0.05$, Mann–Whitney test). Thus, the much smaller Egyptian bee maintained the same metabolic intensity as the European form. But the mass specific heat production rates of the Egyptian bee were distinctly larger than those of the European one at all chosen temperatures (Fig. 3). The highest mean values were 75 mW g^{-1} (at 20°C) for *A. m. lamarckii* and 47 mW g^{-1} (63% of the latter) for *A. m. carnica* (at 25°C). The differences between the two subspecies were significant on the 5% level for all temperatures except 30°C ($p<0.17$). As the differences between the mean rate of the *Carnica* bees at 20 and 25°C were not significant ($p>0.19$) a general decrease with temperature could be assumed in accordance with observations of other authors [10, 14]. This trend shown in Fig. 3 can be approximated by an exponential slope rendering a correlation factor $r=-0.83$ between heat production rate and temperature. Omitting the questionable figure at 20°C leads to a much stronger correlation with a factor $r=-0.980$.

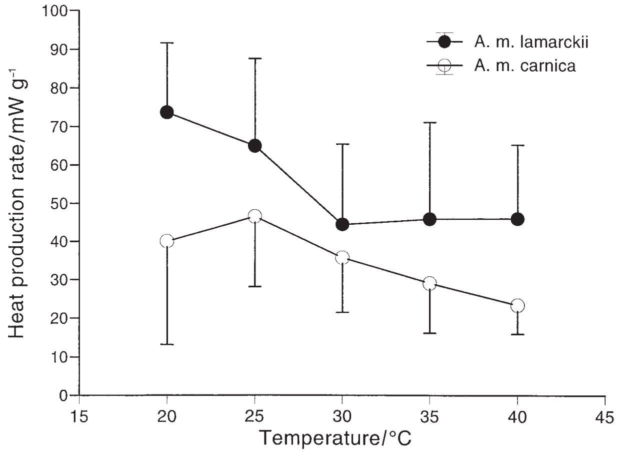

Fig. 3 Mean mass specific heat production rates of both subspecies as function of the experimental temperature. Standard deviations are indicated for 20 experiments per point

The standard deviations drawn in Fig. 3 for the mean heat production rates indicate strong differences between single experiments. They are due to a pronounced activity scatter for the experiments in one temperature group. The maximum values for the mean rates at the five temperatures vary around 94±6 mW g^{-1} for the Egyptian bee at all temperatures while values for the European bee again exhibit a strong exponential decrease with temperature ($r=-0.97$; Fig. 4). Such a clear a dependence on temperature lacks in the corresponding minimum figures. They vary around 14.0±5.9 mW g^{-1} for *Lamarckii* bees and around 12.4±4.9 mW g^{-1} for *Carnica* bees (Fig. 4). The fluctuations in the minimum rates indicate that values of a true resting metabolism are hardly obtained under the chosen experimental conditions and in the short investigation period of 2 h for a discussion of a 'true resting metabolic rate' of honeybees e.g. [15].

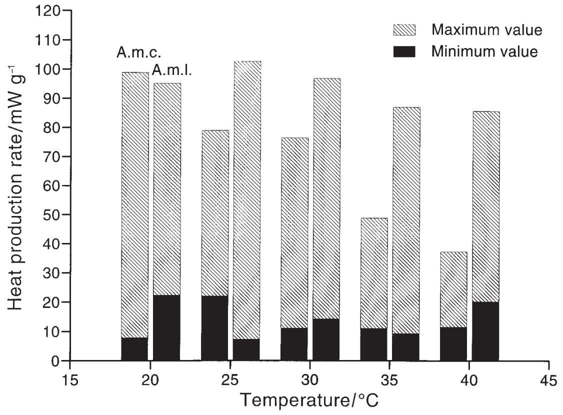

Fig. 4 Comparison of the mean maximum and minimum heat production rates as function of the experimental temperature for European (*A. m. c.*) and Egyptian (*A. m. l.*) honeybees

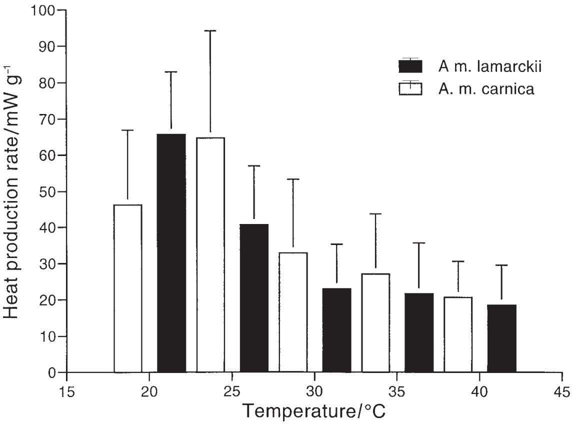

Fig. 5 Comparison of the locomotor activities as function of the experimental temperature for European (*A. m. c.*) and Egyptian (*A. m. l.*) honeybees. Standard deviations for 20 experiments per bar are indicated

The locomotor activity of the bees P_{loc}, defined above as the difference between maximum and minimum rates, also decrease with temperature in the chosen range (Fig. 5). They reduce to 28% for the Egyptian bee from 67 mW g^{-1} at 20°C to 19 mW g^{-1} at 40°C and to 31% for the European bee from 68 mW g^{-1} at 25°C to 21 mW g^{-1} at 40°C. This result indicates that both subspecies become calmer at elevated temperatures and move less frequently, as confirmed by endoscopic observation inside the calorimeter and directly outside, too.

When the obtained calorimetric results are analysed for circadiane changes in the metabolic rates they point for both subspecies to a decrease during daytime from morning to evening (not shown). The effect is most pronounced for *Carnica* bees at 40°C (40% reduction) and for *Lamarckii* bees at medium temperatures (30%). These results are in agreement with those of Southwick for a European colony [16], while Worswick observed a metabolic maximum around 6 pm for an African bee (*A. m. adansonii*) [17].

Discussion

Metabolic and physiologic investigations on different geographical bee races are rare in literature and mainly connected with Africanised bees in South America [3–5]. Because of earlier experiments with the Egyptian honeybee *Apis mellifera lamarckii* we wanted to compare its metabolic activity with that of the European honeybee *Apis mellifera carnica* at different ambient temperatures. To make the experimental conditions as similar as possible both subspecies lived together as a mixed population in a common beehive. Moreover, some preliminary experiments were performed with ‘pure’ swarms of each subspecies. With a few exceptions the mixed swarm accepted the experimental conditions and developed well during the summer.

Table 1 indicates that European and Egyptian bees are quite different in size. Thus, it is necessary to compare the metabolic rates not only per bee but per live mass also. This mass does not only depend upon the age and the size of the bees, but also upon the degree of filling of crop and intestine. Scatter in the mass specific rate is therefore also introduced by the acute state of the individual bee. It was attempted to minimise these errors by catching the bees outside the hive in the free-flight cage in order to obtain a more or less homogeneous group of forager bees.

The present investigation showed a slight, but not significant dependence of the mean heat production rate on temperature for *Lamarckii* bees, but a strong decline with temperature for their *Carnica* counterpart (Fig. 4). A corresponding distinct reduction of food consumption in bee groups was found between 16 and 36°C [18] and a linear decrease of the mean resting metabolism in small worker groups of *A. mellifera* [14, 19]. Allen (1959) observed a decrease of 50% in old worker bees (*A. mellifera*) between 17 and 32°C [20]. A stronger decrease of heat production rate with temperature was calorimetrically determined for isolated bees than for bee groups during the day [6]. At night the opposite relationship held good [21]. In contrast, Rothe and Nachtigall found a ‘significant linear correlation’ between the relative metabolic power of resting bees and ambient temperature [15].

Bergmann’s rule of metabolism for geometrically similar bodies postulates that the smaller one with a higher surface to volume ratio should exhibit the larger heat loss rate per mass. This rule is confirmed by the present results. They show that the significantly smaller Egyptian honeybee dissipates approximately the same heat as the European bee. Heinrich concluded from the equal thoracic temperature of an African subspecies, *A. m. adansonii*, and the European *A. m. mellifera* during flight and attack, that the smaller African bee (66% of mass) must have a higher metabolic rate [22]. Its larger passive cooling rate would otherwise result in a lower body temperature. Moreover, the lacking insulation of tropical bees leads to higher metabolic rates at lower environmental temperatures [23]. Southwick and colleagues compared groups of Africanised bees similar to *A. m. scutellata* and of European bees. With a body mass of only 80% of its European counterpart, this Africanised bee showed up to 109% higher metabolic rates at lower temperatures [4]. Corresponding investigations were performed on African-European honey bee hybrids and their metabolic capacities for flight [24]. As stated by most investigators, the Africanised bees are more active, more aggressive or defensive, form looser clusters and function more efficiently in tropical environments than in temperate zones.

In accordance with several results from the literature, the present paper underlines that the smaller Egyptian bee *A. m. lamarckii* shows a significantly higher mass specific metabolism than the European bee *A. m. carnica*. It is more active, more aggressive and well adapted to its tropical environment. Its foraging strategy aims at dispersed, erratic offers of nectar [25] while the Carnica bees are more efficient in collecting nectar with spatially and seasonally uniform sources. The strong change in agriculture in the upper Nile delta with a transition to monocultures favours the European bees. Therefore, they are imported by beekeepers to Lower Egypt because of their nowadays higher efficiency. In recent years, they have superseded the African subspecies and expelled it to unfavourable ecologic niches [25]. In contrast to South America and its agricultural problems with Africanised bees, the calmer European bee replaces the original African form in this case.

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