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# PHYSIOLOGY AND ENERGETICS OF PRE-FLIGHT WARM-UP IN THE EASTERN TENT CATERPILLAR MOTH *MALACOSOMA AMERICANUM*

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## SUMMARY

Thoracic temperature ($T_{\text{th}}$) during pre-flight warm-up increased linearly with time at all air temperatures ($T_a$). The rate of pre-flight warm-up increased from 3·3 to 12·7 °C/min between $T_a$'s of 14 and 28 °C. Head temperature remained within a few °C of $T_{\text{th}}$ during warm-up, while ventral abdominal temperature remained within a few °C of $T_a$. Pulsation rate of the dorsal vessel in the thorax increased directly with thoracic temperature. Wing-stroke frequency ($n$) varied from 15 $s^{-1}$ at $T_{\text{th}} = 16$ °C to 58 $s^{-1}$ at $T_{\text{th}} = 40$ °C and was similar at any given $T_{\text{th}}$ between $T_a$'s of 14 and 28 °C. While stroke amplitude varied significantly between warm-up and tethered flight, stroke frequency was similar for the two activities in the same $T_{\text{th}}$ range. Calculated rates of heat production were tightly coupled to $T_{\text{th}}$ and did not vary with $T_a$. The change in heat production during warm-up was dependent entirely on changes in frequency of muscle contraction. Stroke work was constant at 0·68 mW between $T_{\text{th}}$ of 15 and 40 °C.

## INTRODUCTION

Insects from a variety of taxa are incapable of immediate flight when muscle temperatures approximate ambient temperatures, because the muscle cannot generate sufficient energy for the wings to support the body weight (Heinrich, 1974). The wing-stroke frequencies of many insects are strongly temperature-dependent. At low thoracic temperatures, the wings are unable to beat rapidly enough to provide the necessary lift, and the work of antagonistic muscles is largely done against each other resulting in heat production rather than useful work for driving the wings (Neville & Weis-Fogh, 1963). Consequently, prior to flight, the insects increase their muscle temperature by a process analogous to shivering in which the normally antagonistic muscles contract in almost simultaneous fashion. This behaviour is well known and has been studied extensively in moths (Dotterweigh, 1928; Krogh & Zeuthen, 1941; Sotavolta, 1954; Dorsett, 1962; Heath & Adams, 1967; Kammer, 1968, 1972; Heinrich & Bartholomew, 1971; McCrea & Heath, 1971; Heinrich & Casey, 1973), bees (Heinrich, 1975, 1976; Kammer & Heinrich, 1972, 1974), beetles

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(Machin, Pringler, Tamasige, 1962; Bartholomew & Casey, 1977) and dragonflies (May, 1976*b*, 1979).

In most cases, studies of pre-flight warm-up have been conducted on relatively large insect species (300–3000 mg). Small size may limit the capacity of insects to warm-up, because rates of heat loss are inversely related to body size (Bartholomew & Epting, 1975; May, 1976*a*). Moths are particularly interesting because they are synchronous fliers; that is, there is a constant phase relationship between impulses from the nervous system and contraction of flight muscles (Kammer, 1968). A similar interrelation between flight-muscle contraction and action potentials occurs during warm-up (Kammer, 1970). Therefore, studies of heat production, wing-beat frequency and thoracic temperature during warm-up may provide important information about the thermal sensitivity and neural patterns controlling a behaviour pattern of obvious adaptive value. In addition, an inverse relationship between frequency of a variety of physiological variables and body size also makes the study of small insects desirable.

The present study examines energetics, regional body temperatures, and wing-stroke frequencies of the Eastern tent caterpillar moth, *Malacosoma americanum* Fabr. (Lepidoptera: Lasiocampidae). This species is of particular interest, because despite its small size (mean body mass = 0·088 g), it regulates $T_{\mathrm{th}}$ during flight, is well insulated, and is an accomplished flier (Casey, 1981). Except for the total cost of warm-up in several lasiocampids (Bartholomew & Casey, 1978), there are no data on the physiology of warm-up in this family of moths.

## MATERIAL AND METHODS

*Animals.* Male moths were collected in the Hutcheson Memorial Forest (Somerset County, New Jersey) by attracting them to a 15 W ultraviolet fluorescent lamp which hung in front of a white bed-sheet secured to a tree limb. The animals could be aged by the degree of wear on the lateral borders of the forewings and by the condition of thoracic insulation. Only 'fresh' moths whose wings were intact and had thoracic insulation covering the entire dorsal surface were collected. The moths were placed in individual plastic coulter counter vials (volume = 35 ml) for transport to the laboratory. The moths were stored in a refrigerator ($T_a$ = 4 °C) between the time of capture and experimentation. All experiments were conducted within 24 h of capture.

*Body temperature.* Thoracic temperature was measured by inserting a 44-gauge copper–constantan thermocouple into the dorsal thorax. A small area of fur was removed with micro-forceps and a hole in the dorsal thorax was made with a micro-surgical needle. The thoracic pile of *M. americanum* was so extensive (see Casey, 1981) that it easily covered the denuded section after the thermocouple was implanted. Thoracic and ambient temperatures were read to the nearest 0·2 °C on a Bailey Bat 4 laboratory thermometer. Thoracic temperature change during warm-up was measured at either 6 or 10 s intervals by connecting the output of the thermometer to a Hewlett-Packard multichannel recording digital multimeter. Alternatively, thoracic temperature was continuously recorded by attaching the output of the laboratory thermometer to the servo-channel (150 mm full-scale deflexion) of a Gilson polygraph.

Anaesthesia was not used during thermocouple and electrode implantation. The moths were placed in a plastic box filled with crushed ice. Thoracic temperature of moths in the box was below 10 °C during implantation, and under most circumstances, all surgical procedures could be performed without causing the moths to warm-up. The moths were left undisturbed for a few minutes following implantation of thermocouples or electrodes. They were then transferred to a constantan temperature-cabinet.

As $T_{\text{th}}$ of the moths approached ambient temperature due to passive warming, they often became active. The activity usually consisted of walking within the confines of the implanted leads and sporadically fluttering their wings prior to exhibiting a typical warm-up behaviour pattern (e.g. Dorsett, 1962). If the moths remained quiescent after $T_{\text{th}} = T_a$ they were gently prodded or pinched with forceps, which caused them to initiate pre-flight warm-up. In several experiments, thoracic insulation was removed by lightly rubbing the surface of the thorax with laboratory tissue or forceps. Rates of warm-up were measured in these moths as detailed above.

Head and ventral abdominal temperatures were measured using a probe consisting of 44-gauge copper–constantan thermocouple threaded into a 1 $\mu$l glass capillary tube which was drawn out to a fine point in a flame. The thermocouple junction was glued to the tip of the probe with a drop of quick-drying liquid glue. The time constant for the probe was less than 1 s. A strip of foam rubber (1·5 cm thick) surrounded the capillary tube to prevent conduction of heat from the fingertips. Moths were seized by the distal portion of the forewings at various durations after the initiation of pre-flight warm-up. While the moth was held upside down, the probe was thrust up from the ventral posterior aspect beneath the labium into the head. The force of the probe moved the head away from the thorax, thereby preventing an inadvertant measurement of thoracic temperature. Immediately after the temperature of the head was measured, the thorax and ventral abdominal temperatures were measured. An entire measurement sequence took place in about 5 s.

*Wing-beat frequency.* Wing-beat frequency ($n$) was measured by implanting 44-gauge constantan wires into two holes in the thorax on either side of the dorsal midline. The wires were attached to an impedance converter. The leads were held in place by coagulated haemolymph. A 44-gauge Cu–Cn thermocouple was also implanted in one of the two holes for continuous measurement of $T_{\text{th}}$ during frequency measurement. Both thermocouple and impedance electrodes were attached to a polygraph. Pulsation frequency of the aorta in the thorax was measured using the same apparatus (see Heinrich & Bartholomew, 1971).

After moths achieved a certain $T_{\text{th}}$, they initiated flight. They then flew for variable periods while tethered by the electrodes and thermocouple. Consequently, we measured $T_{\text{th}}$ and $n$ immediately after take-off. These data are referred to as tethered flight.

*Oxygen consumption.* Total oxygen consumption was measured by placing the animals in small, airtight respirometers. After the warm-up period (timed by stopwatch) was completed, 60 ml air samples were obtained using a syringe through a 3-way stopcock attached to the respirometer. The air samples were injected via [illegible]usion pump through a column of drierite into a Beckman E-2 rapid response $O_2$

analyzer at a flow rate of 54 ml/min. Relative humidity in the room was measured using a Hydrodynamics humidity sensor. Rates of oxygen consumption ($\dot{V}_{O_2}$) were calculated by the equation of Bartholomew & Casey (1978). All values were converted to STPD.

Usually, little harassment was necessary to cause the moths to initiate warm-up after they were placed in the respirometer. In some cases, however, the moths were active for undetermined periods prior to measurement. This undoubtedly had the effect of increasing their thoracic temperature. Unfortunately, the design of our system did not allow us to measure $T_{th}$ during measurement of $\dot{V}_{O_2}$. However, in some cases we can interpret these data based on information for the duration and rate of pre-flight warm-up from other experiments during which we monitored $T_{th}$ continuously throughout the experiment.

*Heat production.* Heat production was calculated from data for $T_{th}$ and thoracic conductance ($C_{th}$). Instantaneous rates of heat production represent the sum of heat storage obtained from warm-up data assuming a specific heat for thoracic tissue of 3·43 J/g °C, and the rate of heat loss calculated as $C_{th}$ ($T_{th} - T_a$) (see Heinrich & Bartholomew, 1971; May, 1976*a*). Thoracic conductance was obtained from cooling curves of dead moths in a small wind-tunnel (see Casey, 1981, for details). $C_{th}$ represents the thoracic cooling constant (2·303$X$ slope of semi-log plot of $T_{th} - T_a$ *v.* time) multiplied by the specific heat. Total heat production was calculated from oxygen consumption data, assuming 1 ml $O_2$ consumed = 20·09 J. Total heat production was also calculated by integrating the relation of calculated heat production based on heat storage and heat loss *v.* duration of warm-up (see Heinrich, 1975).

## RESULTS

*Body temperatures.* At $T_a$ = 22 and 28 °C, thoracic temperature increased linearly with time. Correlation coefficient for individual measurements of the linear regression of $T_{th}$ *v.* time were at least equal to 0·96. At $T_a$ = 14, however, two rather distinct patterns of warm-up were exhibited by different moths. Thoracic temperature could increase either linearly or in an exponential fashion. The latter pattern was unusual and was only observed in two moths. We could detect no difference in the moths which would account for this difference in rate of warm-up. Only experiments in which linear rates of thoracic temperature increase were observed, were used to characterize the rate of warm-up in relation to ambient temperature.

Rates of warm-up were linearly related to $T_a$ (Fig. 1). Variability in rates of pre-flight warm-up were similar at any given $T_a$ (Fig. 1). Mean warm-up rates increased from 3·3 °C/min at $T_a$ = 14 °C to 12·8 °C/min at $T_a$ = 28 °C. Linear regression of mean warm-up rates were highly correlated with $T_a$ ($r^2$ = 0·98). The relation extrapolates to warm-up rate of 0 at $T_a$ = 9 °C. This is consistent with our observation that moths which were chilled to $T_{th}$ less than 10 °C were incapable of initiating pre-flight warm-up.

Thoracic insulation had a significant effect on $T_{th}$ during warm-up. At $T_a$ = 22 °C, the mean rate of warm-up of four moths with thoracic insulation removed was 6·2 °C/min (± 2·2 S.D.), 31 % lower than those in intact animals at the same $T$ However, these moths did not achieve take-off temperature and stopped warm- at $T_{th}$ between 6 and 12·5 °C above $T_a$. Independent experiments indicate that thoracic

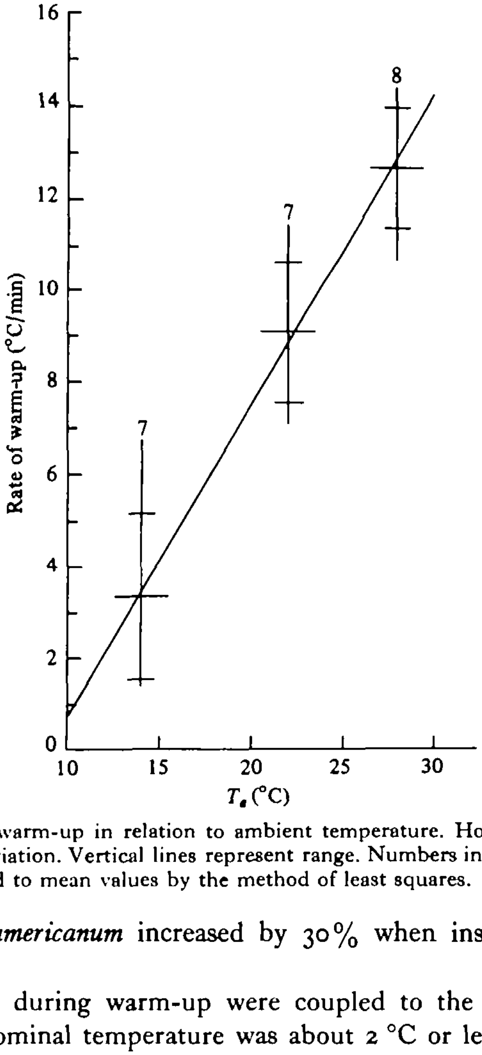

Fig. 1. The rate of warm-up in relation to ambient temperature. Horizontal lines indicate means ± standard deviation. Vertical lines represent range. Numbers indicate the sample size. Diagonal line is fitted to mean values by the method of least squares.

conductance in *M. americanum* increased by 30% when insulation was removed (Casey, 1981).

Head temperatures during warm-up were coupled to the thoracic temperature (Fig. 2). Ventral abdominal temperature was about 2 °C or less above the air temperature throughout the warm-up period, and therefore independent of thoracic temperature (Fig. 3). These data suggest that circulation between thorax and abdomen is interrupted during warm-up as in other moths (Heinrich & Bartholomew, 1971).

Take-off temperatures of the moths were not significantly correlated with ambient temperature at the 5% level (Student's *t* test) and varied from about 38 to 39 °C between $T_a$'s of 14 and 28 °C (Fig. 3).

*Wing-beat frequency.* The wing-beat frequency ($n$) was tightly coupled to the thoracic temperature (Fig. 4). Between $T_a$ of 14 and 28 °C, the relation of $n$ to $T_{th}$ was essentially the same (Fig. 5). The slightly lower values for $n$ at any $T_{th}$ for moths at $T_a$ = 28 °C may be due to the higher mean body mass of this group ($m$ = 0·098 g, compared with $m$ = 0·080 g at $T_a$ = 22, and 0·078 g at $T_a$ = 14 °C). The relation of $n$ to $T_{th}$ for all data, regardless of $T_a$, is:

$$Y = 1{\cdot}88X - 13{\cdot}89 \quad (r = 0{\cdot}98), \qquad (1)$$

where $Y = n$ ($s^{-1}$) and $X = T_{th}$ (°C).

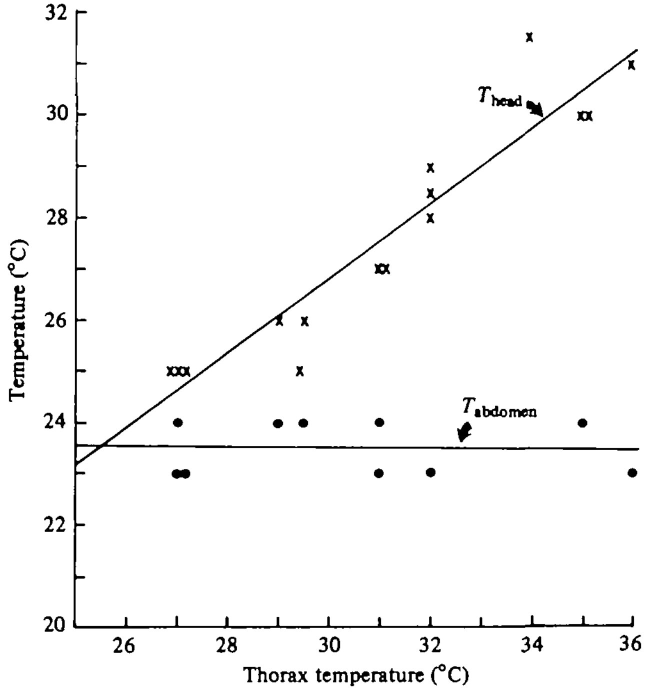

Fig. 2. Head and ventral abdominal temperature in relation to thoracic temperature during warm-up at $T_a = 22$ °C. Each point represents a separate individual. Lines are fitted to the data by least squares.

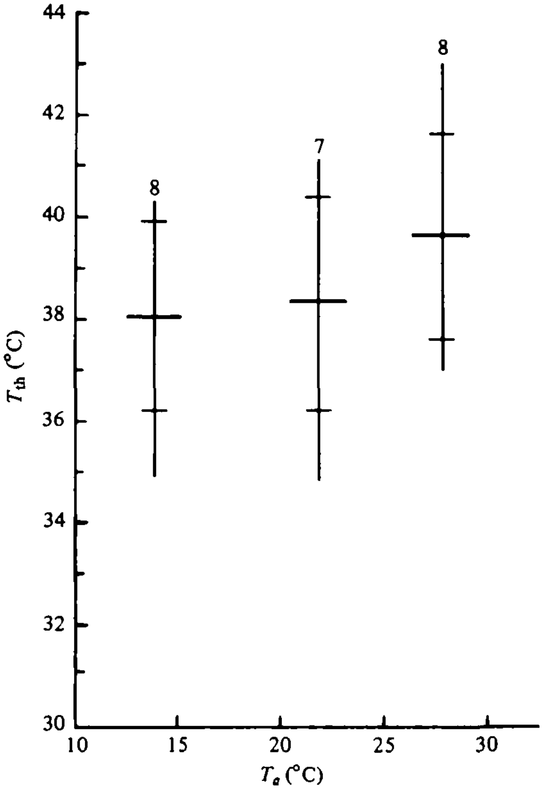

Fig. 3. Thoracic temperature of moths at take-off in relation to ambient temperature.

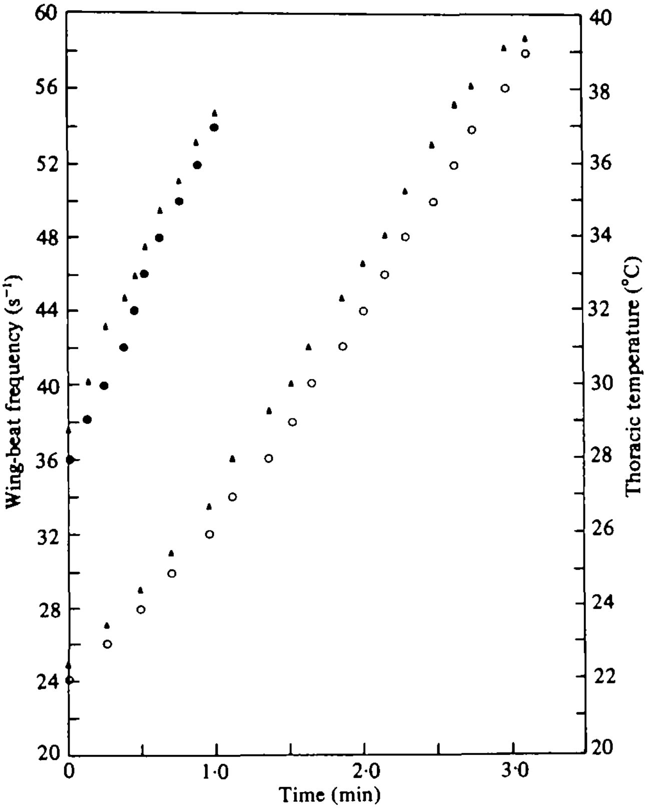

Fig. 4. Time course of wing-stroke frequency (triangles) and thoracic temperature (circles) in two moths during warm-up at $T_a$'s of 22 °C (open symbols) and 28 °C (closed symbols).

The wing-beat frequency of moths in tethered flight immediately after take-off was 55·9 $s^{-1}$ (± 3·7 s.d., $N = 12$). Thoracic temperature of these moths was 38·8 °C (± 1·6). This is similar to the value for *n* predicted in equation 1 which indicates an *n* of 59 $s^{-1}$ for the moths at $T_{th} = 38{\cdot}8$ °C. In addition, these values are similar to *n* of moths measured after 2 min of continuous free flight ($\bar{x} = 58$ $s^{-1}$; $N = 17$; Casey, 1981).

*Oxygen consumption.* Total oxygen consumption during warm-up (Fig. 6) is inversely related to $T_a$, varying from about 0·07 to 0·19 ml $O_2$. The mean value for total $O_2$ consumed during warm-up at $T_a = 22$ °C is essentially the same as that predicted for a 0·09 g moth based on the regression of Bartholomew & Casey (1978).

*Heat production.* Cooling constants of the thorax (*K*) were inversely related to body mass and described by the equation

$$Y = 0{\cdot}744X - 1{\cdot}043 \quad (r = 0{\cdot}85, N = 7), \qquad (2)$$

where $Y = \log K\,(\mathrm{min}^{-1})$ and $X = \log$ body mass (g). These values were used to calculate thoracic conductance.

Calculated heat production, based on rates of warm-up and thoracic conductance, creased linearly with increasing thoracic temperatures during warm-up. The

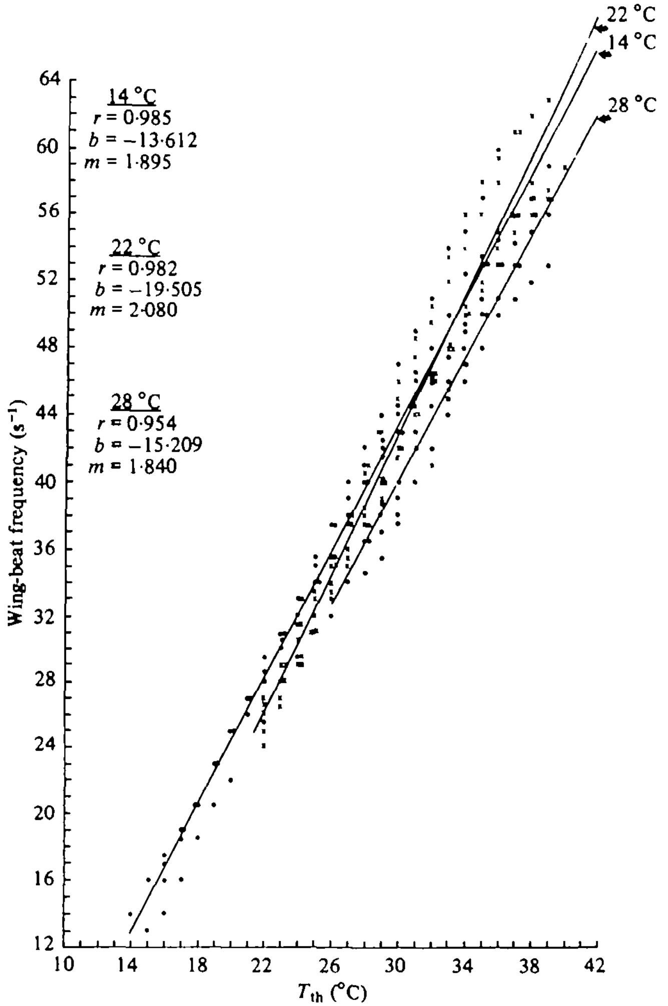

Fig. 5. The relation of wing-stroke frequency to thoracic temperature at 14 (●), 22 (×) and 28 °C (○). Each point represents a separate individual at any given $T_{th}$. Data for regression equations (upper left) describe the lines fitted to the data for various values of $T_a$.

relations of heat production for $T_a$'s of 14 °C, 22 °C and 28 °C (Fig. 7) are not significantly different. The equation for all data, regardless of $T_a$, is:

$$Y = 1{\cdot}23X - 8{\cdot}69 \quad (r = 0{\cdot}913), \tag{3}$$

where $Y$ = heat production (mW) and $X$ = $T_{th}$ (°C).

Heat production at any instant during warm-up is a function of both the wing-stroke frequency and the work done per wing stroke. Dividing calculated heat production at a given $T_{th}$ by $n$ at the same $T_{th}$ yields the stroke work. In *M. americanum*, stroke work is independent of thoracic temperature and amounts to 0·66–0·68 mJ/stroke at all $T_{th}$ between 15 and 40 °C. Specific stroke work during warm-up based on thoracic mass of 0·0385 g (Casey, 1981) equals 17·3 mJ $(\mathrm{g_{th}.stroke})^{-1}$. Therefore, the change in heat production during warm-up can be accounted for entirely by change in wing-stroke frequency.

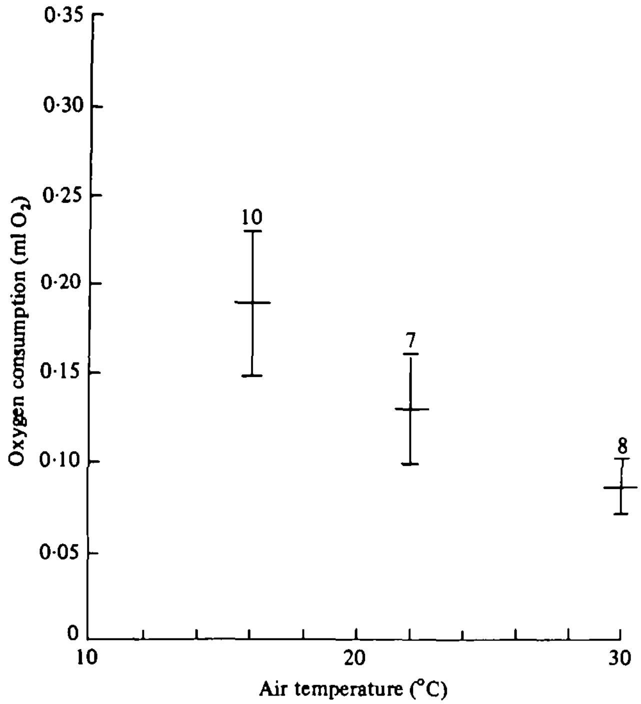

Fig. 6. The relation of total oxygen consumption throughout the entire warm-up period to ambient temperature. Symbols as in Fig. 5.

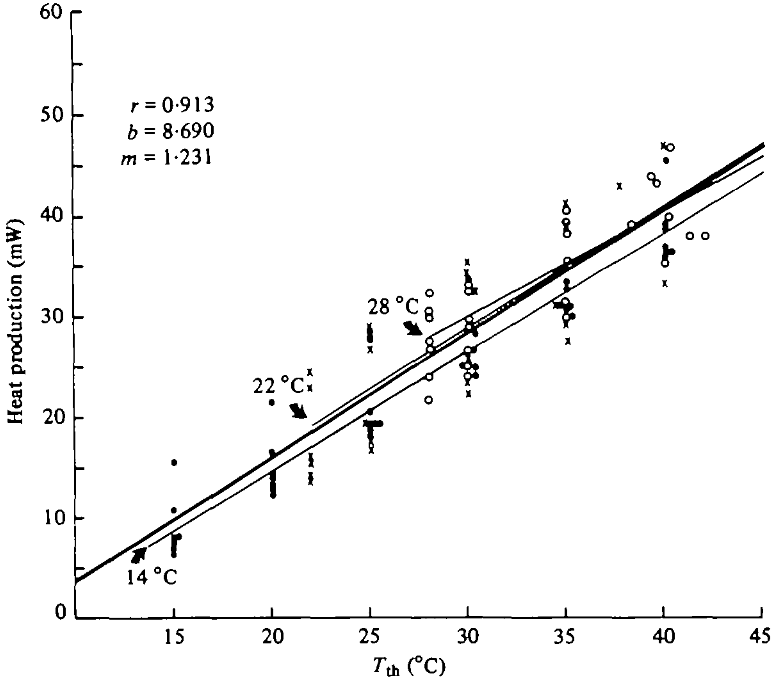

Fig. 7. The relation of calculated heat production to thoracic temperature at $T_a$ of 14 (●), 22 (×) and 28 °C (○). Each point represents a separate individual at any given $T_{th}$. Thin lines are fitted to data for each ambient temperature and the thick line describes the relation of heat production to $T_{th}$ regardless of ambient temperature.

Table 1. *Total heat production during warm-up at several ambient temperatures calculated from (a) total oxygen consumption and from (b) rates of warm-up and thoracic conductance*

(Numbers in parentheses = standard deviation.)

| (a) | | | | (b) | | | |
|---|---|---|---|---|---|---|---|
| $T_a$ | Heat production (J) | Duration (min) | $N$ | $T_a$ | Heat production (J) | Duration (min) | $N$ |
| 16 | 3·81 (0·81) | 2·04 (0·45) | 10 | 14 | 9·32 (2·13) | 7·69 (2·8) | 6 |
| 22 | 2·62 (0·63) | 1·36 (0·12) | 7 | 22 | 3·29 (1·00) | 1·69 (0·21) | 7 |
| 30 | 1·75 (0·31) | 0·52 (0·05) | 8 | 28 | 2·01 (0·28) | 0·98 (0·18) | 8 |

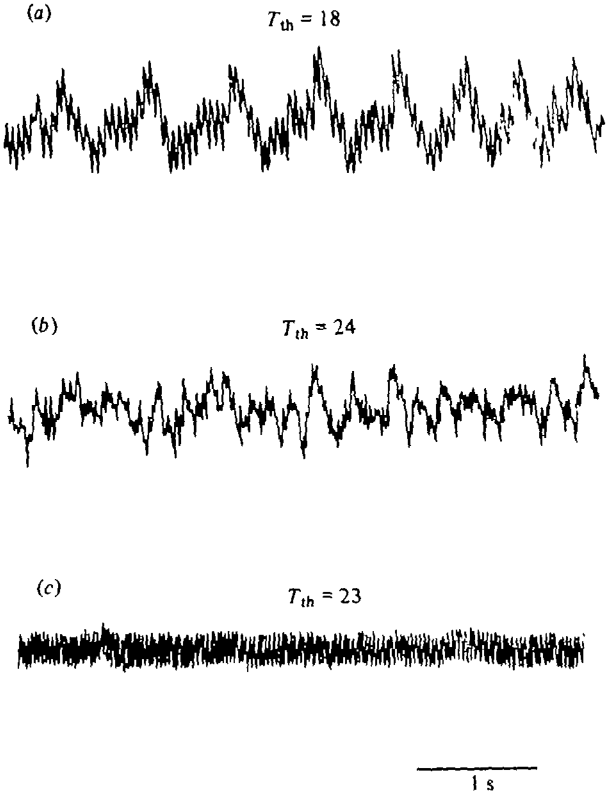

Fig. 8. Sample records of wing-beat traces illustrating (*a*) heart activity superimposed on smaller, more rapid deflexions of wing beats; (*b*) irregular fluctuations; (*c*) lack of heart activity.

Total heat production is inversely related to $T_a$. Similar values for total heat production were obtained from total oxygen consumption data, and from heat storage and heat loss data at high $T_a$. However, at low $T_a$, the total heat production calculated from total oxygen consumption is significantly lower (Table 1). There are two possible explanations to account for this difference. As shown in Table 1, duration of warm-up in the $\dot{V}_{O_2}$ experiments was much shorter at low $T_a$, than in $T_{th}$ experiments. It is therefore likely that the moths were either (1) warmer than

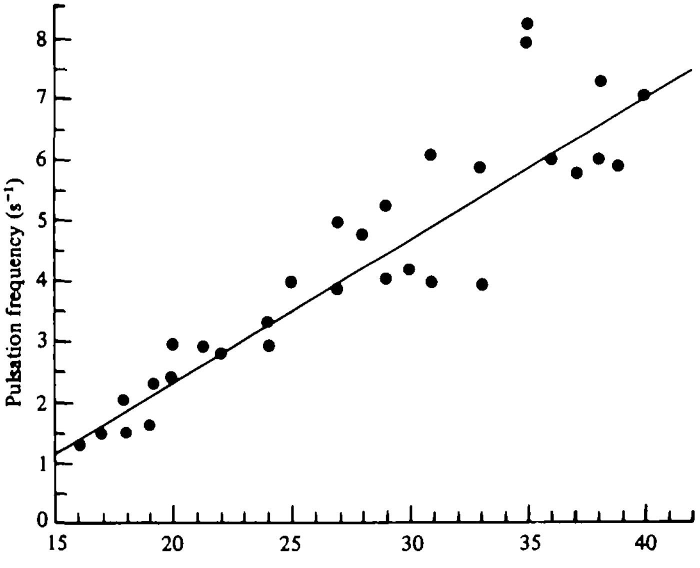

Fig. 9. The relation of pulsation frequency of the aorta in the thorax to thoracic temperature during warm-up.

$T_a$ when warm-up was initiated, or (2) not reaching a true take-off temperature when flight movement was initiated. In either case, a reduced duration of warm-up should result in a decreased energy expenditure.

*Heart pulsation.* Pulsations of the dorsal vessel in the thorax were often detectable from impedence traces (Fig. 8). These pulsations were superimposed as slower deflexions onto the wing-beat record. Pulsations were sometimes observed at high $T_{th}$, low $T_{th}$, or both; but in no experiments were pulsations apparent at all temperatures throughout the entire warm-up. In some cases, the traces showed erratic deviations which could not be quantified, or there was no deflexion at all from the normal wing-beat frequency record (Fig. 8). In a few cases, no heart pulsations were apparent at any time during the warm-up. It is unclear whether this is an artifact due to the positioning of impedance leads, or that heart pulsations did not occur during warm-up. Frequency of pulsations of the dorsal vessel in the thorax were directly related to $T_{th}$ (Fig. 9) and not related to the air temperature. Between $T_{th}$ of 15 and 40 °C, pulsation frequency of the thoracic heart increased from 1 to 7 $s^{-1}$ (Figs. 8, 9).

## DISCUSSION

*Effect of $T_a$.* The rate of warm-up of *M. americanum* is strongly temperature-dependent (Fig. 2) as in other moths (Heinrich & Bartholomew, 1971; Bartholomew & Casey, 1973; Heinrich & Casey, 1973), bumblebees (Heinrich, 1975) and some dragonflies (May, 1976*b*, 1979). Calculated rates of heat production represent the sum of the rate of heat storage in the thorax and the rate of heat loss. The rate of heat loss will be determined by the ambient temperature, since at any given $T_{th}$, the difference in temperature ($T_{th} - T_a$) is the driving force for passive heat loss and therefore greater at low than at high $T_a$. Heat production, however, is a function of $T_{th}$ and is not related to $T_a$ (Fig. 7). Consequently, at any given $T_a$, a larger portion of the heat produced is lost as $T_a$ decreases, and therefore less heat can be stored to elevate $T_{th}$. Our results suggest that *M. americanum*, like sphingid and saturnid moths, warms as rapidly as possible, thereby reducing the time when they are conspicuous to predators while still unable to fly (see Blest, 1957; Bartholomew & Heinrich, 1973, for further discussion).

*Heat production.* The calculated rates of heat production in the present study probably represent an underestimate of the actual situation for several reasons. First, evaporative heat loss from the respiratory tract has not been quantified, and estimating its magnitude is complicated by continuously changing ventilation volumes (see below), temperatures, and vapour pressure during warm-up. May (1979) has estimated that evaporative heat loss during warm-up in dragonflies amounts to about 10% of the total heat production. Thoracic conductance values used in the present study were obtained in still air. If there is significant air movement occurring as a result of wing movements, forced convection effects may cause thoracic conductance to be greater than estimated here (see Heinrich & Bartholomew, 1971). This possibility has been discounted in dragonflies based on lack of significant air movement near the surface of the thorax (May, 1979), but cannot be excluded for *M. americanum* without further data, because the wing movements are more violent than those of dragonflies, and shorter wings should cause greater air movement around the thorax. On the other hand, the dense thoracic insulation should reduce effects of forced convection. Finally, if active heat transfer occurs to the head, conductance of the thorax based on thoracic cooling curves of dead moths will be underestimated (see below). Similar discrepancies between calculated rates of heat production and instantaneous rates of heat production obtained from $\dot{V}_{O_2}$ data amount to 10–20% in bumblebees (Heinrich & Kammer, 1973; Kammer & Heinrich, 1974), dragonflies (May, 1979) and moths (G. A. Bartholomew, personal communication). Assuming a 15% underestimate for our data, heat production per wing stroke during pre-flight warm-up amounts to 0·78 ml/stroke.

The energy expenditure per wing stroke of *M. americanum* during free flight is 1·06 mJ/stroke (Casey, 1981), about 25% greater than the values obtained at all $T_{th}$ during warm-up. However, the wing-stroke frequency during warm-up, tethered, and free flight are all similar at a given $T_{th}$. Our results are very similar to those of the sphinx moth, *Manduca sexta*, which has similar wing-stroke frequency in warm-up and flight at a given $T_{th}$ (Heinrich, 1971*a*; Heinrich & Bartholomew, 1971). The discrepancy between stroke work during warm-up and flight may result from double firing of nerve impulses per muscle contraction during flight, since this will increase the force of contraction and the metabolic rate per wing stroke (Weis Fogh, 1964*b*; Kammer, 1968).

*Head temperature during warm-up.* The head temperature of *M. americanum* is closely related to $T_{th}$ rather than the air temperature (Fig. 4), despite its small size, high surface area, poor insulation, and lack of heat generating tissue. Since the flight muscles are the only major source of heat during warm-up, heat must be transferred from thorax to head. While our data are not sufficient to provide a detailed analysis of the mechanism of transfer, circumstantial evidence suggests that heat transfer physiologically mediated. The fact that the dorsal vessel empties into the head, coupled with the beating of the aorta in the thorax during warm-up (Fig. 9), should result in some heat transfer to the head by blood circulation. Moreover, since the head should cool more rapidly as $T_{\text{head}} - T_a$ increases, the increase in pulsation frequency of the aorta as $T_{\text{th}}$ increases (Fig. 9), would tend to compensate for higher rates of heat loss.

Any explanation implicating heat transfer to the head by blood circulation must also account for a lack of heat transfer from thorax to abdomen because $T_{\text{ab}}$ remained near $T_a$ during warm-up (Fig. 4). It is obvious that the normal circulatory pattern seen in resting insects (Wigglesworth, 1965) cannot be occurring because even small quantities of blood flow to the abdomen should result in elevated $T_{\text{ab}}$, particularly at higher $T_{\text{th}}$ (Heinrich, 1971*b*). In sphinx moths (Heinrich & Bartholomew, 1971) and bumblebees (Heinrich, 1976) the circulatory pattern is interrupted by a lack of coincidence in the pulsation of the aorta in the thorax and the dorsal vessel in the abdomen. If blood is not pumped forward into the thorax, no pressure gradients are present between thorax and abdomen and there is little tendency for blood to flow into the abdomen. If the aorta is not filled after each pulsation with blood from the abdomen, it would refill with some blood from the head. Thus, a local circuit could occur in which the same blood is pumped into the head after it has refluxed and become warm in the thorax (Heinrich, 1980). Even if the heart is not involved in heat transfer to the head, significant amounts of heat are probably transferred from thorax to head via conduction (Heinrich, 1979). During warm-up, some mixing of haemolymph of head and thorax is inevitable, due to pressure changes in the thorax associated with contraction of the flight muscles. Since the frequency of pressure changes in the thorax increases directly with $T_{\text{th}}$ during warm-up (Fig. 5), mixing of haemolymph in the head and thorax should be greater at high $T_{\text{th}}$ than at low $T_{\text{th}}$.

Although it is well known that insects from a variety of taxa maintain $T_{\text{ab}}$ near $T_a$ during warm-up (moths – Heinrich & Bartholomew, 1971; bumblebees – Heinrich, 1976; dragonflies – May, 1976*b*; Heinrich & Casey, 1978; beetles – Bartholomew & Casey, 1977) except for honeybees (Heinrich, 1979, 1980), there are no data available for head temperatures of insects. In view of the complexity of neural control and sensory function associated with flight and thermal sensitivity of the flight motor (see Kammer & Heinrich, 1978), it should be adaptive for species which fly over a wide range of $T_a$ to keep the temperature of the brain as close as possible to that of the thorax. Further work on the control of head temperature is needed, particularly in species which use the abdomen as a thermal window for control of $T_a$.

*Wing movement during warm-up.* Why is there wing movement during warm-up? With the exception of *Perigonia lusca* (Sphingidae) (May, 1976*a*) all moths that warm-up display low-amplitude wing movements corresponding to the frequency of contraction of the dorsal–longitudinal and dorso-ventral flight muscles. Presumably, these movements occur because the synchrony of contraction of the antagonistic muscle sets is not perfect (see Kammer, 1968). While these small-amplitude wing movements make the moths much less conspicuous than full wing movements (Blest, 1957; Heinrich & Bartholomew, 1971), moths which are warming up in the field are much more obvious than those at rest. From the standpoint of heat production, the moths could produce similar quantities of heat if the muscles went into tetany (Heinrich, 1974) and reduce their conspicuousness to predators by eliminating wing movements. We suggest that wing movements are probably related to ventilation rather than heat production. Unlike coleoptera and hymenoptera which ventilate their flight muscles by strong abdominal pumping movements, lepidopterans ventilate the flight motor by pressure changes occurring as a result of thoracic deformation caused by contraction of flight muscles (Weis-Fogh, 1967). Although the insect tracheal system is designed so that diffusion will provide sufficient $O_2$ for a resting insect (Weis-Fogh, 1964*a*), it is unlikely that diffusion would satisfy the oxygen demand during warm-up. For example, the heat production of a 0·088 g moth at rest is about 0·34 mW (Bartholomew & Casey, 1978). During warm-up, however, heat production varies from at least 10 to 40 mW (Fig. 5), 30–130 times the resting level. Therefore, if the moth's flight motor is to be ventilated during warm-up, significant thoracic deformation must occur. Apparently the moths cannot uncouple the wings to prevent wing movement which occurs as a consequence of thoracic deformation.

*Effects of size.* Within the vertebrates there is a strong inverse correlation between the arousal rate (i.e. the rate of increase in core temperature) and body mass, while the insects show no relation between rate of pre-flight warm-up and body mass (Heinrich & Bartholomew, 1971; May, 1976*a*). This difference between taxa is striking, particularly because both insects and vertebrates exhibit a similar relation of thermal conductance to body mass (Bartholomew & Epting, 1975; May, 1976*a*; Bartholomew, 1981).

Warm-up rate for *M. americanum* at $T_a$ = 25 °C is 10·6 °C/min, well above that of any other insect in its size range (Table 2). However, thoracic cooling constants of *M. americanum* and other similar sized insects from several families of lepidoptera, as well as bees, flies, and dragonflies, all are of the same magnitude (see Bartholomew, 1981, for further discussion). It is unlikely that the higher rates of warm-up of *M. americanum* are due primarily to its thoracic insulation since other well-insulated insects, such as bumblebees and sphinx moths (Heinrich, 1975; May, 1976*a*), do not warm up as rapidly. In addition, bees and flies should experience less forced convection than *M. americanum*, since they do not beat their wings during warm-up. The rate of warm-up is a reflexion of the rate at which heat is stored in the thorax and depends on rates of heat production and rates of heat loss. A variation in rates of warm-up from 2·8 to 10·6 °C for insects having similar mass and thoracic conductance indicates that different insects of a given mass have widely different rates of heat production.

Power requirements of insects during flight is not only a function of size, but also overall flight configuration (Nachtigall, 1967; Weis-Fogh, 1973). Wing-stroke frequency during flight can differ considerably in insects having different wing morphology. Moreover, evidence is accumulating that in moths and other synchronous fliers the mass-specific stroke work (energy per wing stroke) does not vary appreciably with body size and that differences in flight metabolism are largely due to differences in stroke frequency (Bartholomew & Casey, 1978; Kammer & Heinrich, 1980; Casey, 1980). It is apparent that the nervous system of synchronous fliers, which determines wing-beat frequency during flight, evolved in parallel with changes in wing morphology such that the frequency characteristics of the flight muscles

Table 2. *Rates of warm-up at $T_a$ = 25 °C in insects of body mass* 60–120 *mg*

| Family | Species | Rate (°C/min) | Mass | Source |
|---|---|---|---|---|
| Anisoptera | *Miathyria marcella* | 2·6 | 0·073 | May (1976*a*) |
| | *Tauriphila argo* | 3·3 | 0·105 | May (1976*a*) |
| | *Triacanthagyna septima* | 3·7 | 0·121 | May (1976*a*) |
| | *Tholymis citrina* | 2·8 | 0·124 | May (1976*a*) |
| Lepidoptera | *Malacosoma americanum* | 10·6 | 0·088 | Present study |
| | *Xylophanes thyelia* | 5·2 | 0·120 | May (1976*a*) |
| Hymenoptera | *Apis mellifera* | 4·5 | 0·110 | Sotavalta (1954) |
| | *Euglossa imperialis* | 7·0 | 0·063 | May (1976*a*) |
| | *Ptiloglossa spp.* | 7·7 | 0·120 | May (1976*a*) |
| Diptera | *Stibasoma chionostigma* | 7·2 | 0·091 | May (1976*a*) |

different species are designed to operate at levels appropriate to the mechanical constraints dictated by wing size and loading. The net effect is that the firing frequency is greater in an insect with small wings, such as a sphingid, than in an insect with large wings such as a saturniid, even if both insects are of similar mass and $T_{th}$.

A similar rationale can be used to explain the wide scatter and lack of inverse correlation of rate of warm-up with size in insects. Since the flight muscles (adapted for flight) produce all the heat during warm-up, difference in morphology should correlate with stroke frequency of the muscles for different species as occurs in flight. Wing beat frequency in warm-up is strongly dependent on $T_{th}$ (Fig. 5), and in several insects the stroke frequency during warm-up is lower for insects with low wing loading than for high wing loaded insects (Casey, in prep.; see also Kammer & Heinrich, 1978 – their fig. 15). In addition, heat production during warm-up of sphingid moths (Heinrich & Bartholomew, 1971), bumblebees (Heinrich, 1975) and tent caterpillars are related to $T_{th}$ during both warm-up and flight. Taken together, these data suggest that differences in heat production during warm-up in different species are a function of differences in stroke frequencies (which reflect action potential frequencies) at any given $T_{th}$. For the tent caterpillar, stroke frequencies at any given $T_{th}$ during warm-up are greater than those of any synchronous flier for which data are currently available (Kammer & Heinrich, 1978), as are its rates of heat production. Similarly, *M. americanum* also has among the highest rates of flight metabolism and stroke frequency (Casey, 1981). Obviously, more data are needed to evaluate this suggestion, but it is clear from the wide range of warm-up rates for insects of a given size range (Table 2) that differences in rates of heat loss between small and large insects (May, 1976*a*) represents only a partial answer to the lack of correlation of rate of warm-up and body mass of insects.

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