

AN ANALYSIS OF PRE-FLIGHT WARM-UP IN THE SPHINX MOTH, *MANDUCA SEXTA*

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INTRODUCTION

It has been known for many years that some insects of the orders Coleoptera, Hymenoptera, and Lepidoptera initiate flight only at body temperatures above 30 °C (Dotterweich, 1928; Krogh & Zeuthen, 1941; Sotavalta, 1954; Dorsett, 1962), and that some species maintain thoracic temperatures above 35 °C while flying. The heat which causes the rise in body temperature during pre-flight warm-up is produced by contractions of the flight muscles.

This study examines the inter-relations of ambient temperature with cardiac performance, wing movements, insulation, convection, and rates of change in thoracic and abdominal temperatures during pre-flight warm-up and post-flight cooling in sphinx moths weighing from 1 to 3 g.

MATERIALS AND METHODS

The moths were reared using a slightly modified version of the method of Hoffman, Lawson & Yamamoto (1966). The eggs and larvae were collected on Jimson weed (*Datura stramonium*) in the Mohave Desert of California. In the 1½-3 days between emergence and experimentation the moths were kept at an environmental temperature of 21-23 °C. Measurements were made in an insulated room in which temperature could be controlled to within 0.5 °C over a range from 0 to 60 °C.

All temperatures were measured to within 0.1 °C using copper-constantan thermocouples connected to a multichannel recording potentiometer. Thoracic temperatures were measured with 40-gauge thermocouples inserted slightly off centre through small holes pierced in the tergum. Care was taken to avoid disturbance of the scales. The thermocouples remained securely in place without further attention. Abdominal temperatures were measured ventrally with 40-gauge thermocouples slipped through the intersegmental membranes.

Wing movements and heart action were recorded from pairs of silver electrodes implanted dorsally on either side of the heart in both thorax and abdomen. The electrodes were wired to two Biocom impedance converters which in turn were connected to different channels of a Grass Polygraph. The changes in impedance which were recorded resulted from alterations in the distance between electrodes and from changes in electrical conduction across the dorsal vessel. In favourable preparations both wing movements and heart action were clearly shown. All measurements of heating and cooling were made in still air.

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Thermocouples and impedance electrodes were implanted 16–20 h prior to measurement in animals anaesthetized with CO_2 . Between implantation and measurement the moths were placed on a moist sponge in a transparent plastic container with room lights on, and kept at a temperature at which they were to be studied. To initiate warm-up, illumination was reduced. At the higher temperatures no further stimulation was needed, but at temperatures of 15 °C and below gentle prodding was sometimes required to arouse the animals.

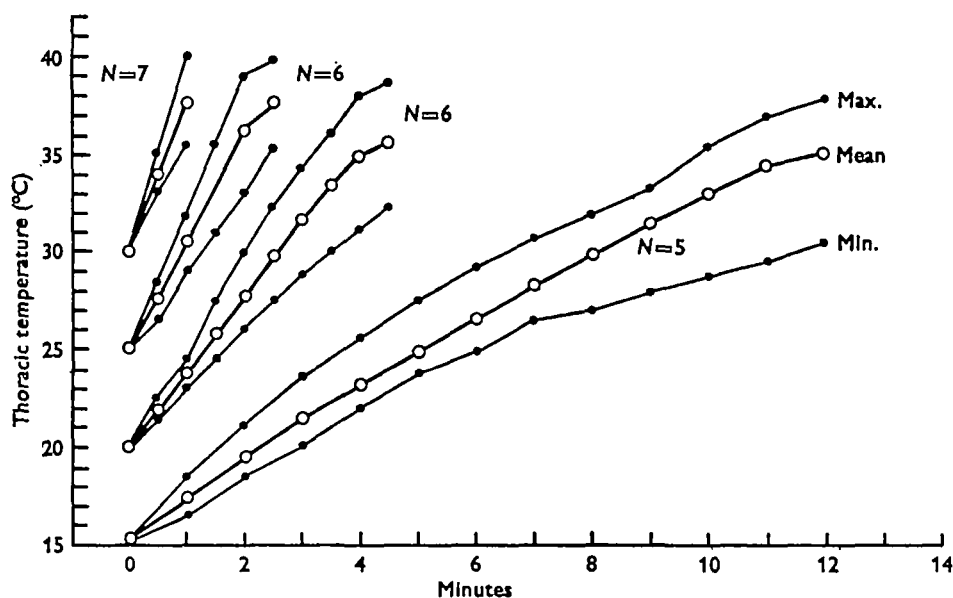


Fig. 1. Mean, maximum, and minimum increases of thoracic temperature during warm-up at ambient temperatures of 15, 20, 25 and 30 °C. N is number of individuals measured.

RESULTS

At rest the thoracic (T_{Th}) and abdominal temperatures (T_{Ab}) of *Manduca sexta* are indistinguishable from each other and from ambient temperature (T_{A}), as is the case with most insects (Krogh & Zeuthen, 1951). However, during pre-flight warm-up T_{Th} rose rapidly while T_{Ab} showed little change.

The increase in T_{Th} during warm-up was approximately linear until flight temperature was approached (Fig. 1). The mean rates of increase in T_{Th} during warm-up increased linearly with T_{A} . At T_{A} of 15 °C the rate of increase was approximately 2 °C/min, while at 30 °C it was about 7.6 °C/min (Fig. 2). The difference between maximum and minimum rates of increase in T_{Th} was greatest (4.5 °C/min) at a T_{A} of 30 °C, and least (1.2 °C/min) at a T_{A} of 15 °C. At the latter temperature the moths sometimes seemed reluctant to initiate warm-up even after repeated tactile stimulation.

Mean thoracic temperatures immediately after initiation of flight varied from 36.8 to 38.8 °C with the lowest figures occurring at ambient temperatures between 12 and 20 °C (Fig. 3).

During warm-up sphinx moths produce heat by contractions of the thoracic muscles which vibrate the wings rapidly through a narrow angle. These wing vibrations are

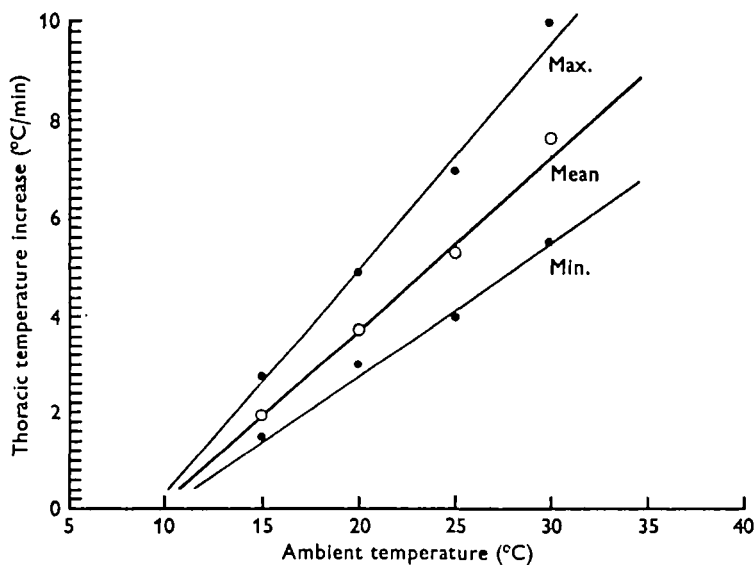


Fig. 2. Rate of warm-up as a function of ambient temperature. The values are taken from the linear portions of the increases of thoracic temperature during warm-up shown in Fig. 1.

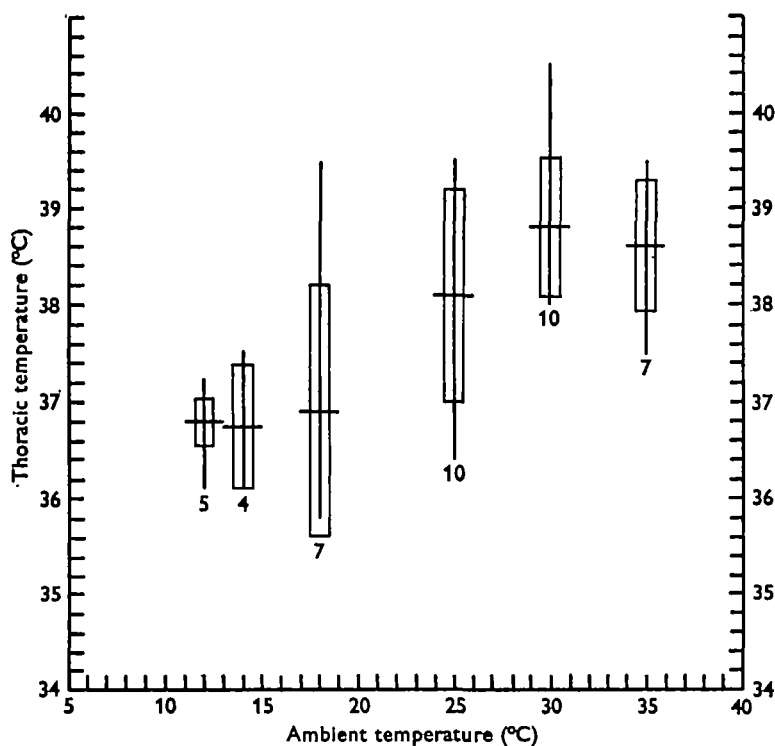


Fig. 3. Thoracic temperatures immediately after initiation of flight. Horizontal lines indicate means, vertical lines indicate the range, and the boxes enclose ± 2 s.e. above and below the means.

sometimes called shivering by analogy with endothermic vertebrates. The rate of wing vibration increased linearly ($r = 0.97$) with thoracic temperature, from about 8/sec at 15 °C to approximately 25/sec at 35 °C (Fig. 4).

When a resting *M. sexta* is held by its legs, it immediately begins to move its wings synchronously through a wide angle as if trying to fly. These 'flying movements' cause a rapid rise in body temperature. The rate of increase in T_{Th} during this forced warm-up closely approximates that observed during normal warm-up (Figs. 1 and 5).

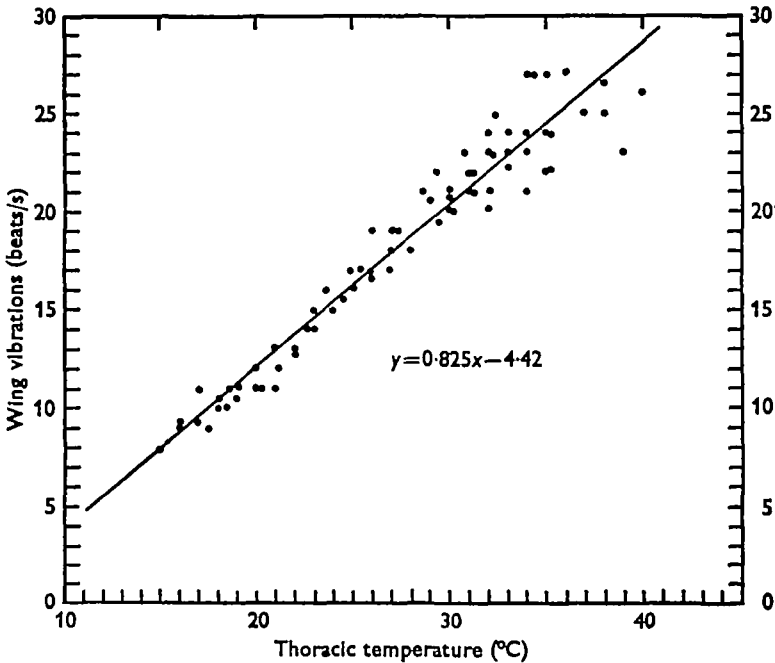


Fig. 4. Rate of wing vibration during warm-up as a function of thoracic temperature. Measurements were made on 10 individuals at various ambient temperatures from 15 to 31 °C. At any given thoracic temperature each point represents a different individual.

Although the rate of wing movement during forced warm-up increased with increasing T_{Th} , at any given T_{Th} it was less than the rate of wing vibration at the same temperature during normal warm-up. In addition, the increase in wing beat tended to show a curvilinear relation to T_{Th} , falling off at temperatures above 30 °C (Fig. 6).

Although the dense covering of scales of sphinx moths affords insulation (Church, 1960; Heinrich, 1971*a*), in still air *M. sexta* is able to warm up to flight temperature even with all thoracic scales removed (Fig. 7).

The cooling curves of moths, immediately after being killed with ether, are straight lines when plotted on semi-logarithmic coordinates (Figs. 8 and 9). The cooling curves of live animals are sometimes linear on such a plot, but are often curved as shown in Fig. 8. In all cases live animals cooled more rapidly than dead ones, and their rates of cooling at a given difference between T_{Th} and T_A (ΔT) tended to be greater at high T_A than at low. Using a ΔT of 15 °C as a starting point, the decrease in mean T_{Th} of nine intact live animals in still air during 4 min was 11.5 °C in a T_A of 25 °C and 8.5 °C in a T_A of 15 °C (Fig. 9).

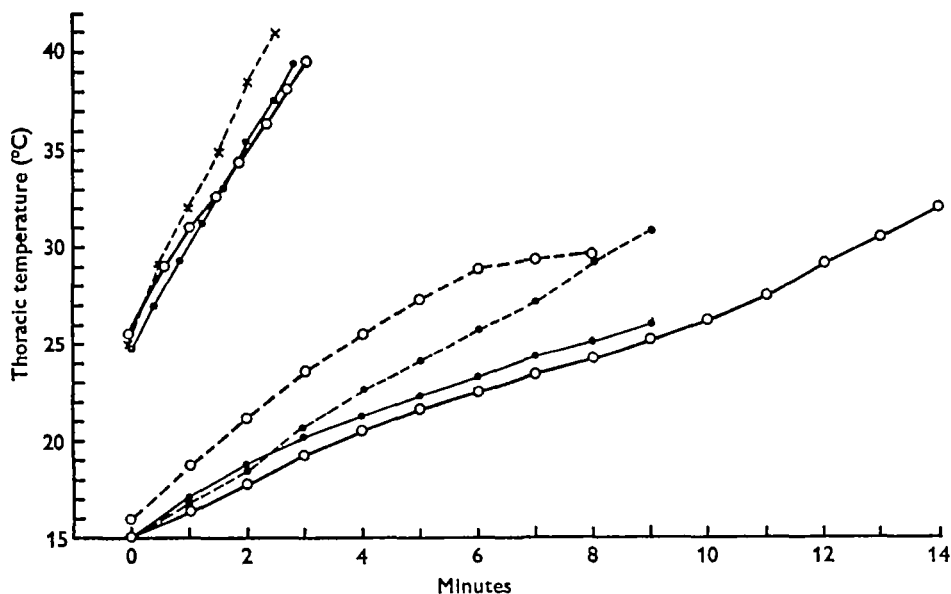


Fig. 5. Changes of thoracic temperatures during warm-up associated with large-amplitude wing beating at ambient temperatures of 15 and 25 °C. Each curve represents a different individual.

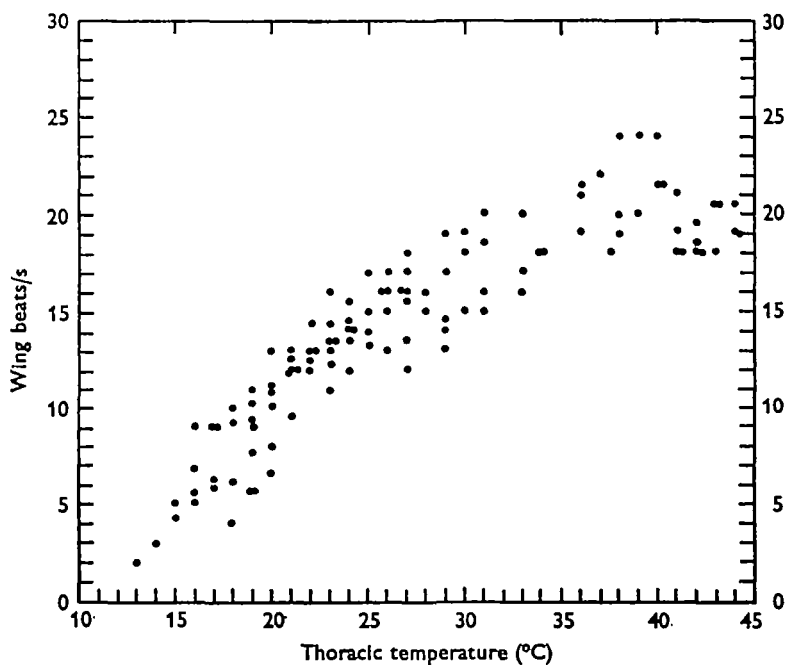


Fig. 6. Rates of reflexly induced, large-amplitude wing beats as a function of thoracic temperature. Measurements were made on thirteen individuals at various ambient temperatures between 13 and 35 °C. At any given thoracic temperature each point represents a different animal.

These differences indicate that the rate of heat loss from the thorax in *M. sex* during post-flight cooling is not completely passive but is affected by physiological factors, one of which appears to be an accelerated transfer of heat to the abdomen. During warm-up the T_{Ab} remained at or near T_A , but after T_{Th} reached the level

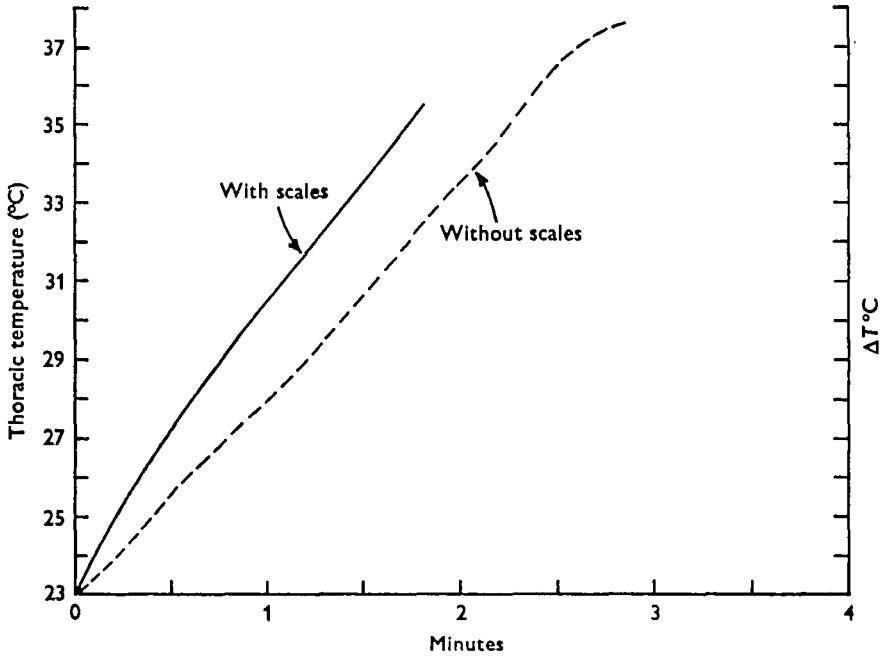


Fig. 7. Warm-up of a 2.3 g moth with and without thoracic scales in still air at an ambient temperature of 23 °C.

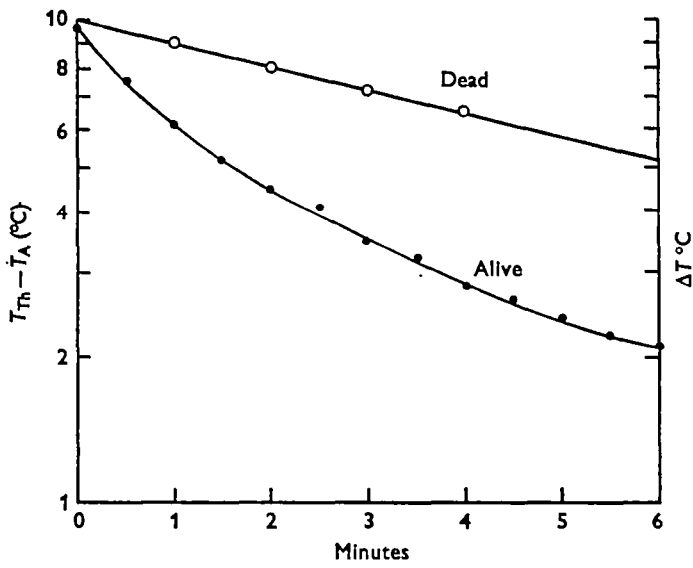


Fig. 8. Cooling rates of a 1.8 g moth when alive and when dead in still air at an ambient temperature of 30 °C.

Characteristic of flight, T_{Ab} rose several degrees above T_A and continued to rise as T_{Th} decreased during cooling (Fig. 10).

Under the conditions of measurement the performance of the heart of resting *M. sexta* was extremely variable. Both rate and amplitude of beating varied widely at

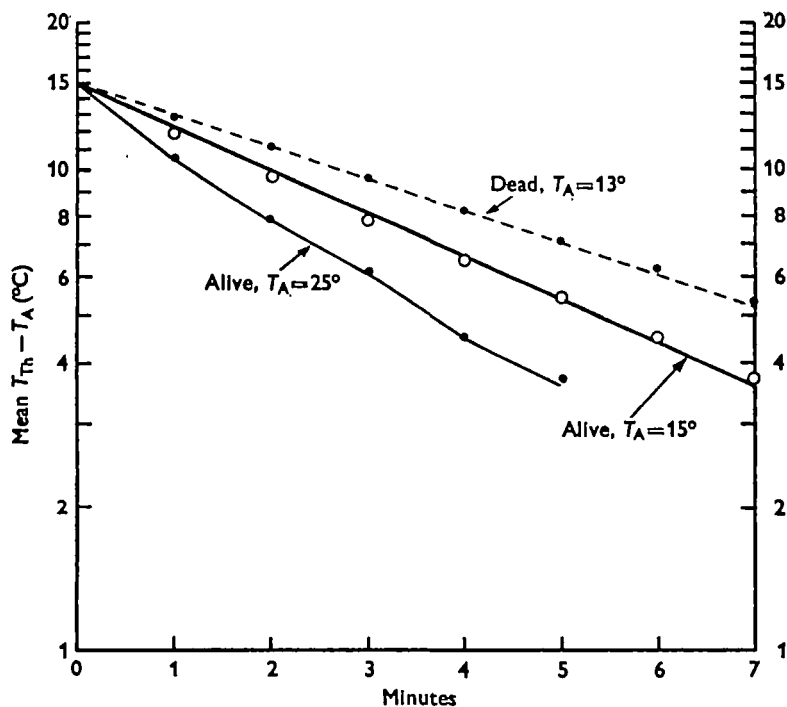


Fig. 9. Mean thoracic cooling rates of ten dead moths at 13 °C, and nine live moths at 15 and at 25 °C.

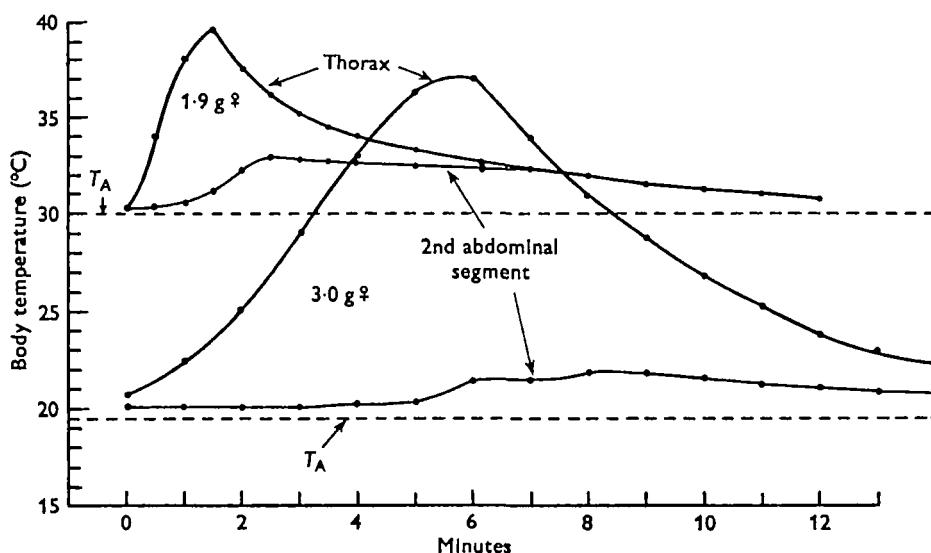


Fig. 10. Thoracic and abdominal temperatures during warm-up and subsequent cooling.

any given body temperature. In a general way heart rate tended to increase directly with resting body temperature, but quantitative characterization of the relation between heart rate and body temperature is difficult because of long periods without beats, periods of reversed direction of contraction, and variable amplitudes of contraction (Fig. 11). Despite the variability of heart performance seen in most animals, in

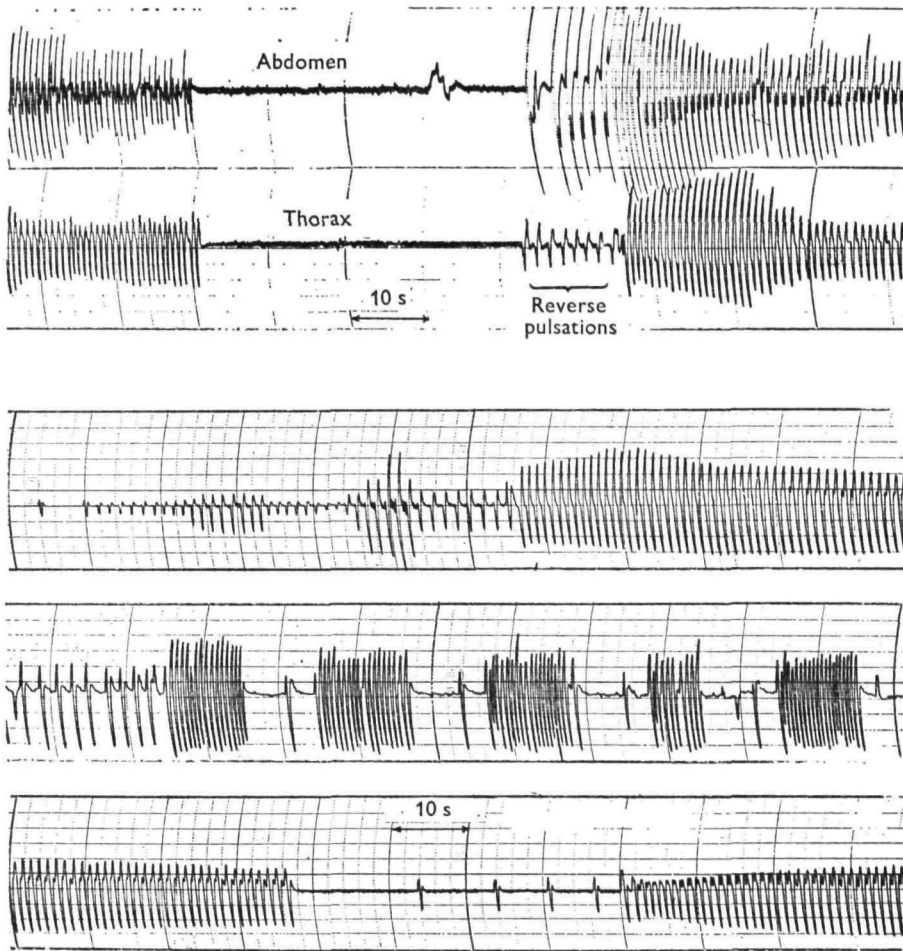


Fig. 11. Records of impedance changes accompanying heart activity of resting moths at an ambient temperature of 25 °C, showing the variability in rate, amplitude, and rhythm. Reversed beats arise in the thorax and travel posteriorly in the abdomen. The two records at the top were obtained simultaneously from the same moth.

some individuals at rest the contractions travelled the length of the heart regularly and smoothly for many consecutive minutes. As previously reported (Heinrich, 1971*b*) records of impedance changes indicate that contractions of the heart travel along the length of the abdomen and continue through the thorax.

During warm-up the records of thoracic heart rate were often either absent or obscured by the movements associated with wing vibrating. However, in some cases both the rates of wing vibration and of thoracic heart beat were clearly recorded

Figs. 12 and 13). The signals from the abdominal electrodes coincided with thoracic heart beats in resting animals, but characteristically became arrhythmic and got out of phase with the thoracic beats during warm-up. In those cases where regularity of

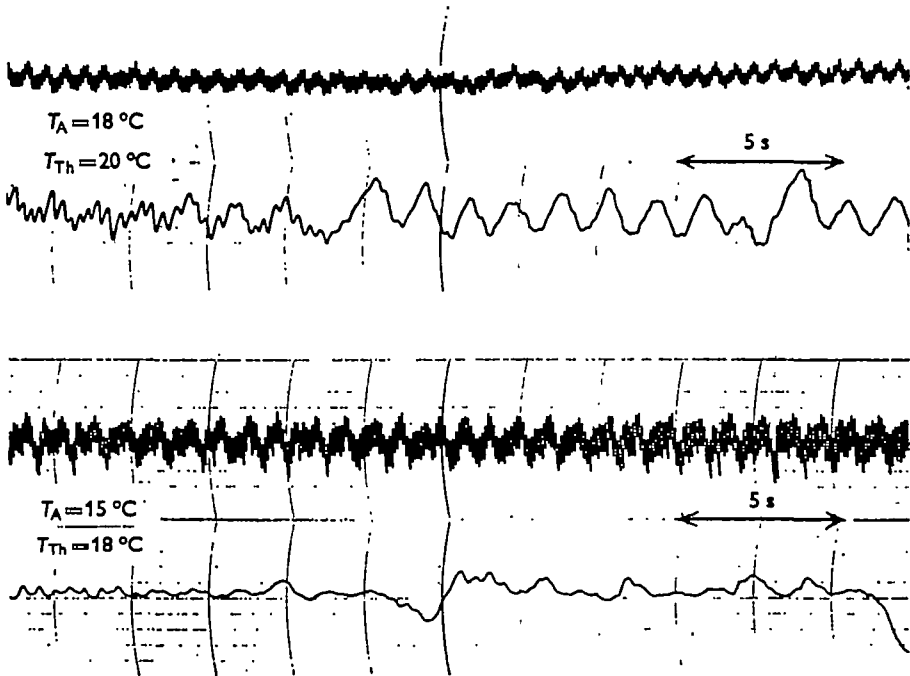


Fig. 12. Two sets of simultaneous records of the changes in impedance accompanying heart activity and wing vibrations during warm-up. Note that the high-frequency wing vibrations are superimposed on the rhythmic activity of the thoracic heart, and that the activity of the heart in the abdomen is variable and differs in frequency from that in the thorax.

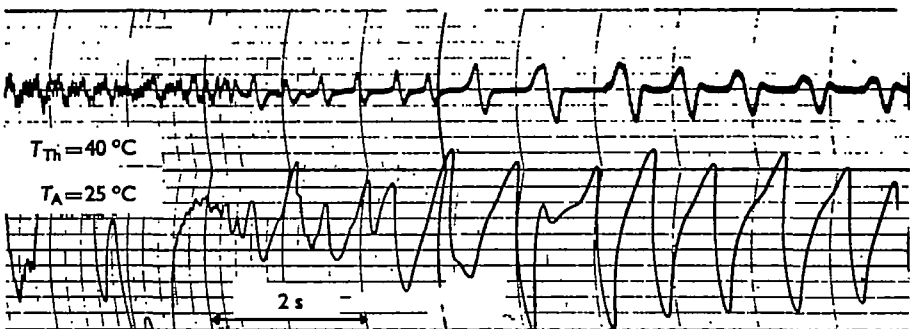


Fig. 13. Impedance records from thorax and abdomen at the termination of warm-up showing heart pulsations in the thorax with and without the superimposed records of wing movements, and the establishment of synchrony between thoracic and abdominal heart beats after cessation of wing movements.

heart beat was maintained the frequency differed markedly from that recorded simultaneously from the thorax (Fig. 12). Temperatures in the abdomen remained near ambient during warm-up. We assume that we were observing fibrillations rather than beats when the signals recorded from the abdomen were at a higher frequency

than those from the much warmer thorax (see upper record, Fig. 12). At the completion of warm-up wing vibrating ceased abruptly and the underlying thoracic heart beat was then more apparent (Fig. 13). Sometimes immediately, and always within several minutes after the termination of wing vibration, synchrony between thoracic and abdominal heart beats was re-established (Fig. 13).

Table 1. *Rates of warm-up and body weight. T_A , 20–25 °C*

Insects	Species	Wt. (g)	Warm-up rate (°C/min)	Reference
1.	<i>Apis mellifica</i>	0.11*	4.5	Sotavalta, 1954
2.	<i>Bombus impatiens</i>	0.20*	8.0	Sotavalta, 1954
3.	<i>B. horti</i>	0.20	3.0	Krogh & Zeuthen, 1941
4.	<i>Celerio lineata</i>	0.39	4.0	Heath & Adams, 1967
5.	<i>Pseudoclanis postica</i>	0.75	11.5	Dorsett, 1962
6.	<i>Geotrupes stercorarius</i>	0.90	4.3	Krogh & Zeuthen, 1941
7.	<i>Deilephila nigrii</i>	1.74	5.5	Dorsett, 1962
8.	<i>Hyalophora cecropia</i>	1.80*	3.8	Hanegan & Heath, 1970
9.	<i>Manduca sexta</i>	2.00	4.1	Present study
10.	<i>Euchloron magaera</i>	2.52	8.0	Dorsett, 1962
Birds				
11.	<i>Archilochus alexandri</i>	3.3	1.35	Lasiewski & Lasiewski, 1967
12.	<i>Calypte anna</i>	3.6	1.25	Bartholomew, Howell & Cade, 1957
13.	<i>Eugenes fulgens</i>	6.8	1.20	Lasiewski & Lasiewski, 1967
14.	<i>Lampornis clemenciae</i>	8.5	0.90	Lasiewski & Lasiewski, 1967
15.	<i>Patagona gigas</i>	21.0	0.66	Lasiewski, Weathers & Bernstein, 1967
16.	<i>Apus apus</i>	29.0	0.30	Koskimies, 1961
17.	<i>Aeronautes saxatalis</i>	30.5	0.40	Bartholomew, Howell & Cade, 1957
18.	<i>Phalaenoptilus nuttallii</i>	40.0	0.45	Lasiewski & Lasiewski, 1967
19.	<i>Colinus striatus</i>	46.0	0.17	Bartholomew & Trost, 1970
20.	<i>Caprimulgus europaeus</i>	70.0	0.43	Peiponen, 1965
21.	<i>Eurostopodus guttatus</i>	75.0	0.27	Dawson & Fisher, 1969
Mammals				
22.	<i>Pipistrellus hesperus</i>	4.0	1.20	Bartholomew, Howell & Cade, 1957
23.	<i>Perognathus longimembris</i>	8.3	0.83	Bartholomew & Cade, 1957
24.	<i>Secista betulina</i>	11.5	0.97	Johansen & Krog, 1959
25.	<i>Marmosa</i> sp.	13.0	0.70	Morrison & McNab, 1962
26.	<i>Microdipodops pallidus</i>	15.2	0.70	Bartholomew & MacMillen, 1961
27.	<i>Perognathus californicus</i>	22.0	0.88	Tucker, 1965
28.	<i>Nyctimene albiventer</i>	28.2	0.50	Bartholomew, Dawson & Lasiewski, 1970
29.	<i>Dipodomys merriami</i>	36.5	0.28	Carpenter, 1966
30.	<i>Eutamias amoenus</i>	50.0	0.65	Cade, 1963
31.	<i>Cercaertus nanus</i>	70.0	0.40	Bartholomew & Hudson, 1962
32.	<i>Citellus lateralis</i>	190.0	0.35	Twente & Twente, 1965
33.	<i>C. mexicanus</i>	190.0	0.32	Neumann & Cade, 1965
34.	<i>C. tereticaudus</i>	229.0	0.25	Hudson, 1964

* Estimated weights.

DISCUSSION

The new information which we have obtained concerning the effects of ambient temperature on pre-flight warm-up and post-flight cooling, the relative effectiveness of wing vibrating and wing beating in heat production, together with data on heart activity and regional differences of body temperature can be used to extend the understanding of the physiology of endothermy in large insects.

In the sphingids and saturniids that have been studied effective flight is possible

Only if the temperature of the thorax is at least 32 °C. The reasons for this have not been analysed in detail in moths. However, in isolated nerve-muscle preparations of *Schistocerca* it has been shown (Neville & Weis-Fogh, 1963) that at low temperatures the duration of the contractions of the upstroke and downstroke muscles is prolonged, causing them to work primarily against each other, rather than on the wings. The maximum mechanical energy for flight becomes available only when thoracic temperatures are high enough to ensure that the twitches of the antagonistic muscles no longer overlap significantly and so act mostly on the wings.

In *M. sexta* the rate of wing vibration during warm-up increases directly with thoracic temperature (Fig. 4), and the frequency of wing movements reaches that characteristic of normal flight, 25–27/sec (Heinrich, 1971*a*), at a thoracic temperature of about 37 °C which approximates the temperature at take-off (Fig. 3). Kammer (1968) has found that during warm-up the flight muscles of sphingids and other lepidopterans contract synchronously, which causes the wings to vibrate rather than beat. However, when resting *M. sexta* are held by the legs they invariably execute wing beats of large amplitude even at low thoracic temperatures. This wing flapping causes a rapid rise in thoracic temperature. The rate of wing flapping increases directly with thoracic temperature but averages slightly lower than the rate of wing vibration. During wing vibration the upstroke and downstroke muscles contract synchronously and work mostly against each other; during wing flapping they contract alternately and work mostly to move the wings. The rate of warm-up is about the same in both situations (Figs. 1 and 5). From these data we infer (1) that in the intact animal the timing of contraction of the antagonistic flight muscles can be either alternate or synchronous over a range of temperatures extending from at least 13 °C to 35 °C, and (2) that the amount of heat produced is very nearly the same whether the muscles are working against each other or are moving the wings.

Using the data for mean rates of warm-up of live moths and the mean rates of cooling of both dead and live moths it is possible to compute approximate upper and lower values for the rates of heat production during warm-up, if it is assumed that all the heat is produced in the thorax and the weight and specific heat of the thorax are known.

If the heat losses caused by respiratory evaporation and the forced convection associated with wing vibration are temporarily ignored, then at any given difference between T_{Th} and T_A (ΔT), the calories produced per minute will be equal to the heat gain plus heat loss. This can be computed from the mean weight of the thorax (0.5 g), its specific heat (0.8), and its change in temperature during warm-up and during cooling, as shown in the following equation:

$$\text{cal/min} = (^\circ\text{C/min warming} + ^\circ\text{C/min cooling}) (\text{sp. heat}) (\text{thoracic wt.})$$

Heat production was computed at 5 °C intervals during warm-up at ambient temperatures of 15 and 25 °C, using mean rates of increase in T_{Th} and two values for T_{Th} during cooling at each T_A – the mean for ten freshly killed animals and the mean for a similar sample of live animals (Fig. 9). The results of these computations (Fig. 14) can be used to obtain estimates of the relation of heat production to body temperature, of the combined effects of evaporation and forced convection, and of the importance of abdominal circulation during warm-up.

From Fig. 14 the following points are apparent:

- (1) In all cases the rate of heat production increases with increasing thoracic temperatures.
- (2) The calculated rates of heat production are higher when the cooling rates of live animals are used than when the cooling rates of dead ones are used, with this difference increasing directly with ΔT .
- (3) The apparent rate of heat production at any given body temperature is greater when T_A is 25 °C than when it is 15 °C.

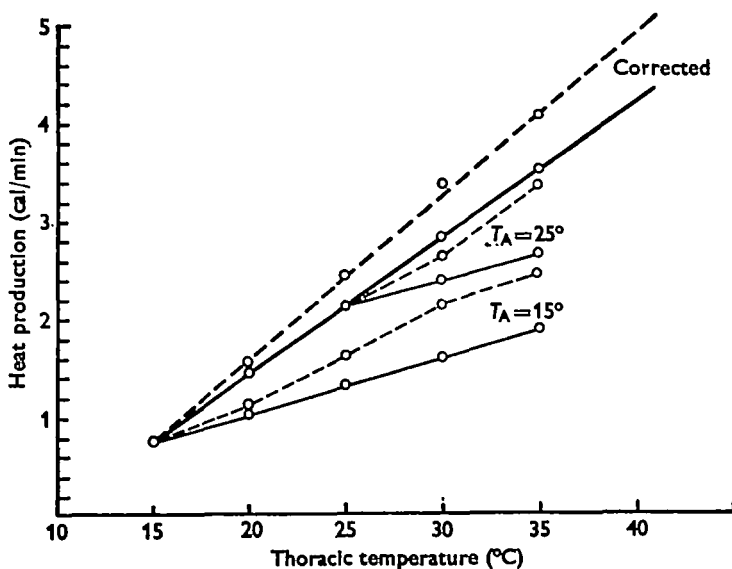


Fig. 14. Calculated rates of heat production during warm-up. The upper limits (---) are calculated from the mean cooling rates of live moths at 25 °C, and the lower limits (—) are calculated from the mean cooling rates of dead animals (Fig. 9). The two sets of thin lines indicate the apparent heat production based on the increases in thoracic temperature (Fig. 1) during warm-up at 15 and at 25 °C. The heavy lines show the relation of thoracic temperature to heat production when the latter is corrected for losses due to forced convection and evaporation (see Discussion).

On the basis of these relationships we can further analyse pre-flight warm-up and add to our understanding of the physiological processes involved.

Abdominal circulation. It appears that heat is actively moved from the thorax to the abdomen, at least during the initial few minutes of cooling, by the circulation of blood. The fact that the rise in T_{Ab} is most conspicuous in the period during which T_{Th} is declining implies that something more than passive conduction is involved. From the data in Figs. 11 to 13 we have previously concluded that during warm-up the action of the abdominal heart is erratic and out of phase with the pulsations of the thoracic heart. From these data we infer that the movement of blood between abdomen and thorax during warm-up is restricted. This should sequester heat in the thorax, and is consistent with the observation that the abdomen remains at or near ambient temperature during warm-up. It has previously been shown (Heinrich, 1970) that during flight at high thoracic temperatures the movement of heat from thorax to abdomen by

ood circulation plays an important role in thermoregulation in *M. sexta*. In Fig. 14 the difference between the upper and lower heat-production curves at both 15 and 25 °C is accounted for in part by the absence of circulation in the dead animals. This gives a rough indication of the amount of heat retained in the thorax by the minimizing of abdominal circulation during warm-up.

Adams and Heath (1964) suggested that the evaporation from a droplet of fluid extruded from the proboscis of a sphinx moth *Pholus achemon* could account for the accelerated cooling seen in this moth. It seems possible that the accelerated cooling could equally well be accounted for by the circulation of blood between thorax and abdomen. We did not at any time observe the extrusion of fluid droplets from the proboscis of *M. sexta*.

Evaporation and forced convection. The difference between the calculated rates of heat production during warm-up at the same thoracic temperature when $T_A = 15$ °C and $T_A = 25$ °C is a measure of the heat lost by respiratory evaporation, and by forced convection due to the air movements associated with wing vibration. (Heat loss due to conduction, radiation and passive evaporation should be the same in freshly killed and in live moths and can therefore be ignored in our calculations of heat production.) Because the wings are motionless during cooling, the cooling curves used in the calculation of heat production include only the effects of passive convection. The heat loss due to forced convection should be a major factor in causing the difference between the heating rates at a given thoracic temperature but differing ambient temperatures. (We have shown in Fig. 4 that the frequency of wing-vibration – and by inference, heat production – are dependent on thoracic temperature and independent of ambient temperature.) For any given thoracic temperature the ΔT during warm-up from 15 °C is 10 °C greater than the ΔT during warm-up at 25 °C. Both upper and lower limits of the calculated rates of heat production for the 15 °C and 25 °C sets of curves shown in Fig. 14 differ by about 0.8 cal/min. From this we conclude that during warm-up at any given thoracic temperature the heat loss due to forced convection and respiratory evaporation is about 0.08 cal/min/°C ΔT . Our data do not allow us to distinguish between heat loss due to evaporation and heat loss due to forced convection.

Rate of heat production. The sets of curves for heat production during warm-up at 15 °C and warm-up at 25 °C can be corrected for heat loss due to evaporation and forced convection by adding to them 0.08 cal/min/°C ΔT . The resulting corrected curves (Fig. 14) give our computation of the relation of rate of heat production to thoracic temperature during warm-up. From the set of corrected curves it appears that rate of heat production during warm-up increased 4.6 to 5.4 times between thoracic temperatures of 15 and 35 °C.

Extrapolation of the corrected rates of heat production during warm-up to a thoracic temperature of 41 °C, which is close to that normally maintained by *M. sexta* in free and unsupported flight, yields values between 4.35 and 5.10 cal/min. Assuming a weight of 1.5 g and that the utilization of 1 ml of O_2 yields 4.8 calories, these figures indicate an oxygen consumption of 36.3–42.6 ml O_2 (g h)⁻¹. These values are slightly below the 40–50 ml O_2 (g h)⁻¹ measured during free flight at ambient temperatures between 15 and 25 °C (Heinrich, 1971a), which is to be expected because oxygen consumption is strongly correlated with the mechanical work required to remain airborne (Weis-Fogh, 1964; Heinrich, 1971a).

Ambient temperature and rate of warm-up. When *M. sexta* was stimulated to initial warm-up after having been allowed to come to equilibrium with ambient temperature, the rate of increase in thoracic temperature increased linearly with ambient temperature (Fig. 2). However, it has been reported in the sphingid *Celerio lineata* (Heath & Adams, 1967) and in the saturniid *Hyalophora cecropia* (Hanegan & Heath, 1970) that rates of warm-up are independent of ambient temperature. We do not know whether this discrepancy is caused by species differences or by differences in experimental methods.

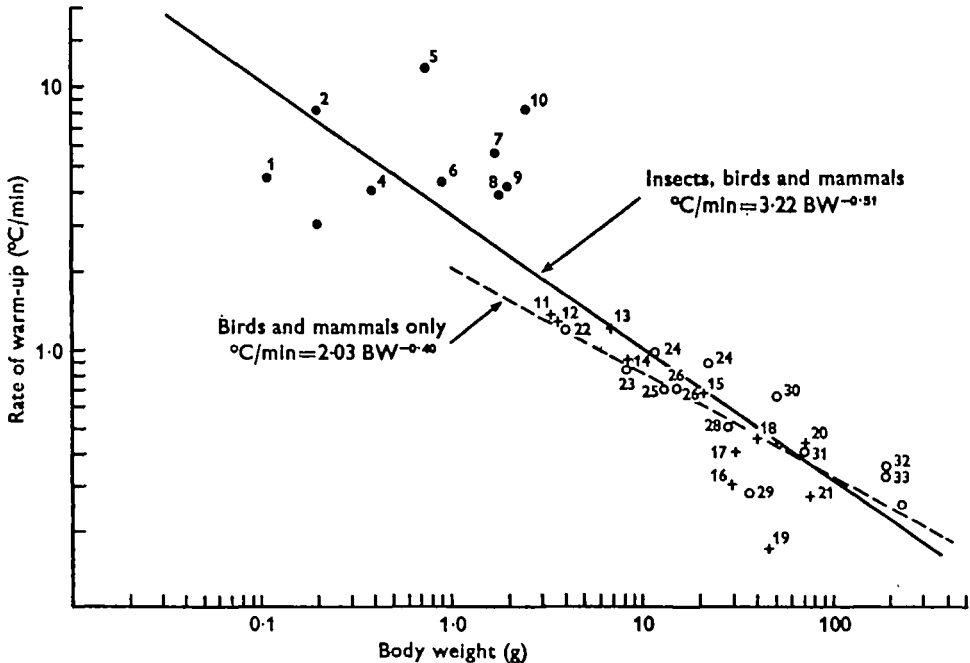


Fig. 15. The relation between rates of increase of body temperature during warm-up in insects (●) and in heterothermic birds (+) and mammals (○). In all cases ambient temperatures and initial body temperatures were between 20 and 25 °C. Most of the rates were obtained from curves showing the rates of increase of individual animals. See Table 1 for references.

Body weight and rate of warm-up. The pre-flight warm-up of large moths shows physiological similarities to the performance of birds and mammals during arousal from the dormancy associated with daily torpor, hibernation, and aestivation. It has long been known that small heterothermic mammals warm up more rapidly than large ones, and a similar situation exists in heterothermic birds (Bartholomew *et al.* 1957; Lasiewski & Lasiewski, 1967). The generalization that rate of warm-up is inversely related to body weight can be extended to include the small sample of insects for which data are available (Fig. 15). For example, in an ambient temperature of 20–25 °C a 100 g mammal warms up about 0.3 °C per minute while a 100 mg insect warms up almost 10 °C per minute. No regular relationship between body weight and rate of warm-up is apparent with the small sample of insects. The larger moths (numbers 7 to 10 in Fig. 15) warm up much more rapidly than do humming-birds and bats which are only slightly heavier.

This difference may be explained by the fact that the moths warm only the thorax whereas their rates of warm-up are plotted in terms of total body weight. Although regional differences in body temperature during warm-up are well known in large mammals, this situation is much less conspicuous in the smallest heterothermic mammals and birds.

SUMMARY

The physiology of pre-flight warm-up in *Manduca sexta* was analysed with regard to rate of heat production, regional partitioning of heat between thorax and abdomen, and the control of blood circulation.

1. When moths which have come to equilibrium with ambient temperature undergo pre-flight warm-up, the thoracic temperature increases linearly until flight temperature (37–39 °C) is approached.

2. The rate of increase in thoracic temperature during warm-up increases directly with ambient temperature from about 2 °C/min at 15 °C to about 7.6 °C/min at 30 °C.

3. The temperature of the abdomen remains near ambient throughout the period of warm-up, but during the initial part of post-flight cooling while thoracic temperature declines sharply abdominal temperatures rise appreciably.

4. During warm-up the rate of wing vibration increases linearly with thoracic temperature. At a thoracic temperature of 15 °C the rate is about 8/sec and at 35 °C it is about 25/sec.

5. When resting animals are held by the legs they at once begin to beat their wings through a wide angle. These wing beats at any given thoracic temperature are slower than the wing vibrations characteristic of normal warm-up, but they cause thoracic temperature to increase at almost the normal rate.

6. The removal of thoracic scales causes a decrease in rate of warm-up, but in still air this does not prevent the moths from reaching flight temperature.

7. During cooling the rate of decrease in thoracic temperature is greater in live animals than in freshly killed ones. At any given difference between thoracic and ambient temperatures cooling rates are directly related to thoracic temperature.

8. In resting moths heart pulsations are usually variable with regard to rate, amplitude, rhythm, and sometimes direction, but the records of cardiac activity simultaneously obtained from thorax and abdomen show close correspondence.

9. During warm-up the records of changes in impedance from electrodes in the abdomen indicate that pulsations of the abdominal heart are either absent, greatly reduced, or at a frequency different from that simultaneously recorded from the thorax.

10. The calculated rate of heat production during warm-up is linearly related to thoracic temperature.

11. Our data are consistent with the assumption that heat produced in the thorax during warm-up is sequestered there by reduction in blood circulation between thorax and abdomen.

12. Rates of warm-up in insects are close to the values predicted on the basis of body weight from data on heterothermic birds and animals.

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