ELSEVIER

Thermochimica Acta 328 (1999) 3–8

thermochimica acta

Direct calorimetric measurement of heat production rates in flying hornets (*Vespa crabro*; Hymenoptera)

Erik Schmolz[a,*], Nina Brüders[b], Burkhard Schricker[a], Ingolf Lamprecht[b]

[a]*Institute of Zoology, Free University of Berlin, Königin-Luise-Str. 1-3, D-14195, Berlin, Germany*
[b]*Institute of Biophysics, Free University of Berlin, Thielallee 63, D-14195, Berlin, Germany*

Accepted 1 October 1998

Abstract

Heat production rates of flying hornet drones, workers and queens have been measured by means of direct calorimetry. A novel kind of calorimeter including a flight roundabout, to which insects can be fixed, has been constructed for this purpose. Heat production rates of flying drones and workers showed a weak negative correlation with ambient temperature. Mean specific heat production rates for workers were 159±38 mW g^{-1} at 20°C and 103±44 mW g^{-1} at 30°C, and for drones 119±27 mW g^{-1} at 20°C and 70±23 mW g^{-1} at 35°C. The same weak negative correlation with ambient temperature could be shown for flight speed, whereas wing-beat frequencies were independent of temperature with values between 85 and 97 Hz. Methodical limitations are discussed in the application of direct calorimetry for flight investigations as well as in some biological implications of our results. © 1999 Elsevier Science B.V. All rights reserved.

Keywords: *Vespa*; Hornet; Direct calorimetry; Insect flight

1. Introduction

The development of wings and the ability to fly can be considered as the most important event in the evolution of insects, which represent an extremely successful group in the animal kingdom. Therefore, the examination of insect flight has been of major interest during the past 60 years to physiological entomologists. The investigations on flight aerodynamics have been the focus of these studies. Moreover, flying insects are known to have the highest specific metabolic rates in the organismic world [1] so that numerous accounts have been undertaken to measure energy consumption during flight [2–4]. In all experiments described up till now, energy metabolism is determined indirectly (e.g. via respirometry and thermometry). In this paper, we report on the possibility to follow the heat production rates of flying insects by direct calorimetry. We have chosen the European hornet *Vespa crabro* as experimental object, because a number of publications concerning heat production rates of individuals [5–7] and of whole colonies [8] are published already. It seemed worthwhile for us to close an important gap in our understanding of the bioenergetics of this social insect. Another reason for choosing this particular insect is that illumination inside a calorimeter is limited for important methodical reasons (see below), but the hornets even fly at very low illumination levels. In addition, hornets are sufficiently robust as test objects because of their rather big size.

---

*Corresponding author. Tel.: +49-30-838-4733; fax: +49-30-838-4323; e-mail: agbienen@zedat.fu-berlin.de

PII: S0040-6031(98)00617-0

Hornets form annual colonies, which means that only young inseminated queens survive at the end of the season and leave the old nest for hibernation at protected places, e.g. under the bark of the trees. In spring, each queen initiate a nest on its own and thus raises the first worker generation by itself. Upon the emergence of these workers, the social phase is initiated, and the queen is restricted to reproduction. In late summer, the reproductive forms (drones and young queens) emerge from their cells [9]. They spend about one week in the nest in order to accumulate food reserves, and leave their colonies without return. Presumably, they do not feed outside the nests and thus are exclusively dependent on only stored body reserves. Therefore, drones and queens represent interesting objects for bioenergetic investigations. While the energetics of queen hibernation have been reported elsewhere [7], in this study we focus on the energetics of drones, which spend most of their stored energy during flight activities while searching for nests containing young virgin queens [10,11]. In order to measure heat production rates of hornet drones during flight at different ambient temperatures, we have developed a new calorimeter prototype for investigations on flying insects, and additionally we applied it to workers and queens of *V. crabro*.

2. Experimental

2.1. Flight calorimeter

A detailed description of the calorimeter prototype shown in Fig. 1 has recently been published elsewhere [12]. Briefly, the calorimeter is placed in an isolated air-bath (temperature range 18–42°C) originally built for an LKB Flow-calorimeter (type 10700, LKB, Bromma, Sweden). The air-bath is connected to a cooling pre-thermostat (type D1, Haake, Berlin, Germany). The calorimeter chamber consists of an aluminum cylinder (diameter 180 mm, height 110 mm, wall thickness 10 mm). The top of the cylinder is closed with a perspex lid. The calorimeter chamber is connected with an outer aluminum cube via 10 Peltier elements (type TEC1-12705, Conrad Electronics, Hirschau, Germany). This cube has a mass of approximately 10 kg and serves as a heat sink. The calorimeter is insulated from the air-bath by an additional outer layer of styropor (20 mm) (Fig. 2)

In order to achieve well-defined flight conditions, a two-armed low-friction roundabout of 62 mm radius is incorporated inside the measuring chamber. The hornets are connected to the roundabout arm by means of a small plastic screw glued on the thorax and then

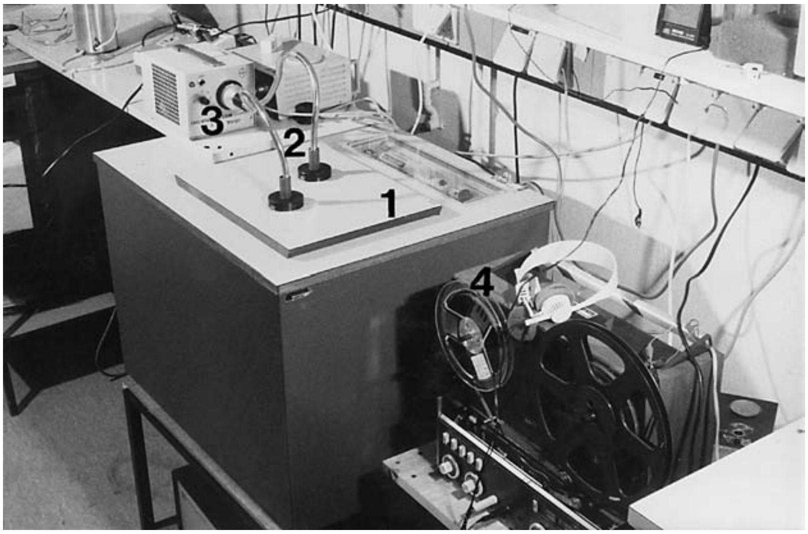

Fig. 1. Photograph of the air-bath thermostat (1), in which the flight calorimeter was placed. Two lightguides (2), connected to a cold light source (3), were inserted into the thermostat. In front is an audio tape (4) for amplification of flight sounds.

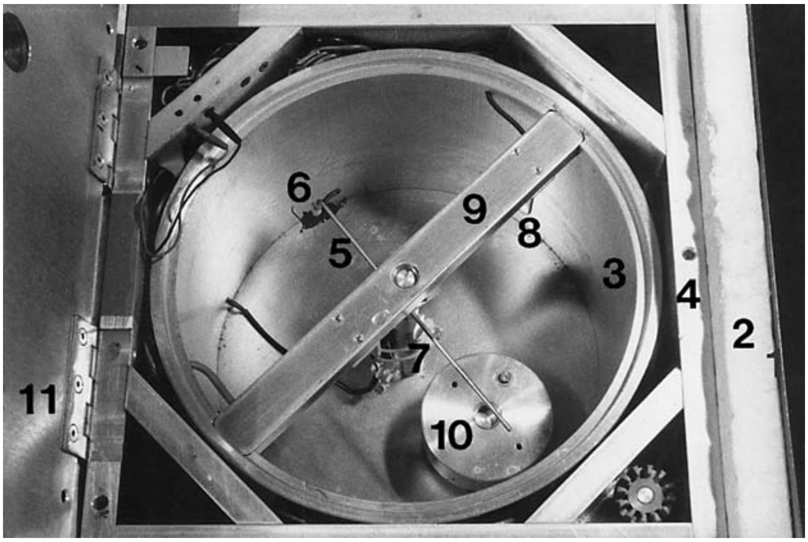

Fig. 2. The flight calorimeter. The calorimeter was placed inside an outer aluminum cube (1) and a styropor layer (2). The inner cylindric aluminum container (3) was connected to the inner cubic aluminum heat sink (4) via 10 Peltier elements (not visible). The flight roundabout (5) with the insect (6) was supported by an adjustable bearing in the central axis (7). A microphone (8) was fixed to the supporting beam (9) of the roundabout axis. The starting table with lowering screw (10) was not used in the experiments reported in this paper. During the baseline runs and experiments, the calorimeter was closed by means of a turnable lid (11).

inserted into a flexible plastic tube fixed to the arm. The flight speed can be measured by means of an inductive proximity switch activated at each revolution of the roundabout arms. Sound generated by the wings is recorded acoustically by a condenser microphone (Sony ECM-144, Japan) connected to a DAT-recorder (Sony, Digital Audio Tape-Corder TCD-D8, Japan). Wing-beat frequencies are later evaluated from these recordings by computer analysis (Avisoft-SASLab Pro 1). The calorimeter interior is illuminated by two lightguides (ϕ=5 mm) connected to a cold light source (Intralux 150h, Volpi, Schlieren, Switzerland). They are introduced vertically through the air-bath and the calorimeter insulation down to a few millimeters above the perspex lid of the calorimeter chamber. Additionally, eight smaller lightguides (ϕ=3 mm) are inserted in the side walls of the calorimeter chamber approximately at the level of the flying insects in order to simulate moving optical marks and thus promote flight activities. The total heat input caused by illumination amounted to 2.5 mW, which can be tolerated compared to the heat production rates of flying hornets of between 50 and 100 mW. The light guides generated an intensity level of approximately 300 lx inside the chamber. In order to calibrate the calorimeter, an electrical resistor was placed at the central axis of the flight roundabout. Calibration of the calorimeter rendered a sensitivity of 63.6 mV W^{-1} and a time constant of 14.3 min.

Experiments with hornets were run at 20°C, 25°C, 30°C and 35°C.

2.2. Experimental procedures with hornets

Between 1995 and 1997, hornets from a total of nine colonies have been used for the investigations. All hornet colonies have been relocated from their original nest sites and placed in artificial nesting boxes at the Institute for Zoology or the Institute for Biophysics of the Free University of Berlin. Foragers had free access to outdoor environment. They were caught for experiments when leaving the colony for foraging flights. Drones and young queens were collected while sitting on the nest envelope prior to their mating flights. After interception, hornets were kept in small containers with sufficient food and then prepared for flight experiments. A small plastic screw (ϕ=2.8 mm, length 10 mm) was glued to the thorax tergites. Then the screw was inserted into a plastic tube connected to the bound end of the roundabout arm. Usually, hornets start flight activity after losing contact with the substratum and continue to fly in the calorimeter when stuck to the roundabout. In some cases, the hornets had to be stimulated to fly by allowing them contact to a substratum (a small piece of styrofoam) and then suddenly removing it. This induced the tarsal flight reflex. The calorimeter chamber was then closed immediately. For approximately 5 min, the calorimeter signal was disturbed because of heat artifacts due to the handling. Hence, heat production rates were only determined after the P(*t*) curves reached a steady state. The calorimeter signal was recorded continuously by means of a chart recorder (BD 41, Kipp and Zonen, Delft, Netherlands). Experiments were terminated, when hornets ceased flight after 30–240 min. Before and after the experiments, hornets were weighted to the nearest 0.1 mg by means of a mechanical fine balance (type 414/13, Sauter, Ebingen, Germany). Mean heat production rates during flight were determined by electronic integration (Digikon, Kontron, Munich, Germany) of the heat production rate P(*t*) over the whole flight time. Experiments were excluded from evaluation once hornets showed unstable flight behavior or defecation. The later caused a strong endothermic disturbance of the calorimeter signal due to evaporation effects. At the end of the experimental procedure the plastic screws were removed and animals were released to their nests. Hence, all specific rates are given per fresh, but not per dry weight.

3. Results

A total of 135 experiments on drones, queens and workers have been performed and 67 of them could be evaluated (see Section 4). The majority of these experiments were made with drones, because they are easier to handle and more willing to fly. The heat production rate showed a weak temperature dependence. Drones had no significantly different heat production rates at 20°C and 25°C (81.2±20.9 mW, n=9 at 20°C; 84.8±6.6 mW, n=8 at 25°C). The same holds true for the values at 30°C and 35°C (42.8±15.3 mW, n=19 at 30°C; 42.5±15.3 mW, n=7 at 35°C). A clear and significant difference existed between 25°C and 30°C (Mann-Whitney U-Test, α=0.05). Values for the specific heat production rates as function of caste and temperature are presented in Fig. 3. The average weight of drones was 619±82 mg (n=43), of workers 447±47 mg (n=17) and of queens 925±95 mg (n=5). Probably, heat production rates of flying workers are also temperature dependent, but not enough usable data

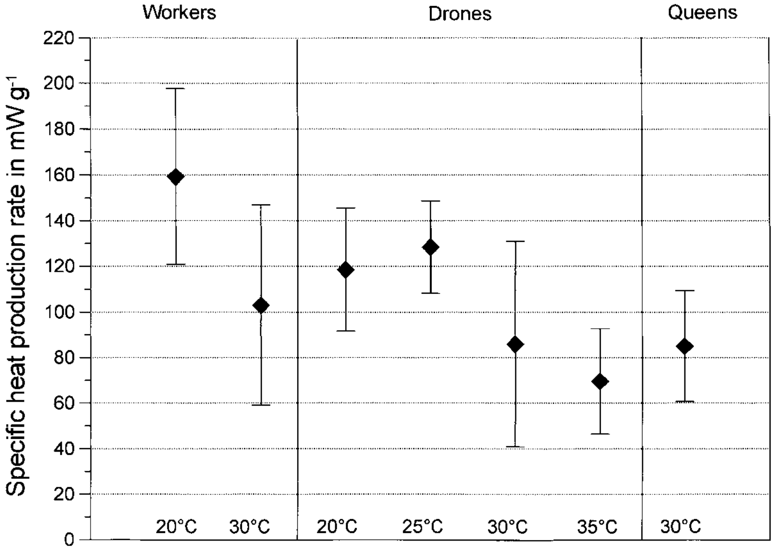

Fig. 3. Specific heat production rates of flying hornets as a function of ambient temperature and caste. The bars indicate standard deviation.

for heat production at 20°C could be obtained to confirm such a correlation (79.1±18.4 mW, n=3 at 20°C compared to 42.3±16.6 mW, n=14 at 30°C). Specific heat production rates of young queens at 30°C (77.7±20.9 mW g^{-1}, n=5) are in the same range as those values for drones, although queens have higher body mass.

With increasing temperatures, flight speed decreased only slightly showing values from 1.1±0.3 m s^{-1} at 20°C, 1.2±0.3 m s^{-1} at 25°C and 0.8±0.2 m s^{-1} at 35°C, with a significant difference between 25°C and 35°C (Mann-Whitney U-Test, α=0.01). Due to technical problems, flight speed could not be evaluated in experiments with drones and workers at 30°C. In 1997, acoustic monitoring of wing-beat frequencies became possible in all experiments with drones at 25°C and 35°C due to improvements in our recording equipment. The mean frequency amounted to 97±13 Hz at 25°C and 85±11 Hz at 35°C with no significant differences between both temperatures. Wing-beat frequency of flying queens at 30°C ranged around 84±7 Hz.

4. Discussion

From a total of 135 experiments, 49.6% could be evaluated. Compared to other studies with flying insects, this success rate seems to be a rather good one. Normally, in such studies, 50–70% of all insects will not fly for a variety of reasons (e.g. motivational status, stress) (personal communications, [2,3]).

For drones, workers and queens of *V. crabro*, specific heat production rates during flight varied between 65.9 mW g^{-1} (drones at 35°C) and 159.3 mW g^{-1} (workers at 20°C). Since these values are the first direct calorimetric data for heat production rates of flying insects, they can only be compared with values obtained by indirect methods like respirometry, thermometry or food consumption. Data from Balderrama et al. [13] for honeybees show values in a comparable range from 58.4 to 60.1 mW g^{-1}. Other papers report much higher heat production rates up to 515 mW g^{-1} for flying honeybees in a wind channel [2]. Lepidopterans (butterflies) show heat production rates between 237 and 393 mW g^{-1} [14,15]; hence it seems that our values for hornets are at the lower end of the spectrum for heat production rates of flying insects. The rather small radius of the roundabout was a critical point in our investigations. It was limited due to technical circumstances, because

1. the calorimeter had to fit properly into the LKB air-bath, and
2. the time constant becomes very large with increasing volume.

It is not clear whether this plays a crucial role, because a manometric study with a roundabout of corresponding size reports intermediate values for heat production rates up to 233 mW g^{-1} for large beetles with a body mass up to 981 mg [16]. Two other factors might have had influence on our data. Firstly, tethered insects may have a lower power output compared to free-flying insects due to the fact that power required for lift is reduced during an experimental flight. Secondly, illumination in the calorimeter was dim. Most likely, the light level has an influence on flight performance and flight speed of insects, although no experimental data are available to this point, and the authors of the studies mentioned above, make no comments on illumination in their experiments. Tethered flight may result in less energy spent for locomotion, since uplift power requirement is reduced by fixation of the insect. For several reasons, we do not believe that tethering resulted in lower heat-production rates:

1. our unpublished experiments in a wind channel with integrated electronical balance showed that hornets lift up their own body weight even when tethered,
2. hornets always exhibited normal flight posture (thorax and abdomen are positioned in a horizontal plane, and legs are held tightly) during roundabout experiments in the calorimeter, and
3. wing-beat frequencies lie within the same range as data from the literature [17].

Heat production rates of flying hornets were not significantly different between castes. However, in honeybees, drones and workers have higher metabolic rates compared to queens [3]. Because of the annual life cycle of their colonies and a solitary phase in spring, hornet queens perform flight activities for longer periods than honeybee queens do, and differences in metabolic rates may reflect this fact. With increasing ambient temperature, the flight speed of hornet drones diminished showing significant differences between 25°C and 35°C. The decrease of flight speed is accompanied by a reduction of heat dissipation. This finding is in accordance with the prevailing aerodynamic theory for flying animals, which predicts an U-shaped curve for the power required for flight as a function of speed with maximum values at slowest and fastest speeds [18,19]. Maximum values of flight speed of hornets as found in literature are up to 6 $\mathrm{m\,s^{-1}}$ [17]. The fastest speed reached during our experiments was 1.2 $\mathrm{m\,s^{-1}}$ at 25°C. Due to technical circumstances, drones did not reach their fastest possible flight speeds in our experiments. Their flight performance may indicate the beginning of such an U-shaped curve, where only slow and intermediate speeds are measured and high speeds are not included. Moreover, in our experiments it could not be shown clearly whether thermoregulation of drones was hindered at high temperatures, and whether drones lower their speed in order to avoid overheating. This would be a reasonable explanation for the flight behavior of drones in this study, and it is supported by recent findings, according to which thermoregulation during flight is mainly achieved by regulation of the metabolic rate [20].

In spite of the methodical problems mentioned above, the energetic strategies of hornet drones can be elucidated, using the results of the present study for some simple calculations. The authors showed in another paper that drones have a fat deposit of approximately 0.4 g with a total caloric value of about 12 kJ [21].

Drones leaving their home nest without the chance to return, must search for other colonies with unmated queens. According to data reported in this paper, drones have heat production rates of approximately 80 mW and a flight speed of about 1 $\mathrm{m\,s^{-1}}$ at ambient temperatures between 20°C and 25°C. This simply means that they spend 80 $\mathrm{J\,m^{-1}}$ flight. Having 12 kJ stored in their fat body, they could fly as far as 150 km in order to look for sexual partners without any uptake of external food. Therefore, even in areas with low hornet population densities, drones will have a fair chance for reproductive success.

In summary, direct calorimetric measurements on flying insects have to face two inherent problems: calorimeter volume, which has to be small, and illumination, which should produce only minimum amounts of heat at light levels high enough to allow and stimulate to fly. Direct flight calorimeters are, therefore, probably best suited for small nocturnal insects with low flight speeds such as moths, for example.

Nevertheless, direct calorimetric measurement of heat production during insect flight may provide the unique possibility to obtain calorimetric and respirometric data from flying insects simultaneously by integration of CO_2- and O_2-measuring devices into the calorimeter chamber. This next step is planned for the near future by the authors of this study.

References

[1] J. Harrison, H.G. Hall, Nature 363 (1993) 258.
[2] W. Nachtigall, U. Rothe, P. Feller, R. Jungmann, J. Comp. Physiol. B 158 (1989) 729.
[3] R. Gmeinbauer, K. Crailsheim, J. Insect Physiol. 39 (1993) 959.
[4] C.P. Ellington, K.E. Machin, T.M. Casey, Nature 347 (1990) 472.
[5] E. Schmolz, I. Lamprecht, B. Schricker, Apidologie 24 (1993) 526.
[6] E. Schmolz, I. Lamprecht, B. Schricker, Thermochim. Acta 229 (1993) 173.
[7] E. Schmolz, B. Schricker, I. Lamprecht, Verh. Dt. Zool. Ges. 90(1) (1997) 147.
[8] E. Schmolz, I. Lamprecht, B. Schricker, Thermochim. Acta. 251 (1995) 293.
[9] M. Matsuura, S. Yamane, Biology of the Vespine Wasps, Springer, Berlin, 1990, p. 156.
[10] R. Edwards, Social Wasps, Rentokil, East Grinstead, 1980, p. 30.
[11] S.W.T. Batra, J. Kans. Entomol. Soc. 53 (1980) 461.
[12] E. Schmolz, I. Lamprecht, B. Schricker, J. Therm. Anal. Cal. 52 (1998) 93.
[13] N.M. Balderrama, B.L.O. de Almeida, J.A. Nuñez, J. Comp. Physiol. B 162 (1992) 440.
[14] T.M. Casey, J. Exp. Biol. 64 (1976) 529.
[15] T.M. Casey, J. Exp. Biol. 64 (1976) 545.
[16] H.W. Ludwig, Verh. Dt. Zool. Ges. 1960 (1961) 355.
[17] A. Azuma, The Biokinetics of Flying and Swimming, Springer, Berlin, Tokyo, 1992, p. 125.
[18] W. Nachtigall, U. Hanauer-Thieser, M. Mörz, J. Comp. Physiol. B 165 (1995) 484.
[19] K.P. Dial, A.A. Biewener, B.W. Tobalske, D.R. Warrick, Nature 390 (1997) 67.
[20] J.F. Harrison, J.H. Fewell, S.P. Roberts, H.G. Hall, Science 274 (1996) 88.
[21] E. Schmolz, I. Lamprecht, B. Schricker, in preparation.