

THERMOREGULATION AND CONTROL OF HEAD TEMPERATURE IN THE SPHINX MOTH, *MANDUCA SEXTA*

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SUMMARY

Head and thorax temperatures (T_h and T_{th}) were tightly coupled during pre-flight warm-up over a range of ambient temperatures (T_a). At $T_a = 21^\circ\text{C}$, the head reached a significantly higher temperature ($T_{th} = 32^\circ\text{C}$) than during exogenous heating of dead moths to the same thoracic temperature ($T_h = 26^\circ\text{C}$). In free-flying moths, slopes of linear regressions for both T_{th} and T_h versus T_a were about 0.4. At any T_a , T_h remained only about 7°C below T_{th} . Abdominal temperature varied with T_a with a slope of 1.2 and remained 2–5 degrees above T_a . Cooling constants (min^{-1}) for the head, calculated from cooling experiments with the thorax either at T_a or maintained constant at about 40°C , yielded similar values. During free flight, as T_a increased from 17 to 32°C , thoracic heat loss decreased from 36 to 20% of the total heat production, head heat loss decreased from 27 to 8%, and abdominal heat loss increased from 17 to 37%. During warm-up at all T_a 's the largest component of energy expenditure was the heat storage and heat loss that occurred from the thorax, followed by that from the abdomen and then by that from the head. Exogenous heating of some live moths resulted in cyclic temperature fluctuations in which T_h and T_{th} changed simultaneously and in opposite directions. During each cycle, the heart beat pattern changed, becoming irregular when T_{th} was increasing and returning to a regular pattern when T_{th} was decreasing. Smaller temperature fluctuations in the head occurred at the same rate as the heart beat. These data suggest that the head temperatures observed during pre-flight warm-up and flight are the result of active heat transfer from the thorax via the blood circulation.

INTRODUCTION

Studies of the physiological regulation of body temperature in moths have dealt primarily with regulation of thoracic temperature. Heat is produced in the thorax as a result of mechanical inefficiency of flight muscle contraction (Heinrich, 1974). In *Manduca sexta*, as in other moths, this heat is either stored in the thorax to increase

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thoracic temperature (T_{th}) as in pre-flight warm-up (Heinrich & Bartholomew, 1971) or some of it is actively transferred to the abdomen to maintain thoracic temperature during flight (Heinrich, 1971*b*). This regulation is brought about by changes in blood circulation pattern between the thorax and abdomen (Heinrich, 1970, 1971*b*).

In most of these experiments, head temperature (T_h) was not measured along with thorax and abdomen temperatures. Because of the close proximity of the head and thorax, and because the dorsal vessel empties into the head after the blood has passed through the thorax, there may be some active transfer of thoracic heat to the head. The effect of this heat on the head temperature is of particular interest, since the neural control centres are located in the head, and nervous output that controls the contraction of flight muscles is highly dependent on temperature (Kammer, 1968).

In the present study, we investigate head temperature of *M. sexta* during pre-flight warm-up and free-flight over a range of T_a 's. We also quantify rates of heat loss from the head, and examine the mechanism of heat transfer between thorax and head in an attempt to evaluate their significance for thermoregulation.

MATERIALS AND METHODS

Pupae of *M. sexta* were purchased from Carolina Biological Supply Co. and were kept in saturated conditions in an emergence chamber. All experiments were conducted within the first three days after emergence.

Head temperatures for heating and cooling experiments were measured by inserting a 44 gauge copper-constantan thermocouple in the centre of the dorsal surface of the head. Thorax temperatures were measured by inserting a 36 gauge thermocouple into the ventro-lateral thorax. The cuticle was punctured with a microsurgical needle. Temperatures were read on two Bailey Bat-4 laboratory thermometers. Head and thorax temperatures were continuously recorded by connecting the output of the thermometers to two servo channels of a Gilson polygraph (150 mm full scale).

Cooling rates of the heads of dead moths (killed by quick freezing in a -80°C freezer) were measured in two ways. First, with the moth on a styrofoam pad and the thorax and abdomen shielded with aluminium foil, the head was heated to about 40°C with a microscope lamp. The lamp was then switched off and T_h was continuously measured during cooling ($T_a = 22^\circ\text{C}$). Alternatively, the head and thorax were heated with two lamps and, while the thorax was maintained at about 40°C , the head was allowed to cool.

Moths to be used for live external heating experiments were precooled to 4°C in a refrigerator. Moths were then secured to a styrofoam pad with crossed insect pins between head and thorax and between thorax and abdomen. Thermocouples were inserted into the head and thorax and the wings were cut off (this caused no visible loss of blood). To measure thoracic heart pulsations, two 44 gauge constantan electrodes were inserted into holes on either side of the dorsal midline. The electrodes were attached to an impedance converter which was connected to the polygraph. All of these preparations could be completed before the moths reached a temperature where they became active. With the head and abdomen shielded with aluminium foil, the thorax was heated using a microscope lamp.

After completing experiments on live moths, some were killed by injecting 0.02–0.05 c.c. of ethyl acetate into the abdomen. The heating was then repeated on the dead moths, with all thermocouples and body positions exactly the same as in experiments using live moths.

During warm-up, T_h and T_{th} were measured with a temperature probe consisting of a 44 gauge thermocouple threaded into a 1 μ l glass capillary tube that had been drawn out to a point in a flame. The end of the thermocouple was secured to the tip of the glass tube with a drop of quick drying liquid glue. The capillary tube with the thermocouple was inserted into a microburet. This arrangement minimized conduction of heat from the finger tips to the probe.

Gentle pinching of the antennae caused the moths to initiate pre-flight warm-up. At various times during warm-up, the moths were seized by the forewings and inverted. To measure T_h , the probe was thrust into the underside of the head (see Casey, Hegel & Buser, 1981 for more details). The T_{th} was measured immediately afterwards by inserting the probe into the centre of the thorax from the ventral side. These measurements took approximately 3 s.

During flight at different T_a 's, T_h , T_{th} and T_{ab} were measured to the nearest 0.2 °C, using a temperature probe consisting of a 36 gauge thermocouple inserted into a 24 gauge hypodermic needle. The moths were induced to fly by gentle prodding and were seized after at least one minute of continuous free flight in a temperature controlled room. Head and thorax temperatures were measured as in the warm-up experiments. Abdominal temperatures were measured by inserting the probe through one of the intersegmental membranes on the ventral surface of the abdomen. All temperatures were measured within 5–6 s.

RESULTS

Head temperature. When dead moths ($n = 8$) were heated exogenously on the thorax to 40.0 ± 2.5 °C ($T_a = 22$ °C), the T_h stabilized at 26.1 ± 1.7 °C. A sample heating curve is shown in Fig. 1. This temperature reached by the head is its equilibrium temperature ($T_{h(eq)}$) and is the result of passive heat transfer from the thorax to the head.

During pre-flight warm-up, the T_h was a linear function of T_{th} (Fig. 2). Actual head temperatures at any given T_{th} were greater at high T_a than at low T_a . Slopes of linear regressions for T_h v. T_{th} (Fig. 2) increased with increasing T_a (0.67 at $T_a = 16$, 0.78 at $T_a = 21$, and 0.97 at $T_a = 30$ °C).

The time course of head temperature during warm-up was derived from data in Fig. 2, assuming an appropriate rate of increase in T_{th} at different T_a 's (Heinrich & Bartholomew, 1971). At all T_a 's, head temperature increased linearly with time during most of the warm-up period (Fig. 3). However, at the beginning of warm-up, the rate of increase of head temperature was initially slow and increased progressively. The rate of warm-up of the head increased directly with T_a (Fig. 3).

Comparison of Figs 1 and 3 shows that at the same T_a , T_h in live moths during warm-up was greater than T_h in dead moths heated to a similar T_{th} . When the thorax reached 40 °C, the head temperature during warm-up averaged 32 °C, while the T_h

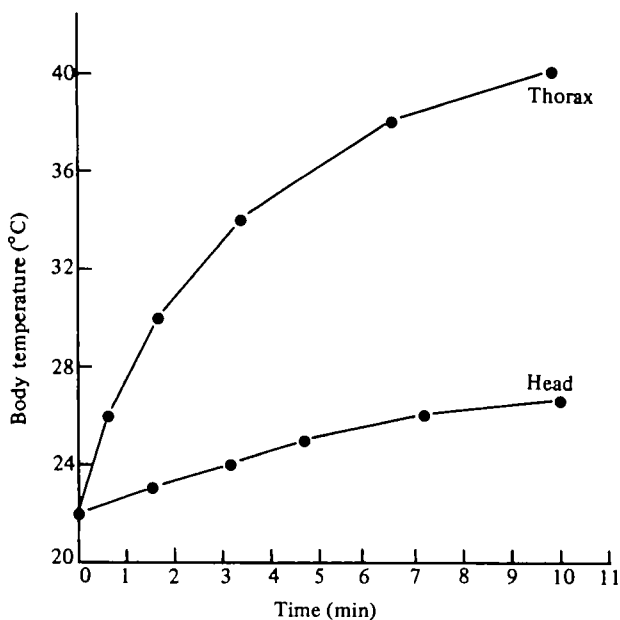


Fig. 1. An example of the relation of head and thorax temperatures with time during exogenous heating of the thorax of a dead moth ($T_a = 22^\circ\text{C}$).

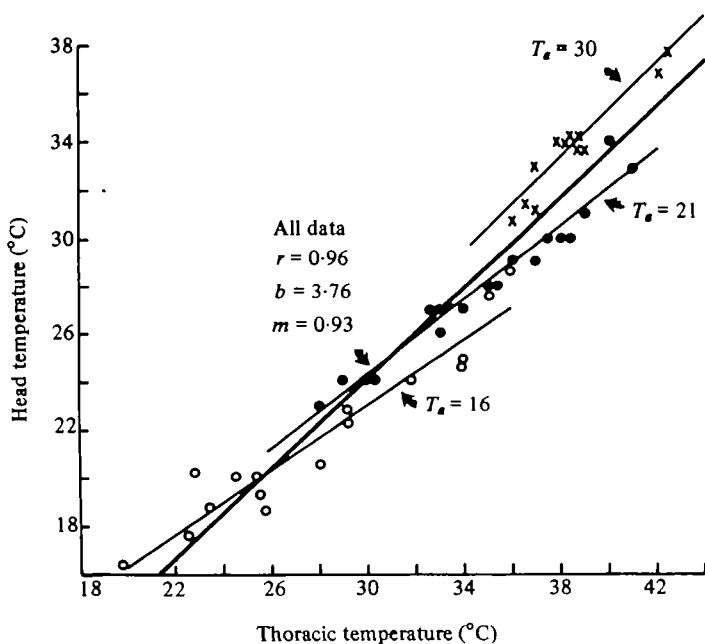


Fig. 2. Head temperature in relation to thoracic temperature during pre-flight warm-up at $T_a = 16^\circ\text{C}$ (○), $T_a = 21^\circ\text{C}$ (●), and $T_a = 30^\circ\text{C}$ (×).

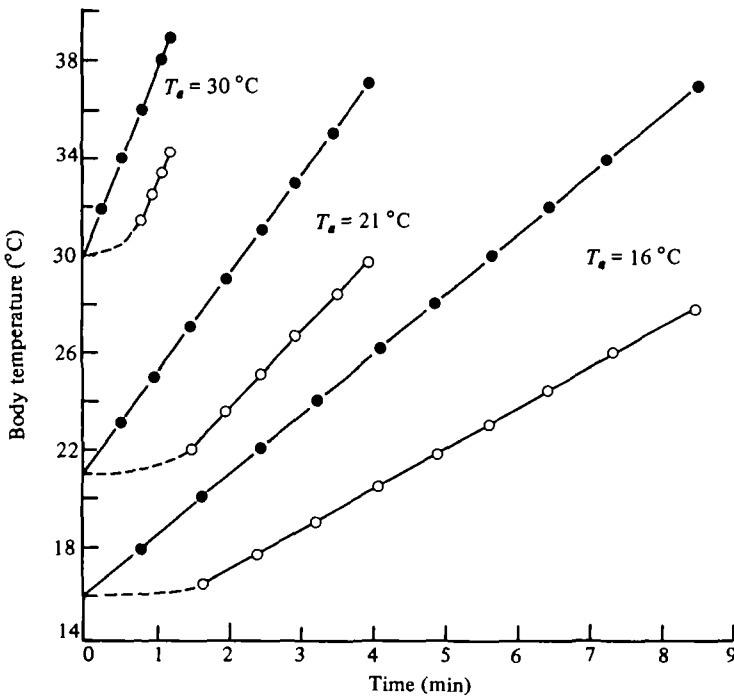


Fig. 3. Time course of temperature increase of thorax (●) and head (○) during warm-up at $T_a = 16, 21$, and 30°C ; calculated from thorax and head temperature data in Fig. 2 and warm-up rates in Table 1.

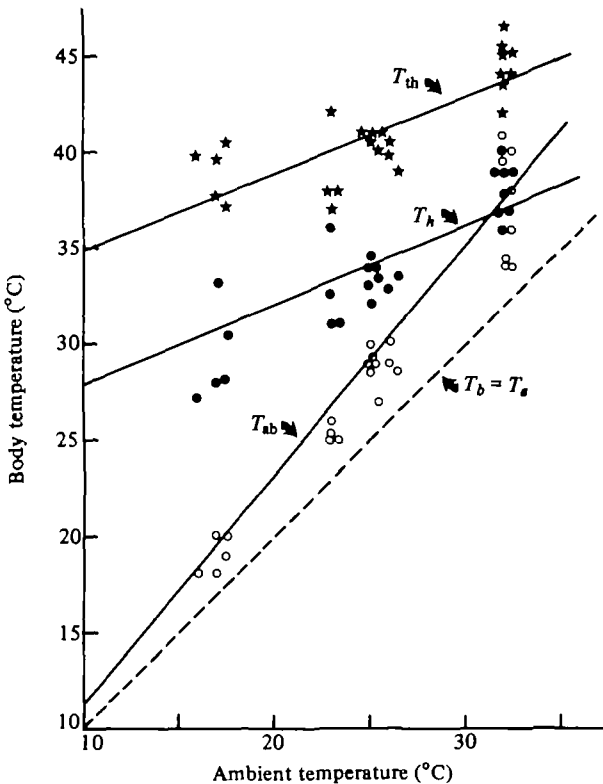


Fig. 4. Thoracic (★), head (●), and abdominal (○) temperatures during free flight plotted against ambient temperature ($n = 26$). The dotted line shows the relation when $T_b = T_a$. Least-square regression equations describing these relations are: $T_{th} = 0.40 T_a + 30.9$ ($r = 0.81$); $T_h = 0.42 T_a + 23.8$ ($r = 0.79$); $T_{ab} = 1.20 T_a - 0.33$ ($r = 0.92$).

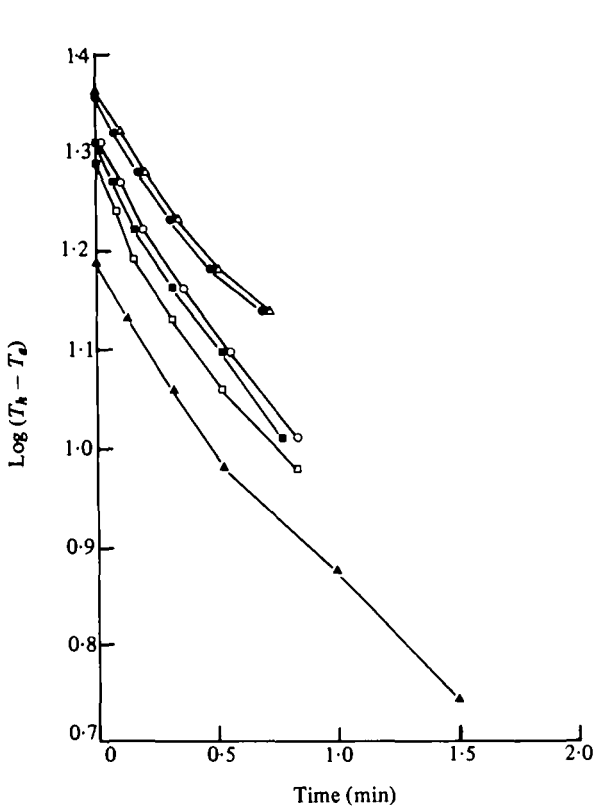


Fig. 5. Cooling rates of the heads of dead moths with the thorax at ambient temperature. Symbols used to differentiate between separate runs.

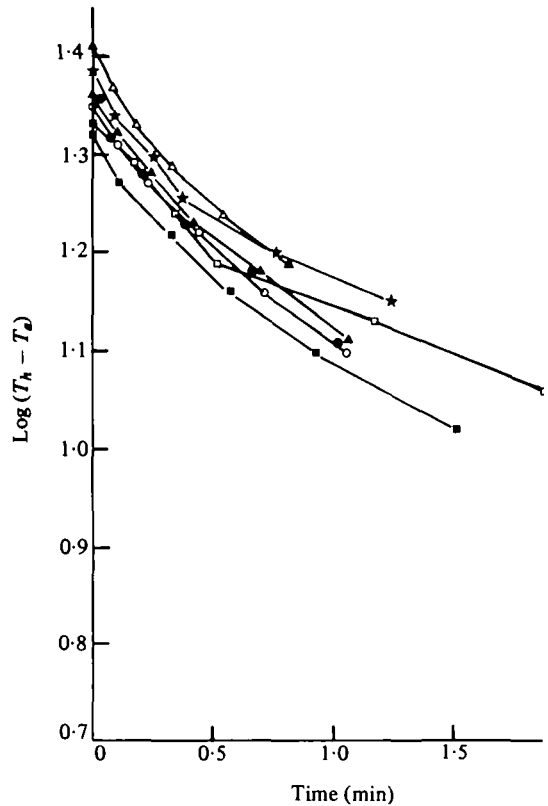


Fig. 6. Cooling rates of the heads of dead moths with the thorax maintained at approximately 40 °C and the driving force calculated as $T_{\text{head}} - T_a$. Symbols as in Fig. 5.

during exogenous heating only reached 26 °C. This indicates that less than half of the heat transfer from the thorax to the head during warm-up can be accounted for by passive heating.

During free flight, regulation of thoracic temperature was apparent over a range of T_a 's (Fig. 4). T_{th} varies from 38 to 44 °C at T_a 's from 17 to 32 °C. There was little change in T_{th} between T_a 's of 17–26. However, between T_a 's of 26–32, mean T_{th} increased by 4–5 °C (Fig. 4).

The abdominal temperature was directly related to T_a (Fig. 4). The difference between T_{ab} and T_a increased from about 2 to 5 °C as T_a varied from 17 to 32 °C. The increase in $(T_{ab} - T_a)$ at high T_a is consistent with the findings of Heinrich (1971*b*) that heat is actively transferred to the abdomen at high T_a .

The slope of head temperature in relation to T_a was essentially the same as that exhibited by the thorax and substantially different from that of the abdomen (Fig. 4). The difference between T_h and T_a decreased with increasing T_a , which suggests that the head temperature is regulated during flight.

Head cooling. Cooling constants (k) of the head were calculated from T_h v. time data from cooling experiments, with T_{th} both at the same value as T_a and maintained

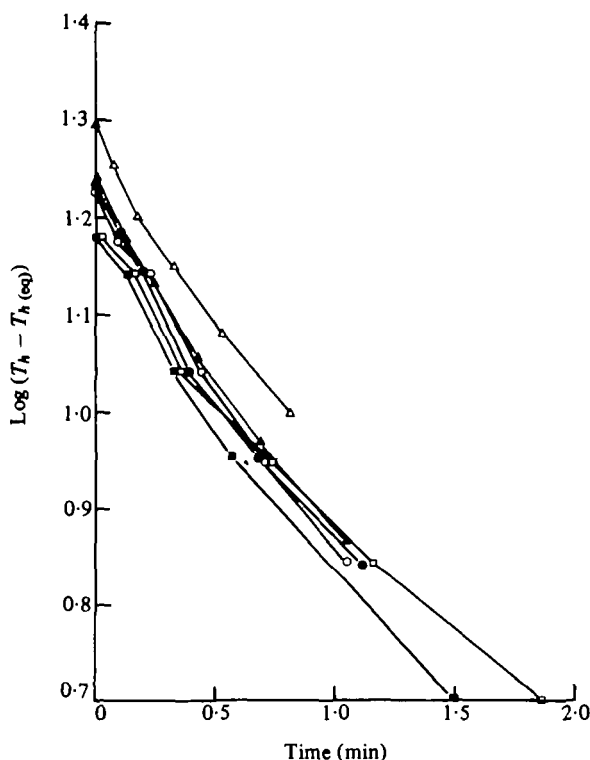


Fig. 7. Cooling rates of the head from the same experiments as Fig. 5, but with the driving force calculated as $T_h - T_{h(eq)}$.

constant at about 40°C . The cooling constant (k) represents 2.303 times the slope of the semi-log plot of $T_h - T_a$ v. time.

The mean cooling constant for the head with the thorax at ambient temperature (method 1) was $0.789 \text{ min}^{-1} \pm 0.058 \text{ S.D.}$ ($n = 6$). Although a slight curvilinearity is apparent, linear regressions of $\log (T_h - T_a)$ v. time for individual runs had correlation coefficients of at least 0.99 (Fig. 5), indicating passive cooling.

Cooling constants for the head obtained from cooling curves in which the thorax was maintained at about 40°C (Fig. 6) were $0.482 \text{ min}^{-1} \pm 0.092$ ($n = 6$) and the relations of $(T_h - T_a)$ versus time were more curvilinear than those obtained using method 1 (Fig. 5). Although the situation with the thorax at 40°C rather than at T_a more closely represents flight conditions, the driving force for heat loss from the head is $(T_h - T_{h(eq)})$ not $(T_h - T_a)$, because heat is constantly being passively transferred to the head (see Bakken, 1976). Using $T_{h(eq)}$ from separate experiments (Fig. 1), semi-log plots of $\log (T_h - T_{h(eq)})$ versus time (Fig. 7) yield straight lines ($r > 0.99$). Mean cooling constants were $0.76 \text{ min}^{-1} \pm 0.096$ ($n = 6$), similar to those obtained from method 1.

The calculated cooling constants can be used with more confidence since similar values were derived from two different methods. Therefore, the head conductance (C_h in $\text{mW/g } ^\circ\text{C}$) calculated from the mean of these cooling constants (k times the specific heat) is an accurate estimate of the actual conductance (see Table 1).

Table 1. *Data used to calculate heat exchange from various avenues (Figs. 8, 9, Table 2) during pre-flight warm-up and free flight in 2.2 g M. sexta*

(Conductance data are given for warm-up and free flight, since the former occurs essentially in still air while the latter occurs in moving air at least equivalent to the induced velocity.)

	Source		
Energy metabolism (flight) (mW)	424	Heinrich, 1971 <i>a</i> ; Casey, 1976 <i>b</i>	
Heat production (flight) (mW)	339	Assuming 80 % of metabolism	
Head conductance (warm-up) (mW/g °C)	44.0	Present study	
Thorax conductance (warm-up) (mW/g °C)	6.8	Heinrich, 1971 <i>a</i> ; Bartholomew & Epting, 1975	
Abdomen conductance (warm-up) (mW/g °C)	10.7	Casey, 1976 <i>a</i>	
Head conductance (flight)* (mW/g °C)	66.1	Present study	
Thorax conductance (flight)* (mW/g °C)	10.3	Bartholomew & Epting, 1975	
Abdomen conductance (flight) (mW/g °C)	16.2	Casey, 1976 <i>a</i>	
Mass (g)			
head	0.10	Present study	
thorax	0.57	Present study	
abdomen	1.40	Present study	
	T_a		
	16	21	30
Rate of warm-up (°C/min)	2.44	4.1	7.6
			Heinrich & Bartholomew, 1971
Relative humidity (%)	80	44	32
			Present study
$T_{th} - T_a$ (flight) (°C)	20.7	16.0	11.7
			Present study (fig. 5)
$T_h - T_a$ (flight) (°C)	13.8	9.2	4.1
			Present study
$T_{ab} - T_a$ (flight) (°C)	2.6	4.1	5.5
			Present study
Heat storage (thorax)† (mW)	80	178	274
			Heinrich & Bartholomew, 1971
Heat storage (head)† (mW)	8	12.6	18.5
			Present study

† Rate of warm-up \times mass \times specific heat (3.43 J/g °C).

* Assuming 50 % increase over still air value (see Heinrich, 1971; Casey, 1976*a*, 1980).

Heat exchange. In a free-flying *M. sexta*, heat is lost at different rates from a variety of sites on the body. Therefore, a heat budget is useful for estimating the relative importance of these various avenues of heat loss. Heat losses from head, thorax, and abdomen and via respiratory evaporation during free flight over a range of T_a 's are given in Fig. 8. Head, thorax and abdominal heat losses were calculated by multiplying the conductance of the specific body part by its mass and its temperature excess over ambient (Table 1). Heat loss due to respiratory evaporation was calculated at the temperature and pressure of the working thorax (Weis Fogh, 1967; Casey, 1976*b*).

Heat loss from the head is a very significant component of the total heat production at low T_a (Fig. 8); more than $1\frac{1}{2}$ times either evaporative or abdominal heat loss. However, as T_a increases, the contribution of the head to the total heat loss decreases to less than one half the evaporative heat loss and less than one fourth the abdominal heat loss. Since heat loss from both the head and the thorax shows a similar relation to T_a (Fig. 8), it is apparent that the head does not operate as a thermal window in flight for stabilizing T_{th} .

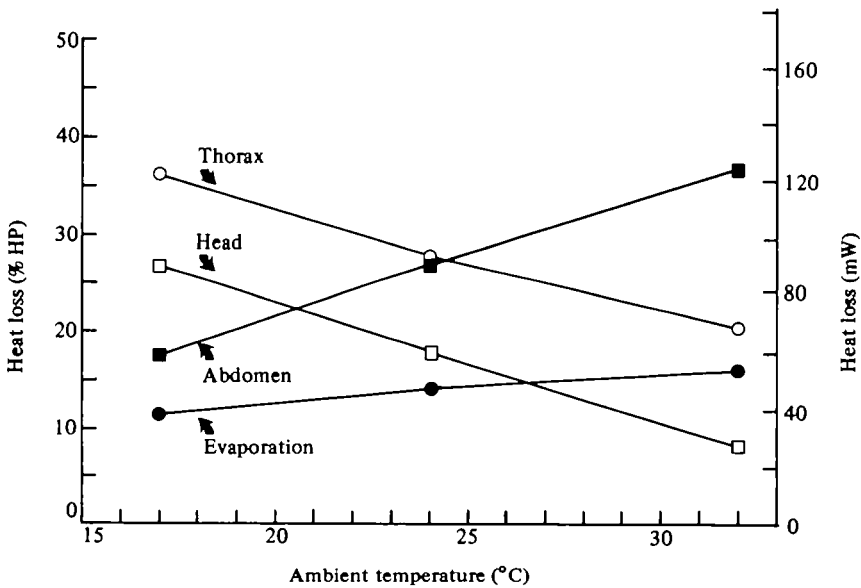


Fig. 8. Calculated rates of heat loss of the thorax, head, abdomen, and respiratory evaporation in mW and % total heat production (Table 1) during free flight at T_a 's of 17, 24, and 32 °C.

In contrast, although the temperature of the abdomen is only slightly elevated above T_a (Fig. 4), due to its large mass, total heat loss from the abdomen accounts for about 17–37 % of the total heat production proceeding from low to high T_a . At most T_a 's, heat loss from the abdomen exceeds that from the head (fig. 8) and at high T_a it also exceeds thoracic heat loss.

The thermal constraints during warm-up are fundamentally different than those present during flight. For example, it is well known that sphinx moths warm their thorax as rapidly as possible (Heinrich & Bartholomew, 1971; Heinrich & Casey, 1973) and that T_{ab} increases only about 1 °C above T_a . For the purposes of calculation, we assume a 1 °C increase in T_{ab} , regardless of T_a (see Heinrich & Bartholomew, 1971). We also assume that evaporation during warm-up is 10 % of the total heat production calculated from other sources and is independent of T_a . This is probably a conservative estimate, since rates of evaporative heat loss during flight range from 12 to 16 % of the total heat loss (Fig. 8).

Rates of heat storage (see Table 1) and heat loss (calculated as above for flight data) during warm-up at $T_a = 21$ °C are given in Fig. 9. Heat storage in the thorax at this T_a amounted to 54 % of the total heat production (Table 2), slightly less than predicted from the regression of Bartholomew, Vleck & Vleck (1981). The heat stored in the head, calculated by assuming a linear increase of T_h with time (Fig. 3), was only about 10 % of the heat stored in the thorax (Table 2). Although rates of warm-up are generally similar for head and thorax (see Fig. 3) the mass of the head is substantially less, which reduces the total input of heat needed to increase T_h . Heat storage in the abdomen is generally considered to be negligible during warm-up in insects (Heinrich & Bartholomew, 1971; Heinrich, 1975; May, 1976; Casey *et al.* 1981). However,

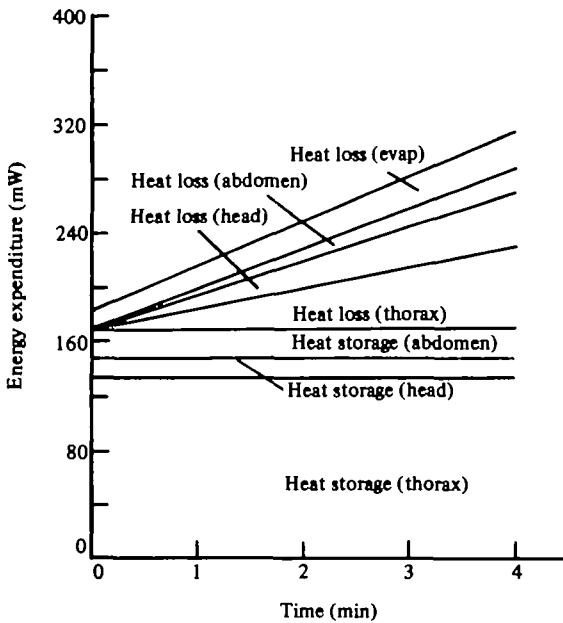


Fig. 9. Calculated rates of heat storage and heat loss of the thorax, head, abdomen, and due to respiratory evaporation plotted against time during pre-flight warm-up at $T_a = 21\text{ }^{\circ}\text{C}$.

Table 2. *Components of total energy expenditure for a 2.2 g M. sexta during pre-flight warm-up at several T_a 's*

(Instantaneous rates of energy expenditure (Fig. 9) are integrated over the entire duration of warm-up.)

Heat production (J)	$16\text{ }^{\circ}\text{C}$	$21\text{ }^{\circ}\text{C}$	$30\text{ }^{\circ}\text{C}$
Thorax-storage loss	40.93 (42.6)	32.28 (53.7)	17.36 (59.9)
Thorax loss	20.75 (21.6)	7.68 (12.8)	1.20 (4.1)
Head-storage loss	3.97 (4.1)	3.18 (5.3)	1.71 (5.9)
Head loss	13.04 (13.6)	4.90 (8.1)	0.76 (2.6)
Abdomen-storage loss	4.78 (5.0)	4.80 (8.0)	4.80 (16.6)
Abdomen loss	3.82 (4.0)	1.80 (3.0)	0.52 (1.8)
Evaporative loss	8.73 (9.1)	5.48 (9.1)	2.64 (9.1)
Total cost	96.02 (100)	60.12 (100)	28.99 (100)

our calculations indicate that in *M. sexta*, abdominal heat storage during warm-up ranges from 5 to 15 % of the total heat production (Table 2). Heat loss during warm-up is greatest in the thorax, followed by the head and abdomen respectively (Fig. 9).

As shown in Table 2, the total cost of warm-up is inversely related to ambient temperature, even though rates of heat production for a given T_{th} should be the same, regardless of T_a (Heinrich & Bartholomew, 1971; Casey *et al.* 1981). This is reasonable, since duration of warm-up is also inversely related to T_a (Table 1), and total cost of warm-up is calculated as the area under the energy expenditure *v.* time plot.

Temperature fluctuations. External heating of the thorax in live moths led to two different sets of results. For some moths, while T_{th} rose, the head temperature did

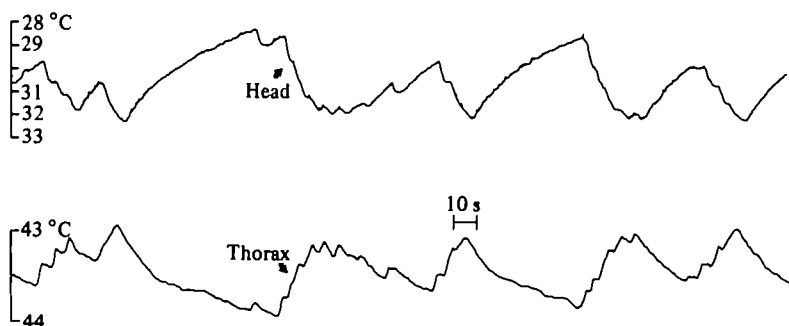


Fig. 10. Sample record from an exogenous heating experiment on a live moth showing head and thorax temperature fluctuations. Downward deflection = increased temperature. Temperature fluctuations of head and thorax $\approx 2^{\circ}\text{C}$ (see Fig. 12).

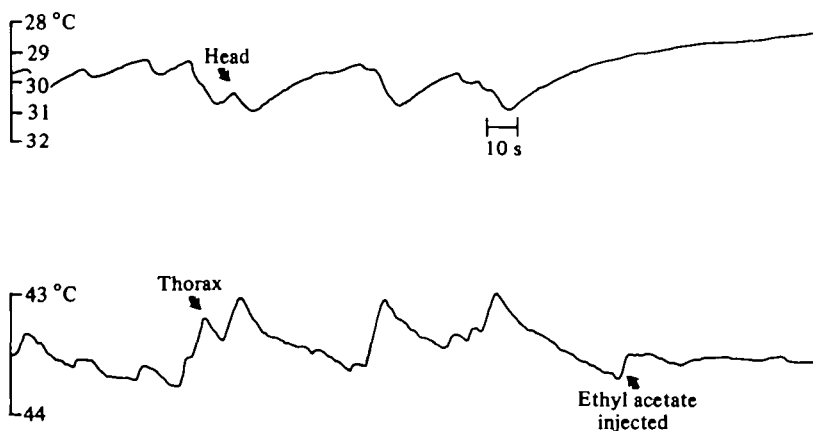


Fig. 11. Sample record of head and thorax temperatures of a moth killed with 0.05 c.c. injection of ethyl acetate during an exogenous heating experiment. Downward deflection = increase in temperature.

not rise much above what can be accounted for by passive heating. When T_{th} reached 40°C , the head usually stayed below 27°C . However, as the thorax in some moths was heated, the head temperature rose significantly higher (to about 31°C), and as T_{th} approached 40°C , cyclic temperature fluctuations were recorded in both head and thorax. The changes in T_h and T_{th} occurred simultaneously and in opposite directions (Fig. 10). As thorax temperature decreased slightly, T_h increased slightly. Then T_{th} would rise again by the same amount and the T_h would correspondingly decrease by the same amount. This cyclic pattern was recorded for over 15 min. Injection of 0.05 c.c. ethyl acetate into the abdomen between the intersegmental membranes caused this pattern to cease. The head then cooled rapidly to the equilibrium temperature and the thorax stabilized at a temperature higher than the temperature reached during the cycling pattern (Fig. 11).

In one experiment, the pulsations of the thoracic heart were recorded simultaneously with head and thorax temperatures. Heart rate at the beginning of the run was at a regular pace of about 32 beats/min. Immediately prior to the onset of the cyclic

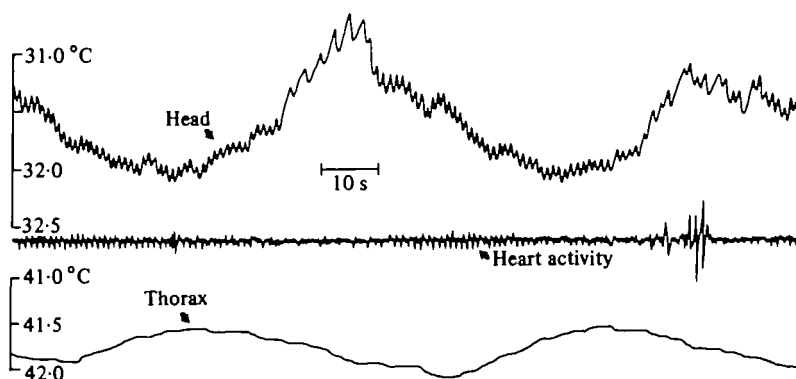


Fig. 12. Sample record from an exogenous heating experiment on a live moth illustrating head and thorax temperature fluctuations and corresponding heart activity. Downward deflection = increase in temperature.

temperature fluctuations, the heart rate pattern changed. As T_{th} increased and T_h decreased in the first half of the cycle, the heart rate became irregular. Just before the other half of the cycle began, the heart rate returned to a regular pattern of about 30 beats/min, which continued as the T_{th} decreased and T_h increased. The heart beat then became irregular again and the cycle repeated. This change in heart rate pattern continued during every cycle (Fig. 12).

As well as these temperature fluctuations, the trace also showed smaller temperature fluctuations in the head (less than 0.1°C) that exactly corresponded to heart rate (Fig. 12). When the heart rate became irregular during each cycle, these temperature fluctuations also became irregular.

DISCUSSION

Head temperature during warm-up. The conductance of the head is five times that of the thorax (Table 1), yet T_h is closely coupled to T_{th} during warm-up (Fig. 3). There must be large amounts of heat entering the head to compensate for this heat loss. Heat comes primarily from transfer to the head of heat produced by the active flight muscles in the thorax. Since passive transfer only accounts for about 45% of the heat in the head, some physiological transfer must also be present. This transfer could occur via blood in the dorsal vessel which empties into the head after passing through the thorax.

As the head temperature increases with T_{th} , the driving force for heat loss from the head also increases. For T_h to keep increasing throughout warm-up, the amount of heat transferred must also increase continuously. The pulsation frequency of the aorta in the thorax is directly related to T_{th} during warm-up in the tent caterpillar moth, *Malacosoma americana* (Casey *et al.* 1981). If pulsation frequency in *M. sexta* shows a similar relationship to T_{th} , the increase in pulsation would provide the added heat that would compensate for the greater heat loss and allow the head temperature to stay coupled with T_{th} .

In warm-up, it should be advantageous to retain heat in the thorax and increase

th as rapidly as possible (see Bartholomew & Heinrich, 1973). It seems counter-productive, then, to transfer heat into the head during warm-up because that would slow the rate of warm-up of the thorax. However, such a pattern is explicable if the moth is attempting to achieve some minimal head temperature prior to take-off. Since the contraction of the flight muscles is controlled by nervous impulses and this neural output depends on temperature (Kammer, 1968), it may be necessary to keep the neural control centres in the head warm in order for effective flight to occur. Since warm-up is a preparation for flight, active transfer of heat to the head during warm-up suggests that the head temperature may be regulated during flight.

Head temperature during flight. The only other data available on the head temperature of insects during flight are from a study on honeybees (Heinrich, 1980*a, b*). At high T_a , honeybees transferred heat from the thorax to the head via blood circulation. Then, most of this heat was lost from the head due to evaporation. This serves as a mechanism to prevent the thorax from overheating during flight at high T_a . Honeybees are unable to use the abdomen as a site of controlled heat loss, due to a specialized counter current exchanger at the junction of the thorax and abdomen (Heinrich, 1980*b*). Unlike honeybees, *M. sexta* uses the abdomen as a thermal window during flight (Heinrich, 1971*b*). The abdomen is well suited as an area for heat loss from the thorax, because small changes in abdominal temperature result in significant changes in heat loss (Figs. 4, 8). Therefore, the moths may not need to rely on the head as a thermal window.

Head temperature data during flight also suggest that the head is not used as a thermal window. If the head operated as a thermal window, $(T_h - T_a)$ should increase with increasing T_a as occurs in the abdomen (Fig. 4), in order to counteract the reduction in passive heat loss from the thorax. However, like $(T_{th} - T_a)$, the temperature difference for the head decreases with increasing T_a (Fig. 4). These data indicate that the head temperature is regulated. This interpretation is consistent with the observation that large quantities of heat are transferred to the head during warm-up.

Heat exchange. Although the heat budgets (Figs. 8, 9; Table 2) derived for warm-up and flight are crude, they provide a quantitative first approximation of the significance of the head in the thermal balance of moths during warm-up and free flight. As shown in Fig. 8, the major portion of energy expended during warm-up results in thoracic heat storage. Since the function of warm-up is to elevate the flight muscles above a minimum flight temperature, the larger the proportion of heat allocated to heat storage, the more rapidly the moth will warm. Because of high head conductance (Table 1), heat loss and storage of the head account for a small, although significant, portion of total heat production. As T_a declines, heat loss from the head increases, due to larger differences between T_h and T_a (Fig. 2). Since about half of the heat transfer between the thorax and head is active (compare Figs. 1, 3), and can be abolished (Figs. 10, 11), it appears that the benefits of elevating head temperature outweigh the energetic costs involved.

Abdominal heat storage and loss are of similar magnitude to that of the head, but they may be overestimated because we assume an average abdominal temperature increase of 1 °C during warm-up (Heinrich & Bartholomew, 1971 their Fig. 10). Data are not available for the temperatures of different locations in the abdomen of sphinx

moths during warm-up. If, as in dragonflies, there can be large differences in temperature between different sites in the abdomen (Heinrich & Casey, 1978), a single measurement of abdominal temperature may not provide sufficient information for calculating heat storage or loss.

The cost of maintaining a regulated head temperature during flight is energetically expensive at low T_a 's, with heat loss from the head accounting for about 25 % of all heat loss at $T_a = 17^\circ\text{C}$ (Fig. 8). At $T_a = 32^\circ\text{C}$, however, less than 10 % of all heat loss occurs from the head. As a consequence of quantifying heat exchange from the head, our heat budget is a better representation of the fate of energy in a flying moth than a previous budget derived for the sphinx moth, *Hyles lineata* (Casey, 1976a). Our calculations account for 92, 87 and 81 % of the total heat production during flight at T_a 's of 17, 24, and 32°C , while the previous budget could only account for 69, 64, and 63 % of total heat production for a 1.5 g *H. lineata* flying at similar T_a 's. It is significant that in neither of these budgets does heat production equal heat loss at the highest T_a 's. Either one of the avenues of heat exchange is underestimated by our approach or an additional site of regulation (see below) has not been examined (see Casey, 1976b).

Mechanism of heat transfer. When the thorax of a live moth is heated to 40°C or more, the cyclic fluctuations of the head and thorax temperature begin (Fig. 10). There is no evidence of this cycling at lower T_{th} . Since the heat input by the lamp is constant, when T_{th} decreases and this is followed immediately by an increase in T_h , it is obvious that active heat transfer is involved. Conversely, when T_{th} increases and T_h decreases, this heat transfer mechanism must have been deactivated. The mechanism whereby heat transfer can be controlled is via blood circulation. As shown in Fig. 12, not only are temperature fluctuations of the head exactly coupled with heart beats, but the overall activity of the heart correlates with observed temperature cycles.

The larger temperature fluctuations resulting from changes in blood circulation patterns (Figs. 10, 11) seem to serve a stabilizing function when the thorax approaches heat stress conditions. At present, we cannot determine whether this type of mechanism is at work at the higher T_{th} 's in flight, or whether it is useful under resting conditions.

The circulation patterns described here for *M. sexta* cannot explain the simultaneous reduction of heat loss from the head at high T_a , and the increase in abdominal heat loss at high T_a during flight. A more complicated circulatory pattern may be involved. It is of interest that the sphingid, *Pholus achemon*, exudes a drop of liquid from its proboscis when overheated (Adams & Heath, 1964). If such a mechanism occurs in sphingids during flight at high T_a , evaporative cooling could keep head temperature low and at the same time provide an additional mechanism for dissipating heat transferred away from the thorax, as in honeybees (Heinrich, 1980a). However, we did not observe regurgitated fluid, either in moths flying at high T_a , or in moths which were externally heated. Therefore, an evaluation of the role of an active mechanism of evaporation in flying sphinx moths must await the acquisition of further data.

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