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Calorimetric experiments on social insects

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Abstract

Direct calorimetric experiments on the social insects: honeybees, bumblebees and hornets are described as function of castes, age, number of animals in a group, temperature, sound generation, hibernation and influence of pheromones. Two honeybee subspecies, the European bee *Apis mellifera carnica* and the Egyptian bee *Apis mellifera lamarckii*, were compared calorimetrically in their energy metabolism which differed considerably in favour of the more alert Egyptian form.

Moreover, thermoelectric cooling boxes for camping were applied as simple heat conduction calorimeters and as artificial nesting facilities for bumblebees and hornets. Their colonies could be monitored calorimetrically and thermometrically throughout the season. In spring, initial nests with only a few workers and one queen were collected in the field and transferred to these boxes where they continued their normal development up to full size of several hundred individuals. By this means, energy turnover of insect colonies could be evaluated under varying conditions. © 1997 Elsevier Science B.V.

Keywords: Calorimetry; Hibernation; Honeybees; Pheromones, Social insects

1. Preface

One late afternoon, Prof. Edouard Calvet, the 'pope' of the French calorimetrists, was working in his Marseillian office when the phone rang. An unknown scientist asked for the maximum vessel size of his famous 'Calvet' calorimeter and if it might be possible to place a monkey in it. Calvet told him the biggest volume and presumed that it would depend upon the mass of the animal. With a 'mercie beaucoup' the connection was broken and Prof. Calvet felt considerably fooled by this interruption of his work. A few minutes later the same voice was at the phone: "Eh bien, monsieur le professeur, I found a similar container and tried. The monkey fits in quite well but the tail has to hang outside!"

This is why so many calorimetrists prefer to work with smaller animals fitting into the usual calorimeters with working volumes up to 100 ml. The present paper deals with such applications for social insects but includes some hints to other organisms and to cooling box calorimeters of by far bigger size.

2. Introduction

Calorimetry on animals began two hundred years ago with Lavoisier's famous ice calorimeter (1780) and the determination of respiration and heat production of guinea pigs, a combination of direct

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and indirect calorimetry at the very cradle of this discipline. Both methods of metabolic research developed separately in the following time. There was a clear accentuation on the indirect one since already Crawford (1788) showed that oxygen consumption is roughly proportional to heat production. Moreover, this approach was cheaper and easier to perform than the direct one. Only in the last decades true (direct) calorimetry was more frequently applied to living systems from microorganisms to man and domestic animals. Due to our experiences with Calvet microcalorimeters of 15 and 100 ml experimental volume the present paper concentrates on own investigations with animals that fit well into such vessels.

Among the small 'calorimeter sized' animals terrestrial insects are the most frequently investigated ones since they are easy to gather, breed, keep, handle and to measure in dry vessels without evaporation problems or high thermal inertia as with aquatic organisms. At heat production rates of 10 to 100 w kg^{-1} and wet weights (ww) between 100 and 1000 mg one expects calorimetric signals of 1 to 10 mV which makes no high demands on the sensitivity of the instrument and on the stability of the baseline. Development and growth was followed calorimetrically for several insects, among them the meal worm *Tenebrio mollitor* L., the cockroach *Blattella germanica* L. and the wax moth *Galleria mellonella* [1–4] while other animals were included in experiments on the influence of xenobiotics (such as pentachlorophenol) in forest ecosystems [5–7].

Insects may live as single individuals through all their life ('solitary insects') or forming large stable colonies for longer periods ('social insects'). In a strict sense only honeybees, ants and termites are counted as superorganisms [8] whose collonies react like multicellular organisms with an egg-laying queen as sole sexual member and the chance to survive the winter. However, bumblebees, wasps and hornets have many ecological, thermal and behavioural aspects in common with bees so that they may be counted – with a few restrictions – as superorganisms.

Termites were excluded from experiments until now for obvious reasons, but forest ants (*Formica rufa*) were investigated calorimetrically as isolated animals of different age [9] or in a more complex way in their social unit – the ant hill – by means of meteorologic techniques [10,11]. In this way it was possible to demonstrate thermoregulatory behaviour for the whole colony and to show the important contribution of microbial metabolism in the nest material to the overall heat balance [9,10]. But as the significance of microbial heat production was jeopardized by other authors [12–16] and corresponding direct and indirect calorimetric experiments are underway now to clarify the differences, ants shall be omitted from this review. Instead, it will concentrate on the three other social insects: honeybees; bumblebees and hornets.

Especially, domestic honeybees were intensively investigated by many authors in different aspects of their social life: development and growth; metabolism as function of caste; age and temperature; orientation; communication and information transfer. Metabolic experiments were usually carried out by indirect calorimetry assuming an exclusive carbohydrate diet and a respiratory coefficient of 1.00. Thus, only a few 'true' calorimetric investigations are found in the literature (for a review see [17]).

3. Material and methods

3.1. Honeybees

Two geographical subspecies were investigated calorimetrically: the European honeybee *Apis mellifera carnica* and the Egyptian honeybee *A. m. lamarckii*. The latter is more aggressive, smaller (78 ± 13 mg ww for workers), slimmer and has shorter wings and legs than the larger (120 ± 29 mg ww) European one of moderate temperament. In both subspecies different castes (queens, female workers, male drones), different ages of worker bees and groups of them in various sizes were investigated, often as a function of the ambient temperature.

An experimental hive of the Carnica bee with free access to the outside was kept in the loft and a Lamarckii hive in a freeflight cage both close to the calorimetric chamber. Thus, transport ways for the bees were rather short between their hives and the calorimeters. Larger numbers were caught in the

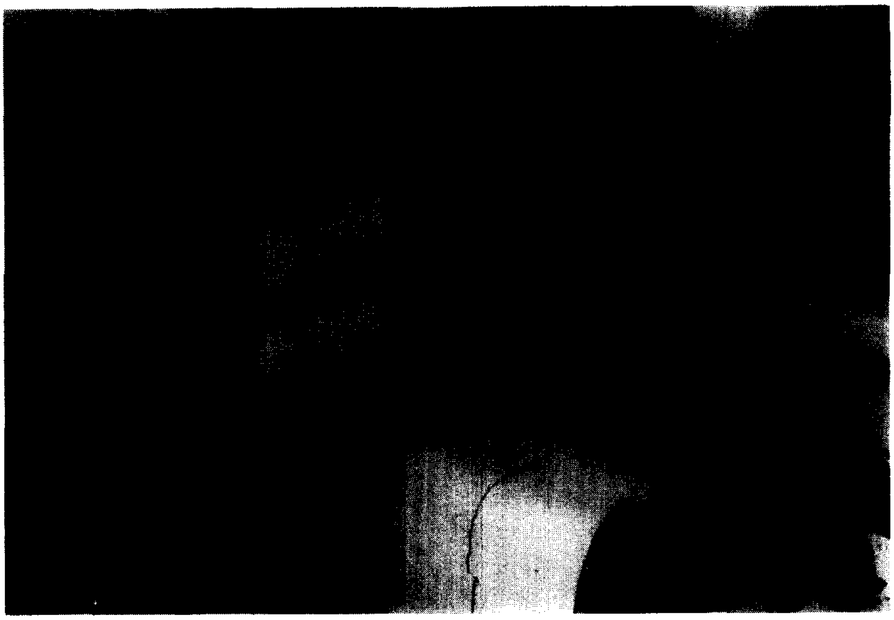

Fig. 1. Opened 8 l cooling box (PMC) used as an artificial nest place for bumblebees. The box is additionally isolated by styropor. The lucit walkway with a bumblebee inside is seen on the right, a few thermocouples inside the box. In front a dual channel recorder for temperature and heat flow [19].

apiary of the department 3 km away from the institute. In all cases the experimental animals were placed back into the hive after measurements. Individual marking of the bees ensured that no bee (except queens) was tested twice.

3.2. Bumblebees

Colonies of the Bumblebee, *Bombus lapidarius*, were kept in artificial breeding boxes or in a PMC ('Poor Man's Calorimeter') instrument [18] from where the individuals were brought to the Calvet calorimeter and placed back after the experiment. The wet weights of workers and drones ranged from 90 to 220 mg, those of young queens were significantly higher from 270 to 650 mg and that of the old queen was 650 mg. In two consecutive years, small initial bumblebee nests were translocated from the original places to the PMC where they continued their usual development (Fig. 1). Around 150 female and male animals lived in the nest during the optimum period in June, a number that steadily declined till the end of July when the queen died and the nest became empty [19,20].

3.3. Hornets

Hornets belong to the social wasps but are larger, more phlegmatic and less aggressive than the 'usual' widespread wasps and thus easier to handle and to investigate. They found colonies in late spring which may count up to a few hundred individuals in September before they die out in late autumn. Only the inseminated queens hibernate at hidden places and start new colonies in the following year.

Similar to the procedure with bumblebees, small initial nests of the hornet *Vespa crabro* with one queen and a few workers, larvae and pupae were translocated from their original sites to appropriate wooden boxes (or PMCs) in the institute. The nests were attached to the top of the boxes (Fig. 2) and the hornets continued to construct them downwards. At the end of the season the boxes were entirely filled by the nests (Fig. 3). These boxes were connected to the outside by walkways so that the usual colony life could proceed. Individuals were caught in the walkways and taken directly to the calorimetric experiments. Hornets are the most heavy insects in these investigations with

Fig. 2. Two young hornet nests at the top of a wooden breeding box. The hornets are seen working at the cells with larvae.

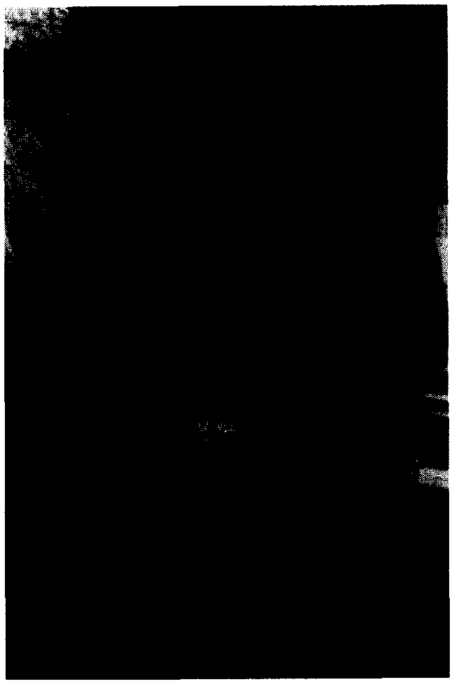

Fig. 3. Hornet nest some weeks later with a third comb and the insulating envelop made from chewed wood.

fresh weights from 400 to 500 mg for workers, 350 to 800 mg for drones and 800 to 1200 mg for queens.

3.4. Microcalorimeter

All calorimetric experiments with individual insects or groups of them were performed with isoperibolic Calvet calorimeters (ms70; SETARAM, Lyon/France) with vessels of 100 ml volume which could house up to 30 bees during investigations. The working temperature varied between 15 and 35°C, the sensitivity amounted to around 54 mV W^{-1}. Typical recorder settings were between 1 and 10 mV full scale.

The calorimeters were equipped with an endoscopic setup for visual and infrared light [21–23] and with a microphone for acoustic responses [22,23]. Both were used to monitor the locomotor activity and the social behaviour of the insects (Fig. 4). These accessories led to a constant baseline shift of the calorimetric signal but produced no further disturbances of the instrument. Observations by infrared light above 780 nm which is invisible for bees show the behaviour of the insects 'in the dark' as normally in calorimetric experiments while visible light allows for the determination of optical influences on the heat production

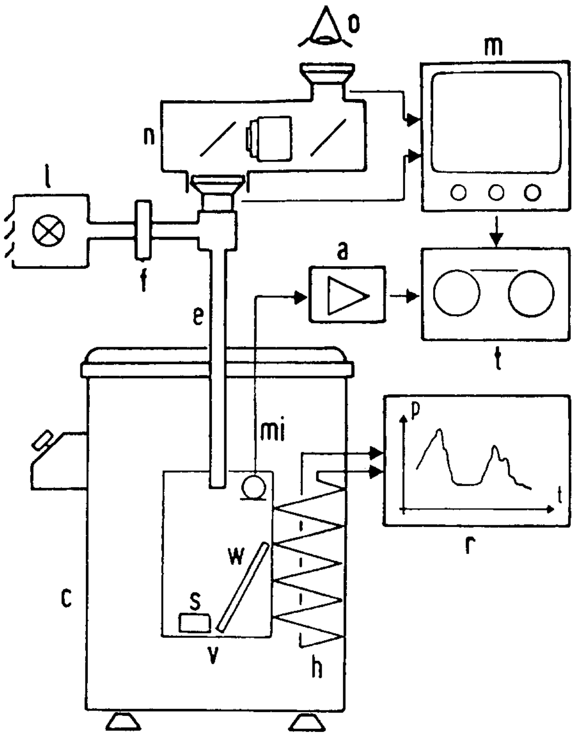

Fig. 4. Calvet calorimeter (ms70) with additional equipment for simultaneous measurements. Calorimeter (c) with 100 ml vessel (v), heat flow meter (h) and recorder (r). In the vessel a cup for hoarded food (s) and a wooden stick for climbing (w). The microphone (mi) is connected to the tape recorder (t) via an amplifier (a). The optical setup comprises the endoscope (e), a lamp (l) and filter (f), a night viewing system (n) plus video camera and monitor (m) or alternatively the naked eye (o) [23].

rate of the insects. For simultaneous indirect calorimetry a constant stream of air was sucked through the vessels and the concentration of oxygen and carbon dioxide determined before and after passing the measuring chamber.

3.5. PMC

To get a broader insight into the energy turnover and thermoregulation of intact insect colonies it was advantageous to use calorimeters big enough to house complete nests. Since commercial calorimeters with appropriate active volumes of several litres are extremely expensive, the idea arose that cooling boxes from camping equipment could serve as a 'Poor Man's Calorimeter' (PMC, [18]). In the bottom of these boxes Peltier elements are embedded which are normally connected to a 12 V car battery and can be used for cooling or heating the box, depending upon the polarity of the DC current applied to the element. In the calorimetric setup this element serves as a heat flow sensor of an appropriate sensitivity (between 7 and 20 mV W^{-1}; [18,20,24–26]). To improve the heat conduction to the sensor the inside of the box was covered with a thin copper foil glued to the walls [25]. The time constant of these calorimeters is rather high (10 to 40 min) but this is no drawback at all as the heat production rate of whole nests fluctuates only slowly and with small amplitudes. Boxes with active volumes between 8 and 24 l from various manufacturers were used, often in a differential setup. They were placed in cellar or loft rooms of the institute with rather stable temperatures (±1°C).

The insects in the boxes had free access to the outside by means of walkways of about 40 to 100 cm, long enough to limit cold draughts and to ensure a stable baseline during the day. Individual insects were caught in these walkways for the microcalorimetric determinations. The reference box just above the first one had a similar walkway but was closed with a grid. At the beginning of the season (and sometimes much later [25]) small initial nests with all the existing members (queen and workers) were relocated from their original sites into the box. Bumblebee nests were placed in the bottom together with some constructing material [20,26], hornet nests were glued to a removable plate and fixed at the top of the PMC [25]. Bumblebees and hornets accepted the translocation in most cases and continued to develop their nests. At the end of the season hornet nests often filled the box completely leaving only minor space at the bottom, that is, at the entrance to their combs.

4. Results and discussion

4.1. Honeybees

Young honeybees hatched from the comb after the larval and pupae stages exhibit a fresh weight of about 110 mg which stays nearly constant throughout their life. But the metabolic level increased with age and changing hive duties so that the final mass specific heat flow is approximately 180 W kg^{-1}, that is, sixfold higher than in the first days. Such values are dependent

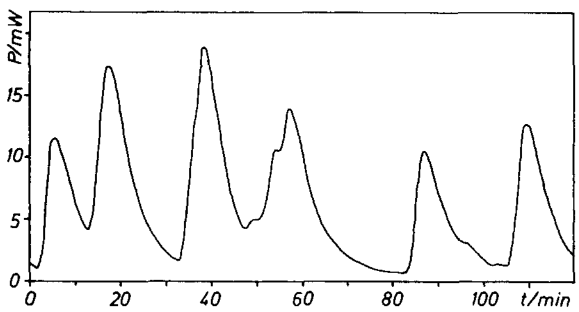

Fig. 5. Power-time curve of a single honeybee (142 mg ww) at 26.5°C. The activity bursts between periods of rest are clearly visible.

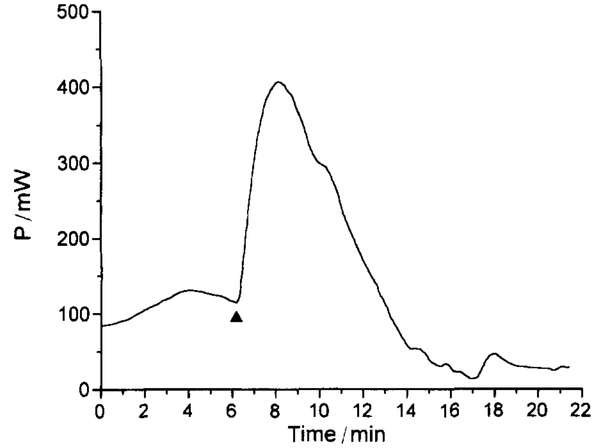

Fig. 6. Power-time curve of a group of 30 honeybee workers (3.28 g ww, 25°C) reacting on a 1 : 10 solution of isopentylacetate in diglyme injected into the air stream through the calorimetric vessel. The addition of the pheromone is marked by the arrow.

on physical parameters like temperature, illumination and day-time, but also on biological facts. Since honeybees are socially living insects the calorimetric power-time curves of single animals may render values which are artificially high. This is due to an enforced locomotor activity which is clearly seen in the calorimetric signal as a chain of periods of rest with low heat dissipation and of activity with high dissipation levels (Fig. 5) [22].

This effect is strongly underlined when honeybee workers are investigated in groups with different numbers. The heat production rate of 15 or more individuals drops to less than 10% of that of an isolated bee. Moreover, endoscopic and acoustical monitoring show that the bees are clustering at the bottom of the vessel around a sugar container and are engaged in social contacts [22,23,27]. Similar reductions are also registered when a few workers are placed together with their queen or combs with brood.

On the other hand, only larger groups of bees exhibit a significantly increased heat dissipation due to agitation when they are exposed to alarm pheromones [28]. Fig. 6 shows a typical response of a group of 30 bees with a wet weight of 3.28 g to the addition of a solution of isopentylacetate dissolved in diethylenglycol-dimethylether (diglyme). This solvent was chosen because of its polar and non-polar regions which help to dissolve all components in case of a complex pheromone. After a more or less constant baseline of about 100 mW the addition of the alarm pheromone led to a steep increase in the heat production rate followed by a smoother drop after a few minutes. In some experiments the calorimetric signal returned to the initial baseline while in many cases it dropped below it due to the physical exhaustion of the bees after the alarm. Deconvolution of the thermal inertia of the calorimeter shows a much more pronounced answer with an instantaneous, nearly steplike upward jump in the signal and a quick return to the former level. Endoscopic and acoustic monitoring in the calorimetric vessel and observation in respiratory experiments outside the calorimeter confirm these observations.

The mentioned preliminary investigation with isopentylacetate as the main component in honeybee alarm pheromones was expanded to other less effective organic compounds and some combinations of them. As with artificial human perfumes the composition of a pheromone is crucial so that synergistic results may be expected. Further experiments are aimed in this direction, not only with honeybees but also with hornets. First calorimetric results are encouraging.

Besides worker bees which are the most interesting and best investigated caste of a colony due to their different duties inside and outside the hive, the other two castes were calorimetrically observed, too. Juvenile drones showed a smaller mass specific heat production rate than the fertile older ones. The increase was threefold at 25°C (up to 184 W kg^{-1}), but up to twenty times at the unphysiologically low temperature of 20°C. The power-time curves of adult drones were highly structured with long periods of rest with low heat dissipation and such with pronounced activity. The cited mean heat production rate equals that of workers with hive duties although they are only half as heavy as the drones. Young virgin queens showed a higher heat production rate than the fertile egg laying queen. This is understandable since the young queen is on its own while the old queen is warmed by the worker bees in the hive [23].

In connection with the discussion about the Africanized 'killer' bee in America it seemed worthwhile to compare the usual European honeybee with an African one. The domestic European honeybee *Apis mellifera carnica* is known to be calmer than the Egyptian one (*A. m. lamarckii*), another form of the known 25 subspecies of *Apis mellifera*. This significantly smaller honeybee shows an alert and more active temperament and an increased readiness for attack. Such differences are reflected in the distinctly increased mass specific heat production rates of bee groups. They occur at all temperatures so that the smaller insects produced as much heat as the larger ones. The results demonstrate that besides morphological differences also physiological ones exist between both subspecies [29].

4.2. Bumblebees

Bumblebees are by far not as intensively investigated as honeybees, because they form only annual colonies and are more difficult to maintain. No direct calorimetric experiments on individual bumblebees are found in the literature, and only few determinations of energy metabolism have been performed by respirometry or calculated from thermometric measurements of thorax temperatures. The same holds true for complete bumblebee nests [30].

Bumblebees perform social thermoregulation: they are able to elevate the nest temperature above that of the surrounding and to keep it constant at about 30°C. Queen and workers produce heat by moving their flight muscles and dissipating it to the nest during brood incubation. In contrast to honeybees these colonies are founded in spring by the queen and die in early autumn. They never produce more than a few hundred workers during the season.

In our experiments, bumblebee queens (*Bombus lapidarius*) were captured after emergence from hibernation and placed in artificial nest boxes. Three weeks later the first workers were seen. After another three weeks such a small initial nest was transferred to an 8 l PMC placed in a cellar room of constant temperature and connected to the outside by a walking duct of 60 cm (Fig. 1). The bumblebees quickly adapted to their new location and the nest developed with a maximum worker number around 150 in the middle of June. Soon after the death of the queen the nest perished in the second half of July [19,20].

The PMC was electrically calibrated with an empty nest and showed a sensitivity of 18.3 mV W^{-1} and a sufficiently stable base line. Simultaneous recording of temperature at four different places in the nest and its heat dissipation were continuously performed during the active period of the nest. The heat flow from the nest – often in a sinusoidal fashion with a maximum in early morning and a minimum in the evening – ranged from 0.3 to 1.4 W supposedly independent of the actual number of workers. From both figures a heat production rate per worker could be estimated being maximal in the first and the last seasonal period of the nest with 30 mW per individuum and minimal in the most active phase with 5 mW. These values transform to 30 to 200 W kg^{-1} at body masses of 150 mg per worker in good agreement with indirect calorimetric data from the literature [19,20].

Members of the different bumblebee castes were taken from the PMC and investigated individually in a 100 ml Calvet calorimeter, prepared for simultaneous respirometric measurements, endoscopic observation and registration of sound generation [19,31]. Female workers exhibited the highest mass specific heat production rate with 110 W kg^{-1}, the male drones followed with 76 W kg^{-1} while the rate of young virgin queens and the old queen were much lower, 27 and 12 W kg^{-1}, respectively. The standard deviations of these mean values were very high. The old queen was measured only once with regard to the social connections in the nest [20]. The comparison of the direct and indirect metabolic rates of the different individuals and castes showed a good linear correlation with a mean respiratory quotient of 0.94 [20].

Endoscopic observations of individual bumblebees in the Calvet calorimeter showed a perfect one-to-one correlation between sound generation and periods of wing motion. Thus, the energetically disturbing endoscopic monitoring could be replaced by the non-interfering microphone registration. In this way a good

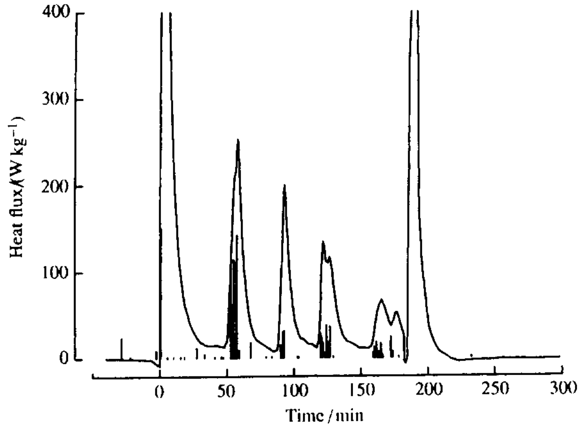

Fig. 7. Simultaneous recording of heat production and sound generation by a *Bombus lapidarius* worker (105 mg) at 26°C. The heat production rate calculated per mass is indicated by the solid line, the microphone signals by the vertical bars. The large deviations from the zero line at the beginning and the end of the curve are calorimetric artifacts resulting from the heat of friction when inserting or removing the vessel [31].

correlation was established between the heat production rate and the sound generation and thus with the wing motion [31]. Fig. 7 shows periods of heat dissipation of up to 200 W kg^{-1} with distinct acoustic signals and consequent drops in 'silent' periods to 10 W kg^{-1}. In one experiment an energy turnover of 350 W kg^{-1} was determined which corresponds well to indirect data of flying Hymenoptera, cited in the literature [31].

4.3. Hornets

Hornets are the largest species among the social insects which were investigated in our experiments. Until now no direct calorimetric determinations of energy metabolism can be found in the literature. The few known investigations used indirect calorimetric evaluations from oxygen consumption and carbon dioxide production and special assumptions on the oxycaloric coefficient.

For individual measurements of workers, drones and queens of the European hornet *Vespa crabro* animals were caught in the walking duct of the artificial nests (see below). They were transferred to a 25 ml batch calorimeter (Bioflux, MV Munich/Germany; sensitivity 55 mV W^{-1}) and monitored at 10, 15 and 20°C. Foragers were gathered at the exit when leaving the nest so that one could assume that they carried enough food to survive the next hours. The animals followed an ectothermic behaviour with a significantly reduced heat production rate at 10 and 15°C compared to 20°C. These reductions amounted to about 60% for drones and workers. Hornet workers showed mean values of 48.4 W kg^{-1} at 20°C, drones of 36.5 W kg^{-1}. At 15°C virgin queens dissipated 12.4 W kg^{-1}, the same amount as workers and drones although the queen had a threefold higher mass (1.16 g) compared to workers (0.45 g) and drones (0.35 g). These values are apparently smaller than those found for honeybees and bumblebees, an observation that might not only be due to the more phlegmatic temperament of the hornets but also to the reduced space in the calorimetric vessel [32].

Drones produce nearly the same heat flow per individuum as workers at 15°C and about 70% at 20°C while in honeybees much larger differences are observed. As the number of drones increases at the end of the season and that of the workers goes down one can assume that drones participate in nest heating in autumn with a significant proportion.

After the death of the colony only young inseminated queens survive the winter with a strongly reduced metabolism. They live exclusively on stored fat reserves established during the summer. In order to check the connection between the reduced heat dissipation rate of hibernation at low environmental temperatures and the decrease in body weight hibernating hornet queens were kept at 5 and 15°C sleeping in individual calorimetric vessels. Every 10 to 20 days the weight loss and the heat production rate were determined for 48 h under red light carefully avoiding any shaking of the insects. At 15°C a correlation between the weight loss and the heat production with mass specific rates of about 1 W kg^{-1} was observed. At a daily weight loss of 2.3 mg, a heat production rate of 0.91 mW (both at 15°C) and with an energy content of 39.8 kJ g^{-1} one can estimate that the fat reserves of approximately 400 mg per queen would endure for 175 days, by far enough for a usual winter season [33]. At lower sleeping temperatures this period would even be prolonged. These figures gained with 10 hornet queens are only rough estimates since the energetic differences between the individuals are large.

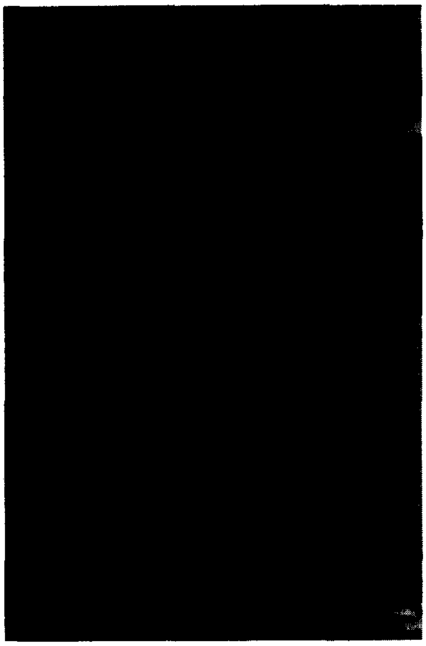

Fig. 8. PMC twin setup for the investigation of intact hornet nests. The upper box serves as a reference, the lower one as calorimeter proper. This box is additionally closed by a grid so that it can be ventilated from time to time keeping the hornets away from the laboratory. Behind the grid a nest can be seen in the upper half of the box. The perspex walkways are seen as white tube (above) and circle in the box (below).

The power-time curves of sleeping hornet queens showed periodical heat bursts due to a discontinuous ventilation that could be also detected in parallel investigations with a carbon dioxide analyzer. Such intermittent breathing with periods of approximately 1 h strongly reduces the insect's water loss.

It is well-known that hornets are social homeothermic organisms able to maintain an efficient thermoregulation of their nests. As described above small but already established hornet colonies were transferred to the institute and placed in closed wooden nesting boxes or PMCs, both connected to the outside by plastic walkways. After two days of confinement the insects had adapted to the new environment and were allowed to continue their usual outside activities. The hornet PMCs were larger than those for the bumblebees (24 l vs. 8 l) and connected as a twin system of working and reference units (Fig. 8). The sensitivity was determined to be 14.8 mV W^{-1}. Once a week the working unit was placed on a balance to determine the actual weight during the active period. At the end of the season the biomass of the hornets could be calculated from those values and consequently the mass specific heat production rates of the animals [25].

One very large hornet nest with 1 queen and 250 workers in 4 combs showed a maximum heat production rate of 12.5 W or 23 W kg^{-1} and a circadiane rhythm of heat production in the most active phase. The rate remained approximately constant till October and then decreased to one third. Workers were the main heat producers in the nest with 69 to 92%, while the contribution of larvae was negligible. Only at the end of the season hornet drones took active part in thermoregulation of the colony [25].

During the whole nesting period two thermocouples were incorporated in the nest for continuous monitoring the interior and the surface temperatures of the nest. At the end of the season the empty nest was heated up to the same temperatures as during the active phase by means of an electric resistor of 10 Ω/25 W. In this way, the heat flow from the nest could be determined in the wooden boxes or as a control of calorimetric measurements in the PMC. In a hornet nest smaller than that mentioned above a typical inner temperature of 26°C and a surface temperature of 23°C, both at ambient 16°C, were obtained with an electric power of 1.8 W. This figure is comparable to those of bumblebee nests of similar size and biomass.

5. Outlook

Investigation of social insects means seasonal working. Hornets and bumblebees exist mainly during the summer with a few weeks in late spring and early autumn. Although honeybees survive the winter they are usually not active in this period except for those kept in free flight rooms. Thus, successful experiments concentrate on a few months. Moreover, 'bad' bumblebee or hornet years occur when the insects appear very late, not at all or are infected by parasites. This makes the scientific progress difficult and time consuming.

Further experiments with bee and hornet groups or with an intact hornet colony in a PMC are aimed at the action of pheromones. These compounds serve as the (chemical) communication among social insects being responsible, for an example, for sex attraction, alarm and appeasement, aggregation and recruiting or clustering. But only with alarm pheromones strong energetic reactions can be expected that are easily detected in batch calorimeters. Therefore, these pheromones will be investigated in more detail looking for the essential ingredients and their concentration, the most effective chemical composition in the sense of synergistic effects, for temperature, group size, duration of exposition and other experimental conditions.

Another approach goes for the energy balance of hornet nests. Direct thermal measurements of heat conductivity of the insulating envelope and theoretical calculation by Newton's cooling law shall render further information on how much energy is needed to keep an elevated constant temperature for the hornet brood. It is known that nest temperature drops in the early morning hours since hornets are not able to store enough food for a continuous intensive heat dissipation through all the night. By electrical heating of the nesting boxes it might be possible to decrease the degree of insulating activities and thus perhaps the energy demand.

Furthermore, a heat conduction calorimeter has been constructed enabling a continuous flight of smaller insects. The animals are tethered to a roundabout of 6.6 cm radius in such a way that they can freely use their wings. An incorporated induction counter together with a computer determines the number of rounds and the flying speed, a microphone the frequency of the wing beats so that further energetic estimations may be performed. Some problems appeared since not all insects fly in the dark. Illumination by light guides of low heat input or other means and optimal intensity levels have to be established for different animals. The connection with a gas analyzer for oxygen and carbon dioxide will be a further development rendering simultaneous direct and indirect determinations of energy metabolism during flight. Preliminary results on hornets and a full description of the new instrument will be published in the near future.

Why are social insects and specially superorganisms so interesting for the calorimetrist? It is the energetic aspect of their life which allows for an existence under often unfavourable conditions and for a quick and efficient development of their brood. Increased heat production and special warming of cells with larvae and pupae are aimed at this end, an energy consuming process for a bumblebee queen in spring being as high as that of flying. European honeybees with a mass of 0.12 g and a surface of 1.76 cm^2 have a surface to mass ratio of 14.7 $cm^2\ g^{-1}$ which is extremely unfavourable concerning heat loss at low temperatures. Bees fall into torpor at 9°C and are unable to thermoregulate. They are fully depending upon the heat production in the winter cluster with a core temperature between 13 and 30°C. 16 000 bees in a typical winter cluster have a total surface of 28 160 cm^2, the cluster itself of only 1257 cm^2. Thus, the surface to mass ratio of the cluster (1920 g) reduces to 0.65 $cm^2\ g^{-1}$, that is, to just 4.5% of that of the isolated bees [8]. This strong reduction in the ratio leads to a corresponding decrease in the heat loss, thus in metabolism and enables the bees to survive 20 times more on their hoarded food in winter.

Comparison of the winter cluster with a typical small hibernating mammal shows how optimal such clustering is: a marmot of corresponding mass (3000 g) has a surface of 3960 cm^2 and thus a two times higher ratio of 1.32 $cm^2\ g^{-1}$. Heat production rate in a small honeybee colony (1500 individuals) equals that of a small mammal (rat). Southwick [34] showed that a double logarithmic plot of oxygen consumption rate vs. mass for honeybee clusters at 15°C renders an allometric straight line just above the famous 'mouse-elefant line' or 'Kleiber line' for mammals [35].

Such energetic aspects become even more pronounced in hornet colonies. One can calculate assuming a mean foraging flight time of 15 min and a mean value of 7.6 mg for the small wooden particles collected to construct the nest envelope that it would take 725 foraging hours for constructing an envelope of 22.1 g. The total energy consumed in these flights corresponds to just 5 days of active colony 'heating' during usual summer days.

Although one has to admit that not everything is really perfect with social insects nowadays (Fig. 9) it can be stated that they form an interesting field for energetic research and that classical direct calorimetry is again an appropriate means to get additional interesting information about complex biological systems without too strong interferences.

Fig. 9. Resignative statement about the modern situation of social insects. Cartoon by Sidney Harris, New Haven.

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