

## MECHANISMS FOR THE CONTROL OF BODY TEMPERATURE IN THE MOTH, *HYALOPHORA CECROPIA*

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### INTRODUCTION

The body temperatures of large moths rise to high and relatively constant levels during activity (Heath & Adams, 1965). When they are inactive, their body temperatures approximate to the temperature of their surroundings, and if the temperatures are low, moths do not initiate flight nor are they capable of flight. Instead, prior to flight they vibrate their wings and warm up 10 °C or more in 1-5 min. (Oosthuizen, 1939; Sotavalta, 1954; Dorsett, 1962; and others). The temperature rise during this interval is linear and only decreases just before take-off. Since the rate of heat loss increases exponentially with increasing gradient between the animal and its surroundings, the rate of heat production during warm-up is not constant but must increase continuously during the warm-up period. Heath & Adams (1967) measured oxygen consumption in two species of moths during the warm-up period and found that it increased with increasing duration of the warm-up period.

This observation would indicate that the metabolic output of the animal is varied to regulate the body temperature. This present study is an attempt to correlate thoracic temperature with the activity of the animal and to determine whether the animal regulates its heat production to maintain a constant thoracic temperature when voluntarily active; or whether the increased thoracic temperature is simply a passive result of flight-muscle activity.

### MATERIALS AND METHODS

*Temperature measurements.* Calibrated thermocouples of copper-constantan were implanted along the dorsal midline of the mesothorax of each animal and glued in position with a small piece of cork. The thermocouple junction penetrated the dorso-longitudinal muscle to a depth of 1-2 mm. If the implant interfered with flight the animal was discarded. The leads of the thermocouple were 1.5 m long and served as a tether. The animal was free to walk and flight was limited only by the length of the tether. Thoracic temperature was recorded on a Honeywell recording potentiometer (Electronik-16) continuously during the life of the animal. Fifteen to twenty animals were run at air temperatures of 17, 25 and 30 °C. The light cycle was 16 h of light and 8 h of dark, approximating the normal photoperiod at the time of emergence.

*Oxygen consumption.* Direct measurements of oxygen consumption in torpid, warming and active moths were made with a Beckman paramagnetic oxygen analyser.

The animals were placed in 125 ml flasks, and the flasks were immersed in a constant temperature bath at 20, 25, 30 or 35 °C. Both air temperature in the chamber and the thoracic temperature were monitored throughout the experiment as previously described. The temperature data and the rate of oxygen consumption were recorded on a Honeywell recording potentiometer. The oxygen consumption values reported were graphically determined over stable periods of 3 min or more.

Oxygen consumption was also determined indirectly from the rate of cooling and warming curves. If there is no significant heat production during cooling the rate of cooling will be a Newtonian process. The heat loss will equal the rate of heat production when the body temperature is constant. Newton's law of cooling states that  $dT_B/dt = AC(T_B - T_A)$  where  $A$  is the area cooled,  $C$  is the thermal conductance,  $T_B$  is the body temperature, and  $T_A$  is the air temperature. The rate of body temperature change ( $dT_B$ ) can be measured from the cooling curve for any value of  $T_B - T_A$  and a given time interval ( $dt$ ). Heat loss (therefore, heat gain at constant temperature), in calories, for any value of  $dT_B$  is  $dH/dt - WSdT_B/dt$ , where  $W$  is the thoracic weight,  $S$  is the specific heat in calories per gram per centigrade degree (0.8 for insect tissue; Krogh & Zeuthen, 1941). Assuming a caloric equivalent of oxygen of 4.8 cal/ml then the oxygen consumption at any given temperature gradient can be calculated.

#### RESULTS

*Temperature measurements and behaviour.* Fig. 1 is a typical thoracic temperature recording on a loosely tethered animal. The behaviour of the animal is noted on the record. The warm-up period is characterized by the linear increase in the thoracic temperature. The increase in thoracic temperature is produced by a shivering mechanism in which the normally antagonistic flight muscles contract simultaneously. Visually, this period can be determined by the vibration of the horizontally held wings. As the thoracic temperature approaches the 'take-off' temperature the animal may begin large flapping movements of the wings and walk towards a point suitable to initiate flight.

With the initiation of flight there is a slight decrease in the thoracic temperature perhaps due to an increased convective heat loss. The thoracic temperature during maintained flight remains relatively constant. During periods of intermittent flight the thoracic temperature is variable. The behaviour of the female at this time is generally directed towards egg-laying. She warms up and flies for a short time, usually less than 1-2 min, and then ceases flight and deposits a small number of eggs. She then begins another cycle of warming followed by flight and egg deposition. The female does not have to be fertile to begin egg laying. All of the females in this experiment were virgin and usually began to lay eggs on the third to fourth day after eclosion.

The males also exhibit intermittent periods of activity, and the temperature recordings look very similar to those of the females. The males during these periods appear to be seeking a female for copulation. After flight they are not torpid but walk aimlessly and exhibit large flapping movements of the wings. In these experiments males and females were run simultaneously in the same room. Presumably, the males could have been stimulated into activity by the females release of the pheromone, and this would account for their 'seeking' behaviour.

*Warm-up.* The rate of warm-up for animals at 17, 25 and 30 °C air temperature are shown in Fig. 2. The rate of warm-up is linear and independent of ambient temperature, but the number of voluntary warm-up periods is reduced at lower air

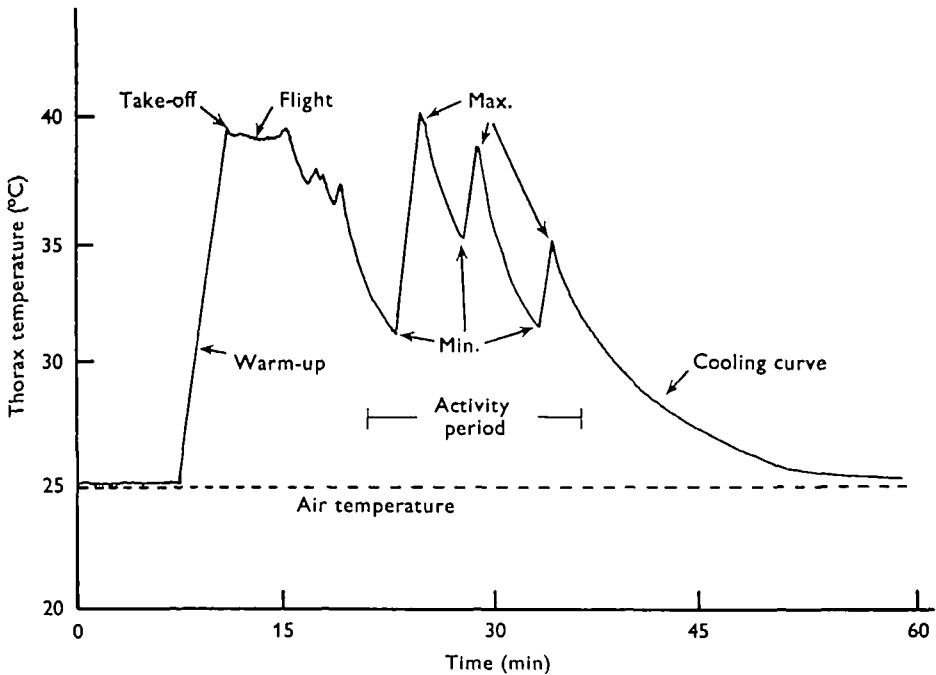


Fig. 1. Continuous recording of thoracic temperature.

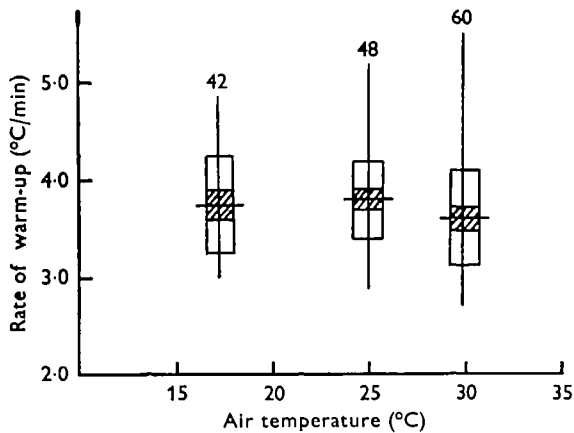


Fig. 2. Rate of warm-up plotted against air temperature. Horizontal line = mean, vertical line = range, unshaded box = 1 s.d., shaded box = 2 s.e., number indicates sample size.

temperatures. The duration of the warm-up period increases with decreasing air temperature from a mean of  $2 \pm 0.3$  min at 30 °C to  $5 \pm 0.5$  min at 17 °C. The warm-up period is a mechanism which raises the thoracic temperature and enables the insect to be active at air temperatures which would prohibit flight.

*Flight initiation.* The thoracic temperature at which flight is initiated was monitored to determine whether there is a specific temperature set point that initiates the flight response. The thoracic temperature at which flight was initiated is plotted against air temperature in Fig. 3. The variation about the means is not excessive and would be expected when comparing individuals. However, the temperature at take-off did vary on subsequent trials within single individuals. If a temperature set point for flight exists, it is not an absolute value and can be altered by other inputs, possibly sensory. The mean temperatures at take-off show a decrease of  $0.25\text{ }^{\circ}\text{C}$  per  $^{\circ}\text{C}$  gradient, indicating a dependence on air temperature.

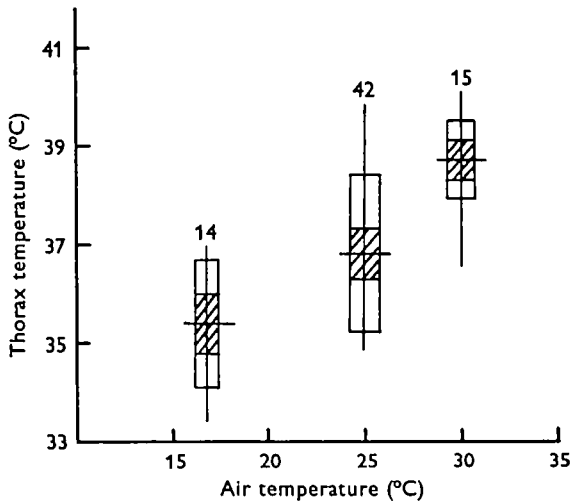


Fig. 3. Thoracic temperature at the initiation of flight plotted against air temperature. Symbols as in Fig. 1.

*Maintained flight.* The thoracic temperature during maintained flight was graphically averaged for flights lasting a minimum of 5 min. The results plotted against air temperature are shown in Fig. 4. The mean values are closely correlated with the flight-initiation temperatures, averaging  $0.4\text{ }^{\circ}\text{C}$  lower. This slight decrease could be due to an increased convective heat loss. The wing movements shift from small amplitude 'shivering', during warm-up to large amplitude, flapping, during flight, which would result in an increased air flow over the surface of the animal.

The mean thoracic temperature during maintained flight also indicates a dependency on air temperature, decreasing  $0.26\text{ }^{\circ}\text{C}$  per  $^{\circ}\text{C}$  gradient. Possibly, this dependence on air temperature is due to an increasing heat loss through the respiratory system as the air temperature decreases.

*Maximum-minimum temperature distribution.* The distribution of the maximum and minimum thoracic temperatures during active periods (intermittent flight) are given in Fig. 5. The means of the maximum and minimum distributions can be considered the upper and lower limits of thoracic temperature for voluntary activity. Within this range the animal does not necessarily regulate its body temperature. However, when the animal approaches the upper limit it voluntarily ceases flight to avoid overheating. Conversely, the metabolic requirements for warm-up increase with decreasing air

temperature (Fig. 7), and the animal cannot 'afford' to allow its body temperature to fall to ambient levels after every short burst of flight. Therefore, during periods of intermittent activity seen in the 'female-seeking' by the male or egg-laying in the female, the body temperature is regulated between the upper and lower temperature limits.

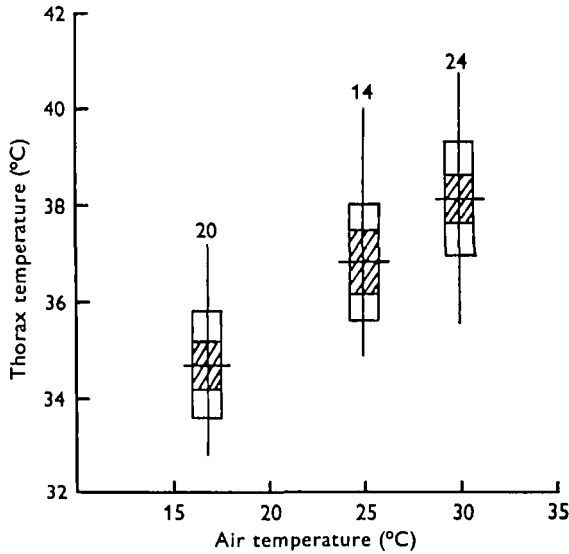


Fig. 4. Thoracic temperature during maintained flight plotted against air temperature. Symbols as in Fig. 1.

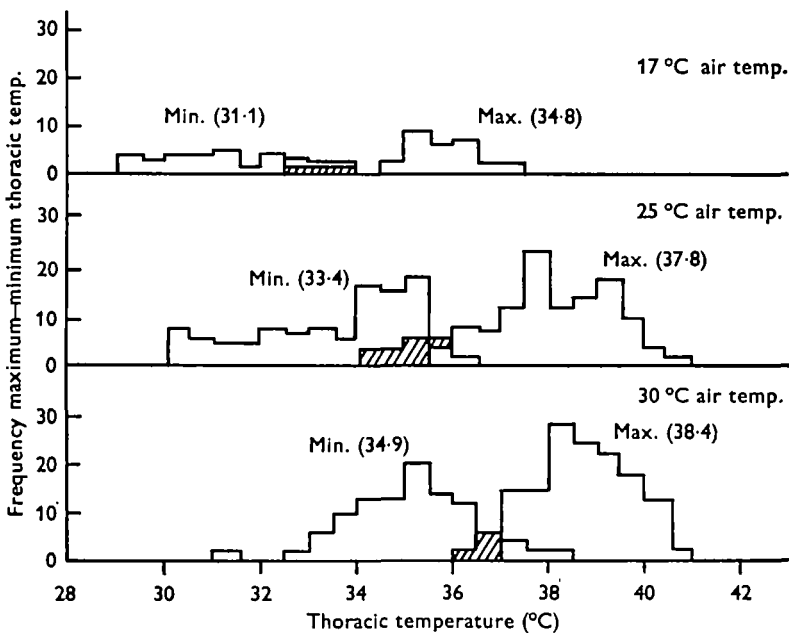


Fig. 5. Histograms of maximum and minimum thoracic temperatures during active periods. Numbers in parentheses are the mean values. Shaded portions are the regions of overlap of the maximum on the minimum distributions.

*Minimum flight temperature.* The means of the minimum and maximum distributions at 25 °C are 33.4 and 37.8 °C respectively. A good estimate of these upper and lower limits can be obtained only by having a very large sample of the thoracic temperatures. At low air temperatures the animals tend to reduce the number of spontaneously active periods, and it would therefore require a large number of animals to get this information. Two experiments were designed to determine these limits directly. In the first experiment ten animals were cooled to 10 °C and then stimulated to fly (air temperature 25 °C) by repeatedly throwing them in the air. When the animal was able to maintain level flight it was immediately captured and the thoracic temperature recorded with a calibrated thermistor probe described by Heath & Adams (1969). The mean thoracic temperature was 34.8 °C with a standard deviation of 1.88. The range was 32.8–38.2 °C. This measured value for the lower limit of activity will be higher than the actual value due to the heat generated during the short flight before capture.

*Shade-seeking.* The upper temperature limit for voluntary activity was measured directly by externally heating the animal and then noting the thoracic temperature at which the animal voluntarily walked or flew from the heated region. A total of fifty-two observations were made on animals at 17 and 25 °C air temperature. Thermocouples were implanted into the animals, which were allowed to move freely on a vertically suspended cheese cloth. An infra-red lamp was used to heat the animals at approximately the normal rate of warm-up. The thoracic temperature at which the animal either walked or flew from the heated region is defined as the shade-seeking temperature. The mean was 38.5 °C ( $n = 30$ , S.D. = 1.33, range = 36.6–42.0 °C) at 28 °C and was 38.3 °C ( $n = 22$ , S.D. = 1.25, range = 36.2–40.2 °C) at 17 °C. In both the minimum flight temperature and the shade-seeking temperature the measured values are in close agreement with those values predicted from the minimum and maximum distributions of body temperature.

*Heat torpor.* In this experiment the animals were heated externally, as in the shade-seeking experiment, but were not allowed to escape the heated region. The mean thoracic temperature at which all voluntary activity ceased was 43.9 °C ( $n = 11$ , S.D. = 2.18 °C, range = 40.0–46.5 °C) and is a measure of the absolute upper temperature limit. This indicates that a safety factor of 5.5 °C exists between high temperature avoidance (shade-seeking) and heat death.

*Oxygen consumption: cooling curves.* Two cooling curves were plotted for each animal at 17, 25 and 30 °C. Fig. 6 is an example of a typical cooling curve. The slope of the line is the combined constants: surface area ( $A$ ) and thermal conductance ( $C$ ). The rate of change in body temperature ( $dT_B/dt$ ) per min per °C gradient was determined graphically. The rate of heat loss was calculated from the equation,  $dH/dT = WSdT_B/dt$ , where  $W$  is the thoracic weight and  $S$  is the specific heat. If the thoracic temperature remains constant, as it does in maintained flight, then heat loss will equal the heat gain. The calculation for heat loss ( $dH/dt$ ) is then equivalent to the metabolic rate (cal/min) to maintain the established gradient. Assuming a caloric equivalent of oxygen of 4.8 cal/ml then the oxygen consumption to maintain the gradient can be calculated.

The rate of oxygen consumption was calculated for individual moths on the basis of the temperature gradient established during maintained flight. These individual

values were then averaged and plotted against the ambient temperature (Fig. 7). It can be seen that at lower air temperatures the rate of oxygen consumption increases in active animals.

These values are under-estimates of the actual oxygen consumption. They account only for metabolism involved in heat production (heat loss) and do not include metabolic expenditures for flight or maintenance of normal physiological functions.

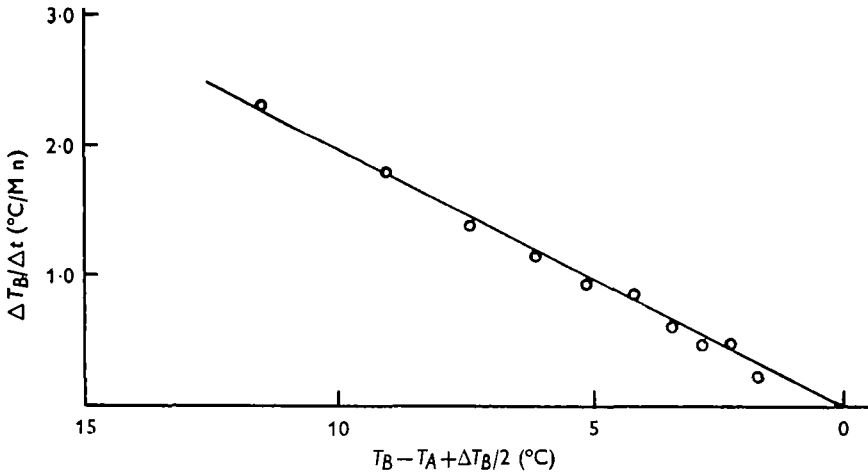


Fig. 6. Linear plot of a representative cooling curve used to calculate oxygen consumption.

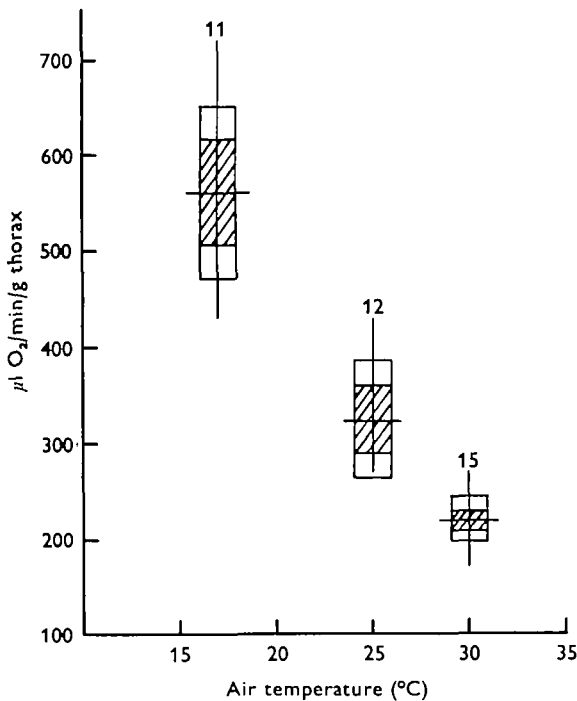


Fig. 7. Calculated oxygen consumption necessary to maintain temperature gradient during activity, calculated from cooling curves. Symbols as in Fig. 1.

During the warm-up period the animal must exhibit a continuously increasing metabolic rate or at least a rate much higher than that required to maintain any given gradient. During this period the animal must maintain the gradient established and

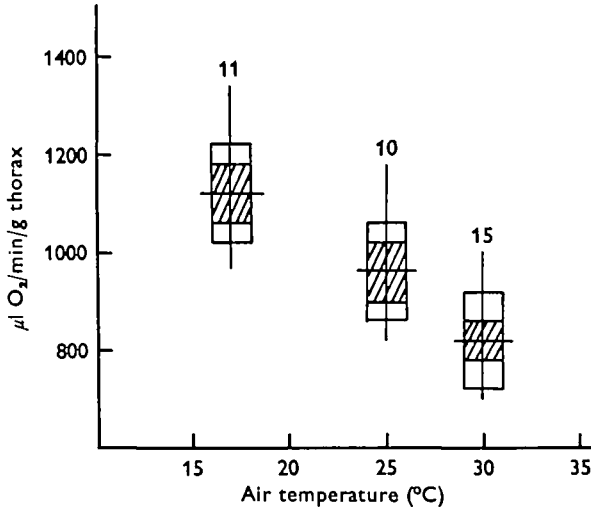


Fig. 8. Calculated maximum oxygen consumption plotted against air temperature. Maximum values calculated by adding the rate of oxygen consumption necessary to maintain the temperature gradient plus the increment required to further increase the body temperature during warm-up. Symbols as in Fig. 1.

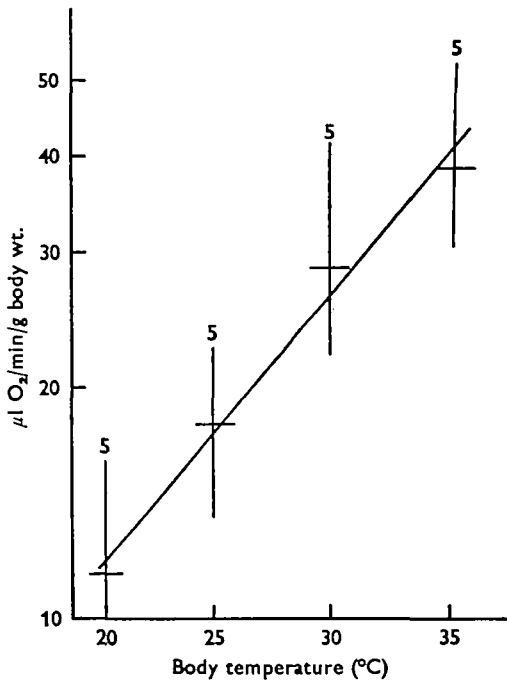


Fig. 9. Rate of oxygen consumption in torpid animals plotted against air temperature (body temperature). Horizontal line = mean, vertical line = range, number = sample size.



also initiate a further rise in thoracic temperature which requires an additional metabolic output. Therefore, at the peak of the warm-up period (transition to flight) the oxygen consumption will be at its maximum rate. The temperature gradient is greatest at this time and over a short period of time ( $dt$ ) the thoracic temperature is still increasing. With the initiation of flight, at least a portion of the metabolic output required for the animal to warm-up is channelled into the mechanical output, i.e. flight.

An estimate of the maximum oxygen consumption can be calculated from the rate of warm-up and cooling curve data. The addition of the rate of oxygen consumption to maintain a given gradient (calculated from the cooling curves) and that required to raise the thoracic temperature (calculated from the rate of warm-up, Fig. 2) will give the maximum oxygen consumption at the given gradient. Individual values were calculated then averaged and plotted against air temperature (Fig. 8).

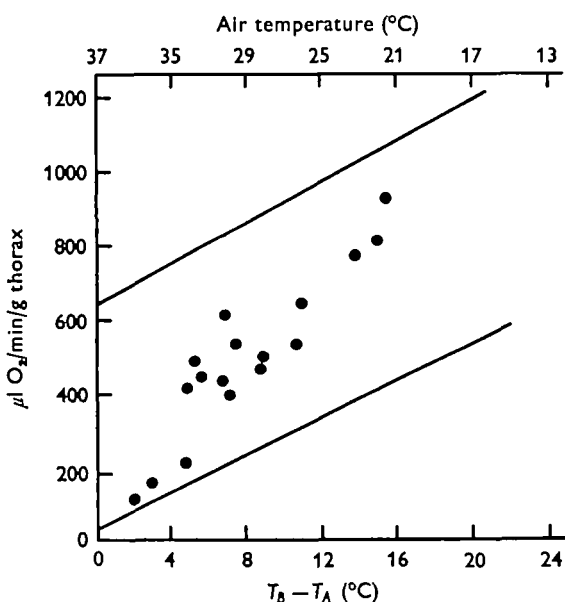


Fig. 10. Directly measured oxygen consumption in active animals plotted against air temperature (developed temperature gradient). Solid circles are values for individual moths graphically averaged over stable periods of 3 min or more. Upper line is the calculated maximum rate of oxygen consumption and the lower line is the calculated rate to maintain the temperature gradient.

*Direct measurements of oxygen consumption.* In torpid animals the effect of increasing the air temperature, in effect the body temperature, was to cause an increase in oxygen consumption (Fig. 9). The  $Q_{10}$  is 2.25 over the range of 20–30 °C.

Oxygen consumption was also measured in active animals at air temperatures of 20, 25, 30 and 35 °C. This is not a true flight situation, since the animals are confined within the respirometer and the air flow differs from that of flight. However, the animals do beat their wings steadily and hold their legs in the flight position indicating that they are at least attempting to fly. In these animals the oxygen consumption decreases with increasing air temperatures (Fig. 10). The solid circles indicate the oxygen consumption of individuals averaged graphically over 3 min intervals. The

upper line is the calculated maximum rate of oxygen consumption. The lower line is the calculated oxygen consumption necessary to maintain the established temperature gradient. These lines represent the limits of oxygen consumption at any given gradient over the range of air temperatures indicated. The directly measured values fall within these limits in all cases.

#### DISCUSSION

*Hyalophora cecropia* is a nocturnal animal and does not normally initiate a warm-up cycle or flight during the day. The body temperature during the day fluctuates with the ambient temperature. If the animal is exposed to direct sunlight the body temperature will rise to 38.5 °C. At this time the animal initiates the behavioural response of shade-seeking and the body temperature does not continue to increase to lethal levels.

This is analogous to the basking behaviour seen in reptiles. The animal uses an external source of heat, solar radiation, to raise its body temperature to an optimal level before initiating activity. In this manner it conserves its energy sources by not going through a warm-up cycle in order to avoid direct sunlight.

During flight the body temperature is maintained at a level approaching the shade-seeking temperature, 38.5 °C. Therefore, it would appear that the animal is faced with the problem of heat dissipation during flight rather than heat production. This problem would become particularly acute at air temperatures above 30 °C. Adams & Heath (1964) have shown that the sphinx moth *Pholus achemon* has developed an evaporative cooling mechanism to depress the body temperature when the animal is thermally stressed. This insect repeatedly extrudes a drop of fluid from the proboscis which lowers the body temperature through evaporation. Since *Hyalophora cecropia* is a nocturnal animal it would rarely encounter air temperatures exceeding 30 °C in the temperate regions where it is normally present. Therefore, no special evaporative cooling mechanisms are found in cecropia moths. The animal relies on behavioural mechanisms to avoid high temperatures encountered during the day and ceases activity at night if the body temperature exceeds the shade-seeking temperature.

*H. cecropia* utilizes metabolic heat production to raise its body temperature to an optimal level before initiating and maintaining flight. During periods of intermittent activity the body temperature is regulated between 34.1 and 38.2 °C over a range of air temperatures of 20–30 °C. After an activity cycle or a period of maintained flight the body temperature is allowed to fall to ambient levels and the animal is in a torpid state.

In modelling the temperature responses of this moth a two set-point system appears to be the most feasible. The upper temperature set point would correspond to the body temperature most favourable for flight. The lower set point would correspond to the lowest body temperature at which the animal can voluntarily initiate and maintain flight. These two set points determine the limits of the range in body temperature over which the animal can be active independent of air temperature. Fig. 11 is a summary of the temperatures responses of *H. cecropia* with the upper and lower set points indicated on the graph.

If the body temperature is below the upper set points it warms up to that level by a 'shivering' mechanism; the normally antagonistic flight muscles, dorsoventrals and dorsal longitudinals, contract synchronously during warm-up producing an excess of

heat (Kammer, 1968). When the upper temperature set point is reached the pattern of contraction of the flight muscles changes. The dorsal longitudinal and dorsoventral muscles contract out of phase with each other and produce the flapping movements seen in flight.

The shade-seeking temperature, the maintained flight temperature, and the mean maximum temperature during active periods are all in close agreement and can be considered to correspond to the upper set point. The body temperature at which the shade-seeking response occurs is perhaps the best estimate of this set point. The response is precise and easily observed, and is solely dependent on body temperature.

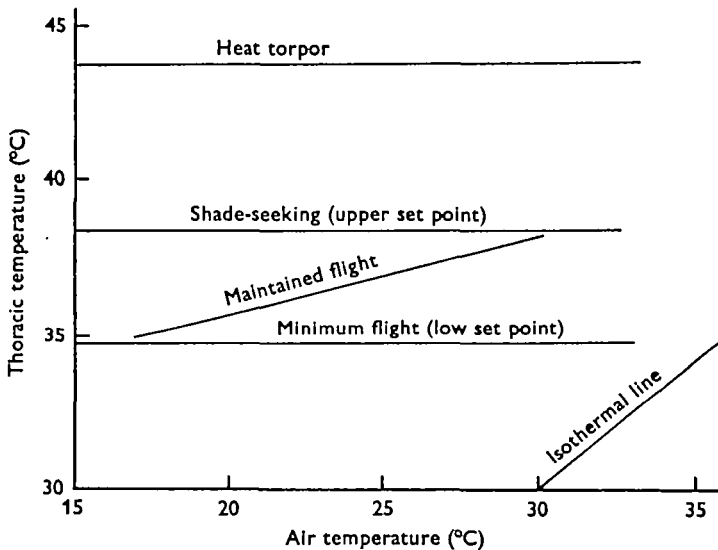


Fig. 11. Summary of the temperature responses of cecropia moths.

A lowering of air temperature has no effect on this response ( $38.3^{\circ}\text{C}$  at  $25^{\circ}\text{C}$  air temperature and  $38.5^{\circ}\text{C}$  at  $17^{\circ}\text{C}$  air temperature). Also the animal does not make any metabolic adjustments to raise the body temperature as in flight or warm-up, and therefore, the body temperature is under the control of the experimenter not the animal. This is essentially an open-loop system. The difference between body temperature and the upper set point is slowly decreased by external heating and the physiological response (shivering) to raise the body temperature is not actuated. When the body temperature reaches the upper set point the behavioural response of heat avoidance is triggered. The only precaution that must be considered is to heat the animal at a rate equal to the normal warm-up rate. Rapid heating may cause an avoidance response at a body temperature lower than the theoretical set point.

The mean maximum temperature during active periods may be misleading as an estimate of the upper set point. If the difference between the upper set point and air temperature ( $B.T = A.T.$  when the animal is torpid) is too great the animal will not voluntarily warm-up. In the few cases where the animal begins a warm-up cycle the attempt may be aborted well before reaching the upper temperature set point. Yet these values are utilized when plotting the distribution and the curve is shifted towards a lower temperature. This shift in the distribution of body temperature during activity

can be seen in Fig. 5. The means for both the maximum and minimum body temperature are shifted towards lower values in those animals held at an air temperature of 17 °C.

The small size of the animal indicates a high surface-to-volume ratio. At low air temperatures the animal may not be able to produce enough heat to offset heat loss and to continue to increase its body temperature to the upper set point. At low air temperatures the heat loss may balance the rate of heat production at a body temperature below the minimum temperature required for flight. Then the animal ceases its warm-up activity to conserve its limited energy reserves.

The maintained flight temperature is a good estimate of the upper set point at high air temperatures, but it is depressed at low air temperatures. The metabolic rate of active animals, measured as oxygen consumption, increases with decreasing air temperatures (Fig. 10). The scope of metabolism is finite and therefore there is a limit to the temperature gradient that can be maintained by the animal.

A low-temperature set point is indicated from two measurements: the minimum flight temperature and the mean minimum thoracic temperature during intermittent activity. As noted above, this set point corresponds to the lowest body temperature at which the animal can initiate activity (flight).

When *H. cecropia* is active the body temperature is maintained between 34.1 and 38.2 °C over a range of air temperature of 20–30 °C. These activity periods generally last 5–15 min although males may remain active for 2 h. The animals do not fly continuously during these periods, but exhibit short flights interspersed with walking, walking accompanied by wing flapping, egg-laying, or what appear to be periods of torpor. It is during these periods of non-flight that the body temperature falls exponentially approaching the ambient temperature. If the animal is to continue its activity, it initiates a short warm-up period raising the body temperature back up to the upper set point. The mean body temperature at which this response occurs was determined from plotting the distribution of minimum body temperatures during these periods of intermittent activity. The mean values as noted in Fig. 5 were 34.1 °C at 25 °C and 34.9 °C at 30 °C which correspond closely to the minimum flight temperature, 34.8 °C.

At the end of an activity cycle the body temperature is not regulated and falls exponentially to ambient levels. It would be far too expensive, metabolically, to maintain a high thoracic temperature during long periods of inactivity. It is during these periods of torpor that the moth responds to temperature as a poikilotherm. The  $Q_{10}$  for rate of oxygen consumption is 2.25 (Fig. 9).

The body temperature for flight initiation and maintained flight is dependent on air temperature, decreasing 0.25 °C per °C gradient. This dependence can be accounted for by an increased evaporative heat loss through the respiratory system. The metabolic rate increases with decreasing air temperature in active animals. Therefore, the spiracles must be opened for longer periods of time at low air temperatures to account for the increased oxygen consumption. The increased time of opening would allow a higher rate of water evaporation, depressing the body temperature.

The decrease in body temperature of flying animals is 2.6 °C (38.1–35.5 °C) when the air temperature is lowered from 30 to 20 °C. This drop in temperature would require the evaporation of 3.2 mg of water in an animal with a 1 g thorax.

The mouth parts in both sexes of *H. cecropia* are rudimentary and the animals do not feed or drink as adults (Rau, 1910). Therefore, evaporative water loss during flight would rapidly lead to desiccation and death unless production of metabolic water balanced evaporative loss.

One of the basic substrates for flight-muscle metabolism in *H. cecropia* is palmitic acid (Domroese & Gilbert, 1964). Complete combustion of this 18-carbon chain by 250  $\mu$ l of oxygen (the increase of oxygen consumption in flying animals when the air temperature is lowered from 30 to 20 °C, Fig. 10) yields 13.8 mg of water. Therefore, the metabolic water produced by flight-muscle metabolism is more than sufficient to account for evaporative water loss.

#### SUMMARY

1. Thoracic temperature in the moth, *Hyalophora cecropia*, is correlated with gross patterns of behaviour.

2. The animal warms up to a minimum of 34.8 °C body temperature before initiating flight. The rate of warm-up is linear and the duration of the warm-up period increases with decreasing air temperature.

3. Thoracic temperature at the initiation of flight and during maintained flight remain constant at any given air temperature, however, decreases 0.25 °C per °C gradient as air temperature is decreased.

4. Distribution of the maximum and minimum thoracic temperatures during active periods indicate that the animal maintains its body temperature within a favourable range. The animal uses behavioural mechanisms to maintain the thoracic temperature within this range when the body temperature reaches the limits, 33.4 and 37.8 °C.

5. The minimum thoracic temperature for flight (34.8 °C) and the shade-seeking temperature (38.5 °C) correspond closely to the limits predicted from the maximum-minimum distribution of thoracic temperatures.

6. The theoretical minimum and maximum rates of oxygen consumption were calculated from cooling curves and warm-up curves. Both rates increase when the gradient between body temperature and air temperature increases (air temperature is lowered, body temperature remains relatively constant).

7. Directly measured rates of oxygen consumption in flying animals increase as air temperature decreases. These values fall within the calculated maximum and minimum in all cases.

8. Oxygen consumption measured in torpid animals indicates a normal poikilothermic response, increasing with increased air temperature. The  $Q_{10}$  for this response is 2.25 over the range 20–30 °C.

9. A model for the regulation of body temperature in active moths is discussed.

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