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A THREE-COMPARTMENT MODEL DESCRIBING TEMPERATURE CHANGES IN TETHERED FLYING BLOWFLIES

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Summary

A three-compartment model is presented that describes temperature measurements of tethered flying blowflies, obtained by thermal imaging. During rest, the body temperature is approximately equal to the ambient temperature. At the start of flight, the thorax temperature increases exponentially with a time constant of 30s; in steady flight, a temperature of approximately 30°C is reached (ambient temperature approximately 25°C). After flight, the temperature of the thorax decreases exponentially with a time constant of 50s. Fitting the time courses of the three body compartments, i.e. head, thorax and abdomen, with the model allows the thermal parameters to be calculated. The metabolic heat produced by a blowfly during tethered flight is estimated to be approximately 23mW.

Introduction

Non-invasive temperature measurement of insects with a thermal imaging camera was first applied to honeybees, *Apis mellifera*, by Cena and Clark (1972), and subsequently by Schmaranzer (1983), Stabentheiner and Schmaranzer (1987, 1988) and Stabentheiner and Hagmüller (1991). That the infrared radiation emitted by the tiny bodies of insects can be accurately monitored over time with considerable spatial resolution was further demonstrated by Schmaranzer and Stabentheiner (1988, 1991; honeybee *Apis mellifera*, fly *Musca domestica*, beetle *Melolontha melolontha*, katydid *Conocephalus dorsalis*) and Heinrich (1987; moth *Eupsilia morrisoni*). These results

confirmed previous measurements with thermocouples showing that the temperature of the three body compartments, head, thorax and abdomen, can differ substantially (e.g. Heinrich, 1974, 1975, 1980*a,b*; moth *Manduca sexta*, bumblebee *Bombus terricola*, honeybee *Apis*).

In the present paper we use thermal imaging to investigate the thermal effects of blowfly flight. The experimental results are interpreted using a simple model that explicitly treats the insect body as a three-compartment system. The model is used to quantify the blowfly's heat budget.

Materials and methods

Tethered flight

Blowflies (*Calliphora vicina*) were tethered via a V-shaped aluminium wire glued with a small drop of wax at the junction between the head and thorax (see Fig. 1A). A blowfly, thus tethered dorsally, remains at rest when it is offered a substratum, e.g. a small ball of paper tissue. Taking away the substratum initiates flight and this results in warming up. The reverse process, the end of flight and cooling down, was induced by replacing the substratum.

Thermal imaging camera

The changing temperature was monitored by adjusting the fly in the focal plane of a thermal imaging camera system (Fig. 1B–F). This was a Barr and Stroud IR-18 equipped with a telescope. The measured images yielded apparent temperatures that were transformed into body temperatures assuming 100% emissivity of the fly body. Stabentheiner and Schmaranzer (1987) found an emissivity of $99.4 \pm 2.8\%$ for the honeybee *Apis mellifera*. Assuming an emissivity of 97%, a recent estimate by Stabentheiner (personal communication) yields an increase of the steady-state thoracic temperature (30.1°C) of only 0.17°C . The temperatures of the fly body compartments (see Fig. 2) were calculated by taking the average temperature of a selected area, as indicated by the boxes in Fig. 1E.

Three-compartment model

The measured temperature changes were simulated with a three-compartment model for the fly body, assuming the following: (1) heat production in the thorax is due to flight muscle activity; (2) heat is lost to the surroundings from three compartments, the head, thorax and abdomen; (3) heat is transferred from the thorax to the head and to the abdomen (see Heinrich, 1970, 1972, 1976, 1979). Formally:

$$W_h \frac{dT_h}{dt} = -C_h(T_h - T_a) + E_h(T_{th} - T_h), \quad (1a)$$

$$W_{th} \frac{dT_{th}}{dt} = M - C_{th}(T_{th} - T_a) - E_h(T_{th} - T_h) - E_{ab}(T_{th} - T_{ab}), \quad (1b)$$

$$W_{ab} \frac{dT_{ab}}{dt} = -C_{ab}(T_{ab} - T_a) + E_{ab}(T_{th} - T_{ab}), \quad (1c)$$

or, equivalently:

$$\frac{dH_h}{dt} = -L_h + F_h; \quad \frac{dH_{th}}{dt} = M - L_{th} - F_h - F_{ab}; \quad \frac{dH_{ab}}{dt} = -L_{ab} + F_{ab}. \quad (1d)$$

Here T_i , where i is h , th , ab or a , is the temperature of the head, thorax or abdomen or the ambient temperature; dH_i/dt is the rate of heat change of body compartment i ; W_i is the heat capacity; $W_i=c_i m_i$, where c_i is the specific heat and m_i is the mass; M is the rate of heat production by the thoracic muscles; C_i is the thermal conductance (see, for example, May, 1985); E_h and E_{ab} are the thermal exchange coefficients of the thorax to the head and abdomen, respectively. The terms $L_i=C_i(T_i-T_a)$, $i=h, th, ab$, of equations 1a–c represent the rate of heat loss of the three compartments to the surroundings. The terms $F_i=E_i(T_{th}-T_i)$, $i=h, ab$, represent the rate of heat flux from thorax to head and abdomen, respectively.

Equation 1 simplifies greatly in the steady state. Then, $L_h=F_h$ and $L_{ab}=F_{ab}$, or:

$$C_h/E_h = (T_{th} - T_h)/(T_h - T_a) \quad (2a)$$

and

$$C_{ab}/E_{ab} = (T_{th} - T_{ab})/(T_{ab} - T_a). \quad (2b)$$

Furthermore, the rate of heat production by the thoracic muscles in the steady state is (cf. Casey, 1992):

$$M = L_h + L_{th} + L_{ab}. \quad (3)$$

Generally, an insect exists in a non-steady state and, therefore, the set of coupled linear differential equations of equations 1a–c cannot be solved straightforwardly. Analytical solutions can be obtained when the body parameters, and specifically the heat production, are constant. However, it is much simpler to run an appropriate simulation program; we obtained Figs 3 and 4 using the program PSI/e (BOZA, Pijnacker, the Netherlands).

Results

Thermal imaging of flies

Fig. 1B shows that the heat radiation from the body compartments at rest is about equal to that of the surroundings, indicating that the temperatures of the head, thorax and abdomen are approximately equal to the ambient temperature. Fig. 1C–F, the images obtained at $t=15s, 30s, 60s$ and $90s$ after the onset of tethered flight, shows that the radiation of the thorax increases rapidly upon initiation of flight, followed by a more moderate radiation increase from both the head and, to a much lesser extent, the abdomen. The highest intensity of radiation emanates from the dorsal part of the thorax, where the flight muscles are concentrated.

Quantitative evaluation of the thermal images yields the time course of the temperature changes. The three body compartments were sampled in each frame as indicated by the

rectangles in Fig. 1E. Fig. 2A demonstrates that the temperatures of the three body compartments in the resting state are close to the ambient temperature of 25.0°C. Flying causes the thoracic temperature to rise, reaching approximately 30°C in steady flight. The

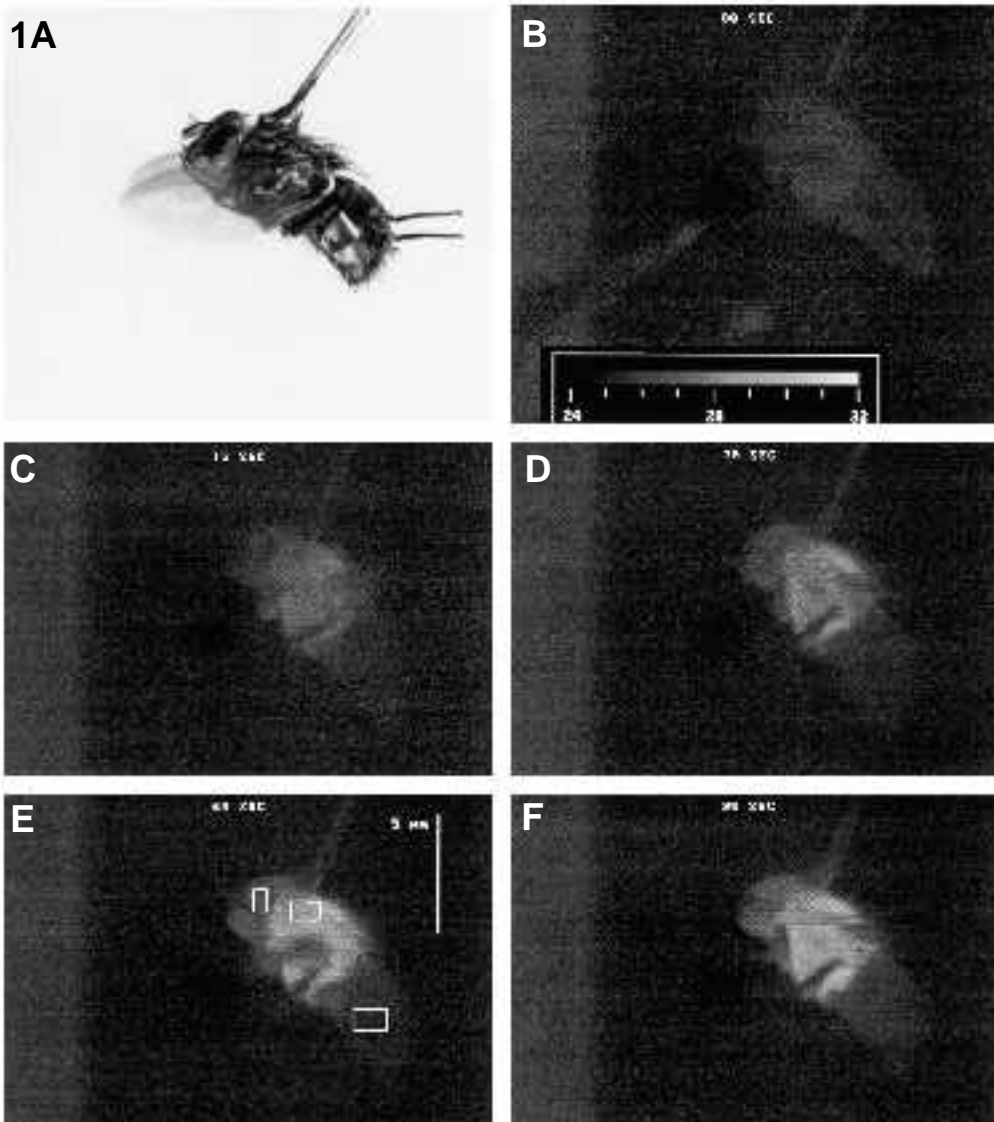


Fig. 1. Photograph (A) and thermal images (B–F) of a tethered flying blowfly at flight onset, $t=0s$ (B) and at $t=15s$ (C), 30s (D), 60s (E) and 90s (F). The tether, the V-shaped aluminium wire, can be seen pointing upwards from the thorax. The background (in B–F), behind the fly, consisted of a temperature-controlled plane, maintained at 24.5°C. Adjacent to the fly was another temperature-controlled plane, set at 25.7°C. The grey scale (in B) indicates the temperature in °C. The rectangles in E indicate the areas sampled for obtaining the temperatures of the three body compartments. Note that the legs obstruct the radiation emitted by the thorax.

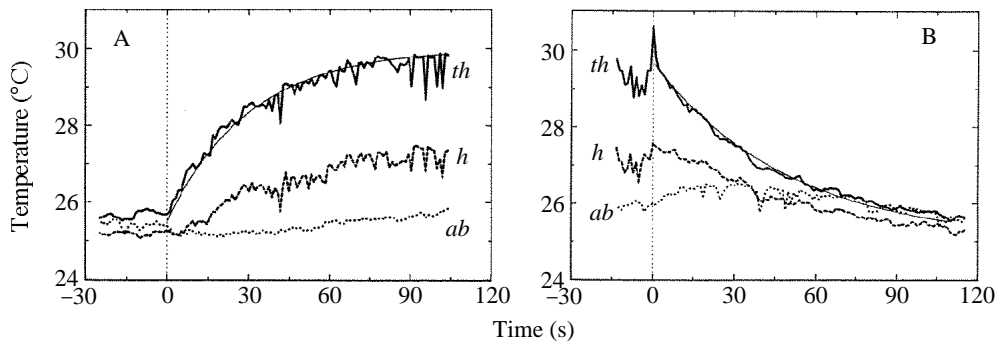


Fig. 2. Time course of the temperature in the thorax (*th*), head (*h*) and abdomen (*ab*), showing warming up during flight (A) and cooling down after flight (B). Thin lines are simple exponential functions with time constants of 30s (A) and 50s (B).

time course approximates a simple exponential function with a time constant of 30s (Fig. 2A).

Fig. 2A shows that the temperatures of the head and abdomen also increase. Presumably, the latter body parts do not produce extra heat themselves, but receive heat from the thorax, because the temperature time courses of both head and abdomen more or less approximate an exponential with a similar time constant of about 30s, except for a distinct delay.

At the end of flight, the temperatures of the fly's body compartments fall back to the ambient temperature (Fig. 2B). The time course of the cooling phase of the thorax is again approximately exponential, but the process is distinctly slowed down, as the time constant is now about 50s (Fig. 2B). The time courses of head and abdomen temperatures indicate that heat transfer from the thorax continues during the cooling phase.

Modelling the temperature distribution in a blowfly

The findings from the thermal imaging experiments are incorporated in the three-compartment model (see Materials and methods) with the following assumptions: (1) the heat capacities of the head, thorax and abdomen depend solely on their mass; (2) the thermal exchange coefficients of thorax to head and to abdomen are equal, i.e. $E_h = E_{ab}$; (3) evaporative heat loss is negligible; and (4) the heat power produced by the thoracic muscles, M , is negligible at rest and at its steady-value during flight. The average masses were: $m_h = 5.0\text{mg}$ and $m_{th} = m_{ab} = 40\text{mg}$. Taking a specific heat $c_h = c_{th} = c_{ab} = 3.4\text{J g}^{-1}\text{K}^{-1}$ (following, for example, Heinrich, 1975), the heat capacities are $W_h = 17\text{mJ K}^{-1}$ and $W_{th} = W_{ab} = 136\text{mJ K}^{-1}$. The warming-up curves of Fig. 2A can then be approximated satisfactorily using the model, equations 1a–c, by taking, for the produced heat power, $M = 1.38\text{J min}^{-1} = 23.0\text{mW}$ (for similar values for the metabolic power of the honeybee, see Nachtigall *et al.* 1989); for the thermal conductances, $C_h = 75\text{mJ min}^{-1}\text{K}^{-1} = 1.25\text{mW K}^{-1}$, $C_{th} = 183\text{mJ min}^{-1}\text{K}^{-1} = 3.05\text{mW K}^{-1}$ and $C_{ab} = 244\text{mJ min}^{-1}\text{K}^{-1} = 4.07\text{mW K}^{-1}$; and for the thermal exchange coefficients, $E_h = E_{ab} = 67\text{mJ min}^{-1}\text{K}^{-1} = 1.12\text{mW K}^{-1}$ (Table 1). Substitution of these values into equation 1 yields Fig. 3A.

Table 1. *Body parameters of the blowfly used in modelling the thermal distribution of tethered flying blowflies*

| | Head | Thorax | Abdomen |
|--|------|--------|---------|
| Mass m (mg) | 5.0 | 40 | 40 |
| Specific heat c ($\text{J g}^{-1} \text{K}^{-1}$) | 3.4 | 3.4 | 3.4 |
| Heat capacity W (mJ K^{-1}) | 17 | 136 | 136 |
| Thermal conductance C (mW K^{-1}) | | | |
| Tethered flight | 1.25 | 3.05 | 4.07 |
| Rest, after flight | 1.00 | 1.83 | 1.63 |
| Thermal exchange coefficient E (mW^{-1}) (from thorax) | 1.12 | – | 1.12 |
| Steady-state temperature ($^{\circ}\text{C}$) ($T_a = 25.0^{\circ}\text{C}$) | 27.4 | 30.1 | 26.1 |
| Steady-state heat loss to surroundings L (mW) | 3.0 | 15.6 | 4.4 |

The warming-up and cooling-down curves of the thorax (Fig. 2A,B) have time constants of 30s and 50s, respectively. This indicates that the thermal conductance of the thorax drops during the cooling phase by a factor of 0.6, or, during the cooling phase $C_{th}=1.83\text{mW K}^{-1}$. Assuming that the exchange coefficients remain unchanged, the three cooling curves of Fig. 2B can be approximated with equations 1a–c, using $C_{th}=1.83\text{mW K}^{-1}$, $C_h=1.00\text{mW K}^{-1}$ and $C_{ab}=1.63\text{mW K}^{-1}$ (see Fig. 3B). This indicates that the thermal conductances of the head, thorax and abdomen at rest, after flight, are lowered by factors of 0.8, 0.6 and 0.4, respectively. We presume that the thermal conductances at rest, in still air, are lower than those during flight, owing to air currents around the fly's body, produced by the wings.

The sudden drop in the thermal conductances at the end of flight results in a seemingly paradoxical temporary temperature increase in the head and abdomen. The same phenomenon was observed in temperature recordings of the abdomen of a tethered flying giant tropical fly (Bartholomew and Lighton, 1986).

Using the parameters obtained from fitting the time courses with the model, we can

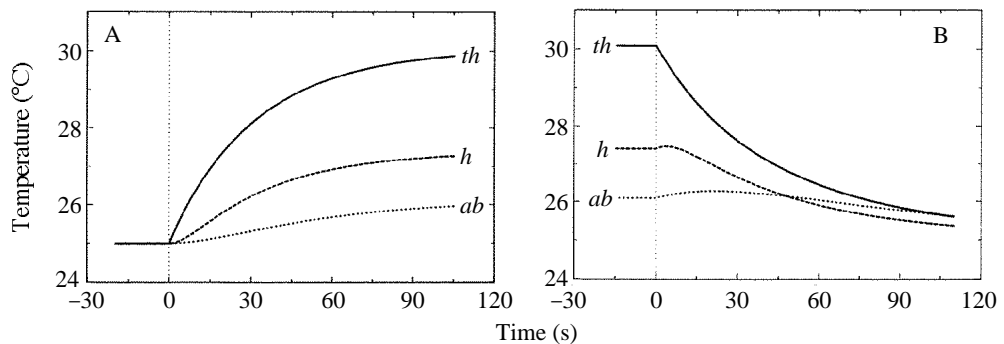


Fig. 3. Time courses of the temperature of the three body compartments, similar to Fig. 2, calculated using equation 1 and the body parameters listed in Table 1.

calculate the energy relationships of the blowfly. Fig. 4 shows that the major part of the total heat loss to the environment (L_{tot}) occurs through the thorax (L_{th}). Smaller, but non-negligible, amounts of heat are lost *via* the head (L_h) and abdomen (L_{ab}) (see Fig. 4A,B). The latter compartments thus act as a heat sink for the thorax, as in other insects (Heinrich, 1970, 1972). The heat power flowing from thorax to the head (F_h) and abdomen (F_{ab}) appears to remain rather small (Fig. 4C,D).

After the warming-up phase, in the steady state, $L_{th}=15.6\text{mW}$, $L_h=3.0\text{mW}$ and $L_{ab}=4.4\text{mW}$. The total heat losses, L_{tot} , equal the heat power produced, M . Hence, the heat fluxes from the thorax to the head and abdomen in the steady state are $F_h=3.0\text{mW}$ and $F_{ab}=4.4\text{mW}$. With an ambient temperature $T_a=25.0^\circ\text{C}$, the temperatures in steady flight are calculated to be: $T_h=27.4^\circ\text{C}$, $T_{th}=30.1^\circ\text{C}$ and $T_{ab}=26.1^\circ\text{C}$. Note that the thermal conductances and the exchange coefficients can be conveniently checked with the temperature values in the steady state using equations 2a,b.

Presumably, the heat exchange between the body compartments is mainly due to haemolymph flow (e.g. Heinrich, 1970, 1972). If the haemolymph is mainly water, with a heat capacity of $4.18\text{Jg}^{-1}\text{K}^{-1}$, an exchange coefficient $E_h=E_{ab}=67\text{mJmin}^{-1}\text{K}^{-1}=1.12\text{mW}\text{K}^{-1}$ gives a flow rate of 16.0mgmin^{-1} . In a 85mg

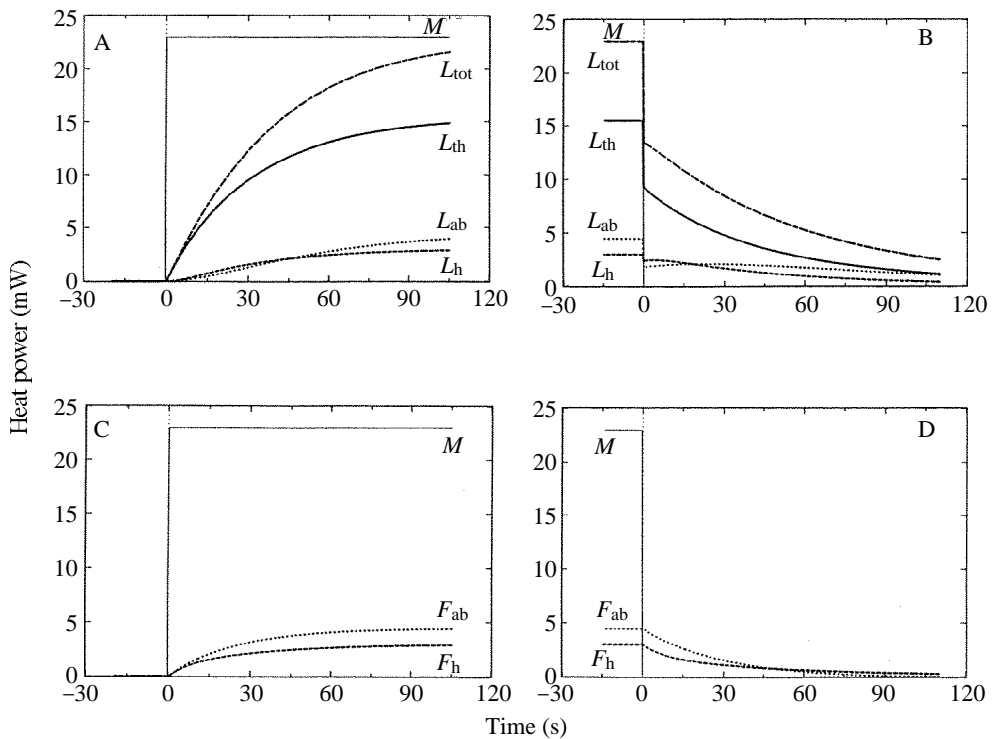


Fig. 4. (A, B) Heat power produced by the thoracic muscles (M) and lost to the surroundings by the head (L_h), the thorax (L_{th}) and the abdomen (L_{ab}) during the thermal processes of Figs 1–3. (C,D) Heat power exchanged from the thorax to the head (F_h) and abdomen (F_{ab}). L_{tot} , total heat loss.

blowfly, this means that about one-fifth of the body mass is transported per minute from thorax to abdomen (see Heinrich, 1976, 1979, for a related calculation in the case of the bumblebee *Bombus terreicola*). If the total haemolymph volume is 15 μl (Normann, 1972), a blood flow of 16 mg min^{-1} means that the total volume circulates through the body in approximately 1 min. This is quite compatible with the observations of Weyrauther *et al.* (1989) on the eyes of a white-eyed mutant blowfly (*chalky*, *Calliphora*). After injection of 1–2 μl of the fluorescent dye Lucifer Yellow into the thorax, the fluorescence of the eyes increased within several seconds, apparently due to rapid transport of the injected dye solution into the head.

In summary, the heat distribution in an insect body can be well described with a three-compartment model. The metabolic power calculated for the blowfly appears to be very similar to the value obtained for the honeybee (Nachtigall *et al.* 1989).

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Note added in Proof

In his recent comprehensive book *The Hot-Blooded Insects* (1993, Springer Verlag: Berlin, p. 365), Bernd Heinrich presents the thermal contour maps of a few insects immediately after flight, derived from measurements with a thermal imaging camera.