J. exp. biol. (1980), **88**, 133–145
With 6 figures
Printed in Great Britain

FLIGHT ENERGETICS AND HEAT EXCHANGE OF GYPSY MOTHS IN RELATION TO AIR TEMPERATURE

BY TIMOTHY M. CASEY
Coordinated Department of Physiology, Cook College, Rutgers University, New Brunswick, NJ 08903

(*Received* 19 *December* 1979)

SUMMARY

Gypsy moths elevate thoracic temperature (T_{th}) during flight by endogenous heat production but do not regulate it. Thoracic temperature of moths in free, near-hovering flights exceeded air temperature by approximately 6–7 °C at all T_a's between 17 and 32 °C. Mean rates of mass specific oxygen consumption varied between 40 and 47 ml O_2 $(g \cdot h)^{-1}$ and were not correlated with air temperature. Wing-beat frequency increased from 27 to 33 $(s)^{-1}$ between air temperatures of 18 and 35 °C. Thoracic heating and cooling constants are similar in live and dead moths, and removal of thoracic scales increases heating constants by about 12 %. Preflight warm-up occurs at low T_a's but the moths are capable of immediate, controlled flight at T_a's above 22 °C. Relatively low levels of heat production by the flight muscles are a consequence of low power requirements associated with the flight morphology of gypsy moths. Calculated rates of thoracic and respiratory heat loss of free-flying moths are slightly lower than values of heat production.

INTRODUCTION

In recent years, several studies have examined the flight energetics and thermoregulation of flying moths (see Heinrich, 1974; Kammer & Heinrich, 1978, for review). Detailed studies of the sphingid moths *Manduca sexta* (Heinrich, 1970, 1971 *a*, *b*) and *Hyles lineata* (Heath & Adams, 1965; Casey, 1976 *a*) indicate that these species regulate thoracic temperature (T_{th}) over a wide range of air temperatures (T_a) and that flight effort is essentially independent of T_a. Comparative studies of T_{th} during flight (Bartholomew & Heinrich, 1973), thoracic conductance (Bartholomew & Epting, 1975) and flight metabolism (Bartholomew & Casey, 1978) indicate that moths from several taxa exhibit qualitatively similar flight characteristics and patterns of thermal homoeostasis.

Relatively little is known about the flight energetics and thermal balance of very small moths. Several factors should reduce the capacity of small moths to achieve high thoracic temperatures during flight. In general, as body size decreases within the lepidoptera, wing loading is reduced (Greenewalt, 1962; Bartholomew & Heinrich, 1973), thereby reducing power requirements necessary for flight. At the same time, decreased body mass causes increased rates of passive heat loss from the thorax (Bartholomew & Epting, 1975). The present study examines the flight energetics of male gypsy moths (*Lymantria dispar*, Lymantriidae) (body mass $\simeq$ 100 mg) at several air temperatures and quantifies rates of heat production and heat loss during free, near-hovering flight.

MATERIALS AND METHODS

Male gypsy-moth pupae were obtained from the Beneficial Insect Laboratory, New Jersey Department of Agriculture, Division of Plant Industry, Trenton, New Jersey. Adult moths were also collected by attracting them to a white sheet illuminated by an ultraviolet light in the Hutchinson Memorial Forest, Somerset, New Jersey. Experiments were performed on moths within 3 days of eclosion, or within 24 h of field capture.

Body mass and mass of various body parts was measured to the nearest milligram on a top loading balance. Wing length was measured to the nearest 0·2 mm with a millimetre ruler. Wing area was obtained by taping the wings, overlapped in natural flight position, on to a piece of paper, and tracing their outline with a planimeter. Thoracic mass was measured after head, legs, and wings were removed with iridectomy scissors. Pile depth was measured using a calibrated scale inserted into the ocular of a 10-power dissecting microscope.

Moths flew inside an airtight glass jar (volume = 825 ml) for at least 2 min, timed by stopwatch. If they attempted to land, the jar was gently rotated or tapped, causing the moths to resume flight. In all experiments the moths were continuously airborne (here defined as having the entire body off the floor of the chamber). Data for flights which did not meet this criterion were discarded. The moths' flight performance did not appear to be impaired by the size of the chamber and continuous flight durations in excess of 15 min were occasionally obtained.

Thoracic temperature (T_{th}) was measured using a probe consisting of a 44-gauge copper–constantan thermocouple threaded into a 26-gauge hypodermic needle. The needle was attached to a 3 ml syringe filled with white glue. The probe was stabbed into the centre of the thorax. Moths were held by the distal portion of the forewings to reduce the effect of handling on thoracic temperatures. Only data obtained within 5 s of capture were recorded.

Wing-beat frequencies were recorded on a portable cassette tape-recorder by holding a directional microphone at the lid of the flight jar. After the experiment the recording was played into a storage oscilloscope using sweep duration of 200 or 500 ms. Wing beats were either counted directly from the stored trace or the sweep duration was decreased and the interval between wing beats was measured to the nearest 0·2 mm.

Oxygen consumption ($\dot{V}O_2$) was measured by removing a 60 ml air sample from the flight jar through a 3-way stopcock cemented to the lid. A parafilm layer was inserted between the lid and the mouth of the jar to ensure an airtight seal. The air was delivered to a Beckman E-2 rapid response oxygen analyzer by an infusion pump at the rate of 54·5 ml min^{-1}. Relative humidity in the laboratory varied between 40 and 75 %. Humidity inside the flight jar could not be measured. Calculations of $\dot{V}o_2$ were made using the formula given by Bartholomew & Casey (1978), assuming R.H. = 50 %. All gas volumes were converted to STPD.

Heating and cooling curves were measured by implanting a 44-gauge copper-constantan thermocouple into the centre of the thorax while the moths were lightly anaesthetized with carbon dioxide or immediately after they had been killed with ethyl acetate vapour. The thermocouple was attached to a portable laboratory thermometer whose output was connected to the servochannel (150 mm full scale) of a Gilson polygraph.

Several methods were employed to hold the moth during heating and cooling experiments. For measurements in still air, the moths were either heated or cooled to the appropriate temperature in a constant-temperature cabinet. When they reached the desired temperature the moths, with thermocouples attached, were grasped by the forewings with forceps and transferred to a small plastic box whose floor was lined with styrofoam. The moths were placed approximately 1 cm above the styrofoam on a tripod formed by the heads of three no. 1 insect pins. To measure cooling curves in relation to wind speed, the moths were held by the dorsal margin of the forewing between two toothpicks, which were clamped to a ring stand. The thoraxes of moths were heated to approximately 45 °C using a microscope lamp. The moths were positioned in front of a squirrel-cage blower attached to a variable transformer, with the long axis of the body parallel to the direction of wind movement. Wind speed was measured immediately prior to, and following each experiment using a hot-wire anemometer. Heating and cooling constants (min^{-1}) were calculated as 2·303 × the slope of the linear regression of log $(T_{th} - T_a)$ *v* time. Heating and cooling constants were converted to conductance assuming a specific heat of 3·42 J $(\text{g}\cdot{}^{\circ}\text{C})^{-1}$.

RESULTS

Morphology. In male gypsy moths the thorax is essentially spherical in shape, having a diameter of 4–5 mm. The entire thorax is insulated by pile which varies in length from 0·87 mm on the lateral surface to about 1·25 mm on the dorsal surface. Scales are longest (2·12 mm) near the lateral border where the wings attach.

The abdomen is long (11–12 mm), slender (diameter 2–3 mm) in shape, and poorly insulated. The dorsal surface of the first three abdominal segments is loosely covered with long, hair-like scales (1 mm) but they are much less dense than those on the thorax. The remaining abdominal segments contain no long scales. The lateral and ventral abdomen has no pile.

Morphometric parameters of male gypsy moths are summarized in Table 1. The moths have large wings relative to their body size. Mean wing areas for moths mounted with wings in flight position was 5·4 cm^2, yielding a mean wing loading of 1·83 N m^{-2}. Wing mass amounted to approximately 10 % of the total body mass. Thoracic mass of male gypsy moths is 41 % of the total body mass (Table 1).

Flight performance. Several different flight patterns were seen in gypsy moths forced to fly in the jar. True hovering flight (see Weis-Fogh, 1973) occurred in all experiments, although it was rare for a moth to exhibit this pattern throughout an experiment. Usually, hovering was interspersed with attempted forward flight, during which the long axis of the body was nearly horizontal while the wings beat in a vertical plane. When attempting forward flight the moths flew into the side of the jar. The prothoracic legs could not gain foothold on the curved wall and after a few seconds

Table 1. *Morphometric parameters of male gypsy moths*

	$\bar{x}$	S.D.	Range	N
Body mass (mg)	100·8	21	45–162	22
Thoracic mass (mg)	41·4	9·8	23–60	20
Wing mass (mg)	10·06	2·92	4–14	17
Wing length (cm)	1·99	0·14	1·70–2·25	15
Wing area (cm^2)*	5·39	1·71	3·35–8·90	14
Wing load (N m^{-2})	1·83	0·60	1·13–2·98	14

* Both pairs.

hovering or climbing flight occurred. In a few instances the moths would climb abruptly and vigorously and the upward momentum caused them to follow the contour of the walls, resulting in a complete loop. I could not determine the amounts of time spent in each flight pattern during individual experiments.

The capacity for flight by gypsy moths is apparently not affected by air temperatures between 17 and 34 °C. Neither flight duration nor control of flight seemed to vary qualitatively over the range of T_a examined. Wing-stroke amplitude was not systematically measured in this study, but it could often be estimated. Amplitudes varied from 110 to 150° with no obvious differences in stroke amplitude in relation to T_a. The wing tips never touched at the top of the upstroke during flight.

Wing-stroke frequency (n) of moths flying at least 2 min showed a significant positive correlation with T_a (Fig. 1). Between T_a's of 18·5 and 34 °C mean n increased from 27·1 to 33·3 s^{-1} (about 23 %). However, between 29 and 32 °C, mean n did not vary significantly (Fig. 1).

Oxygen consumption. Mean rates of mass specific oxygen consumption of moths during free, continuous flight were 40-47 ml O_2 $(g \cdot h)^{-1}$ and were not correlated with air temperature (Fig. 2). The relatively large variability at any given T_a is probably related to the individual differences of flight patterns within the jar. At T_a = 25 °C, mean $\dot{V}O_2$ (40·2 ± 6·5 = 2 S.E.) was lower but not significantly different at the 5 % level from $\dot{V}O_2$ at $T_a = 18$ (T = 1·32) or at $T_a = 30$ (T = 0·62). Neither total nor mass-specific oxygen consumption was significantly correlated with body mass at $T_a = 25$, but in view of the small range of body mass (0·079–0·180 g), and variation of flight performance, this result is not surprising. Assuming fat utilization (RQ = 0·7) mean rates of power input of male gypsy moths are 22–26 mW (220–259 mW/g body mass). Since the thorax is composed primarily of flight muscle which is responsible for virtually all of the energy expenditure, power input (P_i) per unit mass of thorax should provide an index to the P_i of the flight muscle. Mean rates of power input per unit mass of thorax ($\bar{x}M_{th}$ = 0·041 g, Table 1) = 536 – 631 mW/gth.

Thoracic temperature. During flight, T_{th} of flying moths was, in all cases, greater than the air temperature and was not regulated between air temperatures of 19 to 32 °C (Fig. 3). Minimum $T_{th} - T_a$ (ΔT) was 6·05 °C (at T_a = 27 °C) and maximum ΔT was 7·05 °C (at T_a = 32 °C); these mean values are not significantly different ($P > 0·1$). Since there was no significant radiant input, and the power input is similar at all T_a's (Fig. 2), the similarity of ΔT at all T_a's indicates that T_{th} of flying gypsy moths is a function of the heat produced by the flight motor as a byproduct of the flight effort.

Thoracic heating and cooling constants. In still air the thorax of living moths heated

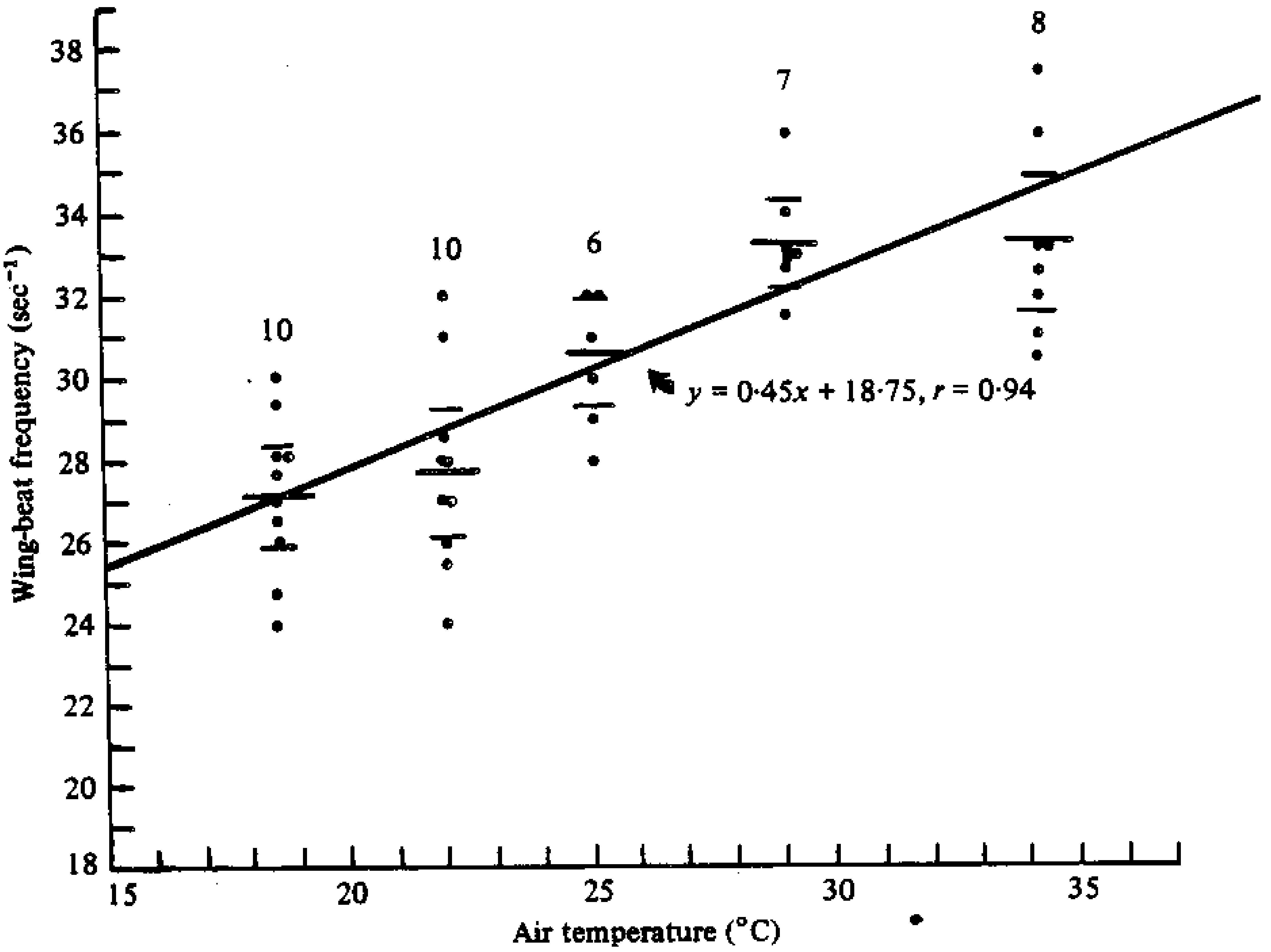

Fig. 1. The relation of wing-beat frequency of free-flying moths to air temperatures. Horizontal bars indicate mean values ± 2 times standard error. Straight line is linear regression of mean n in relation to T_a

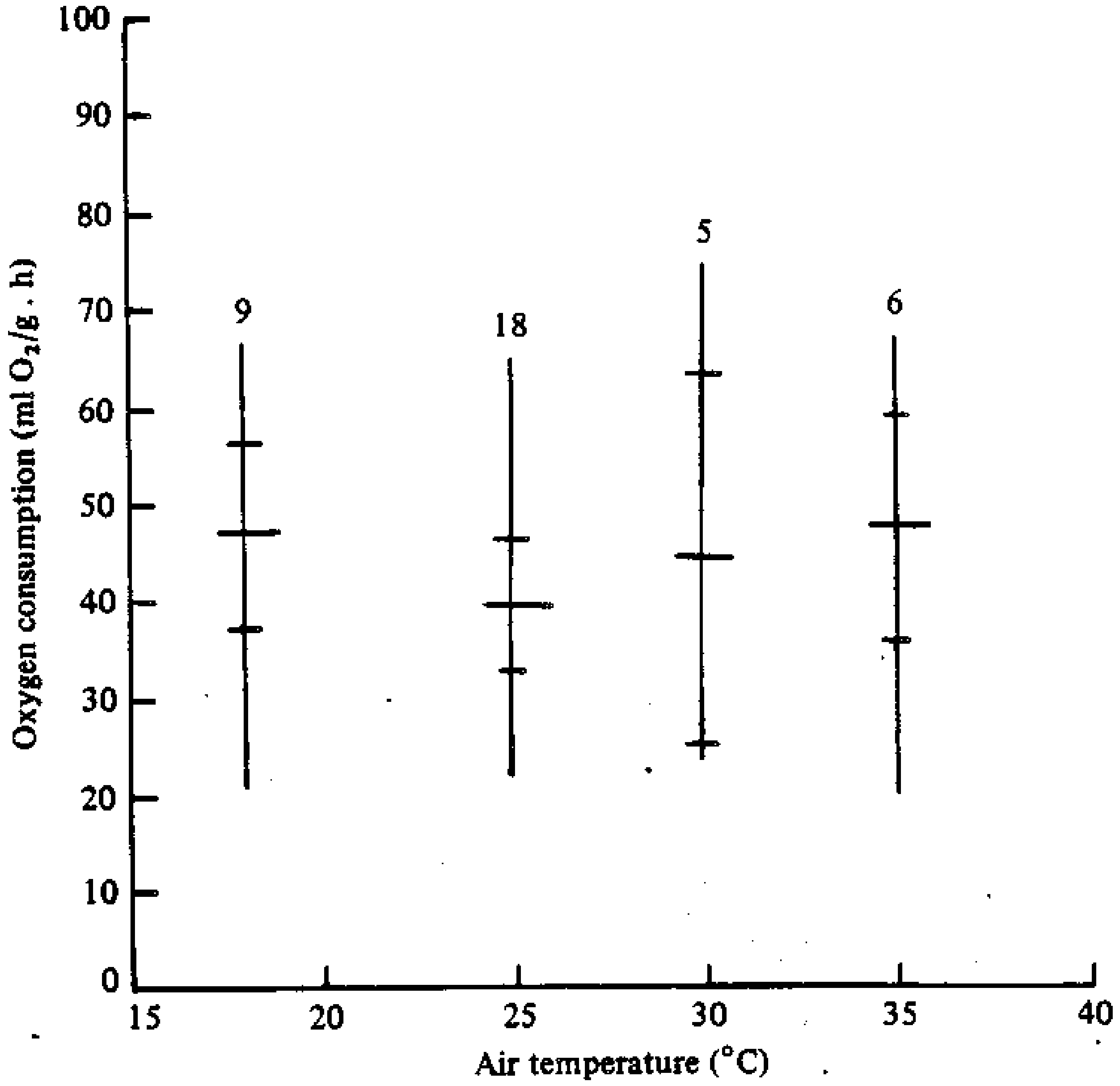

Fig. 2. The relation of mass-specific oxygen consumption to air temperature of gypsy moths during flight. Vertical bars represent range, horizontal bars = means ± standard error. Numbers indicate sample size. No moth was flown at more than one air temperature or more than once at the same temperature.

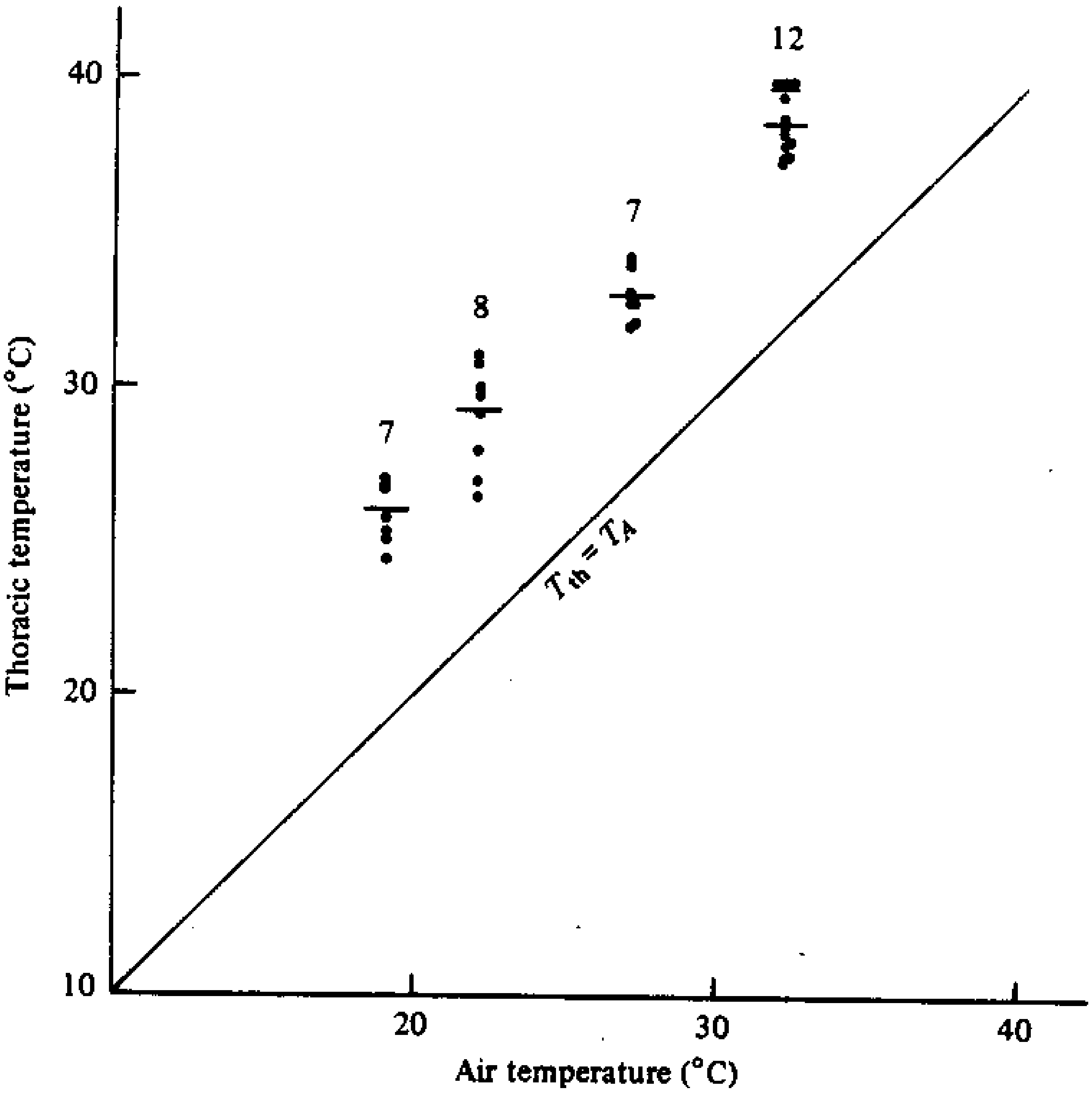

Fig. 3. The relation of thoracic temperature of gypsy moths after flights of at least 2 min to air temperature. Each point represents a separate individual. Horizontal bars indicate mean temperature.

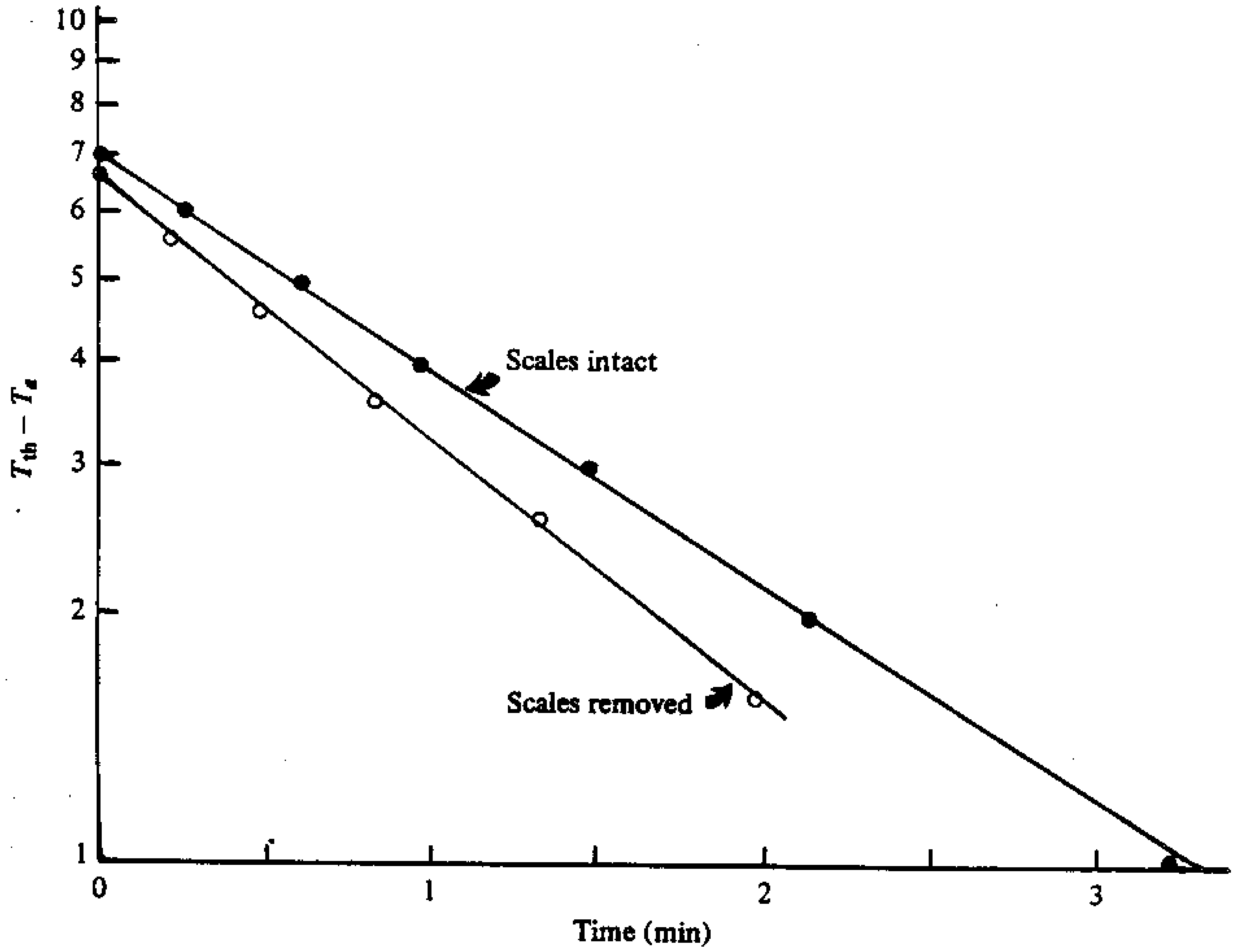

Fig. 4. Heating of 0·085 g moth in still air with thoracic scales intact and after thoracic scales were removed. After moths were cooled in a refrigerator they were transferred to a plastic box at room temperature. The thermocouple was in the same location for both experiments.

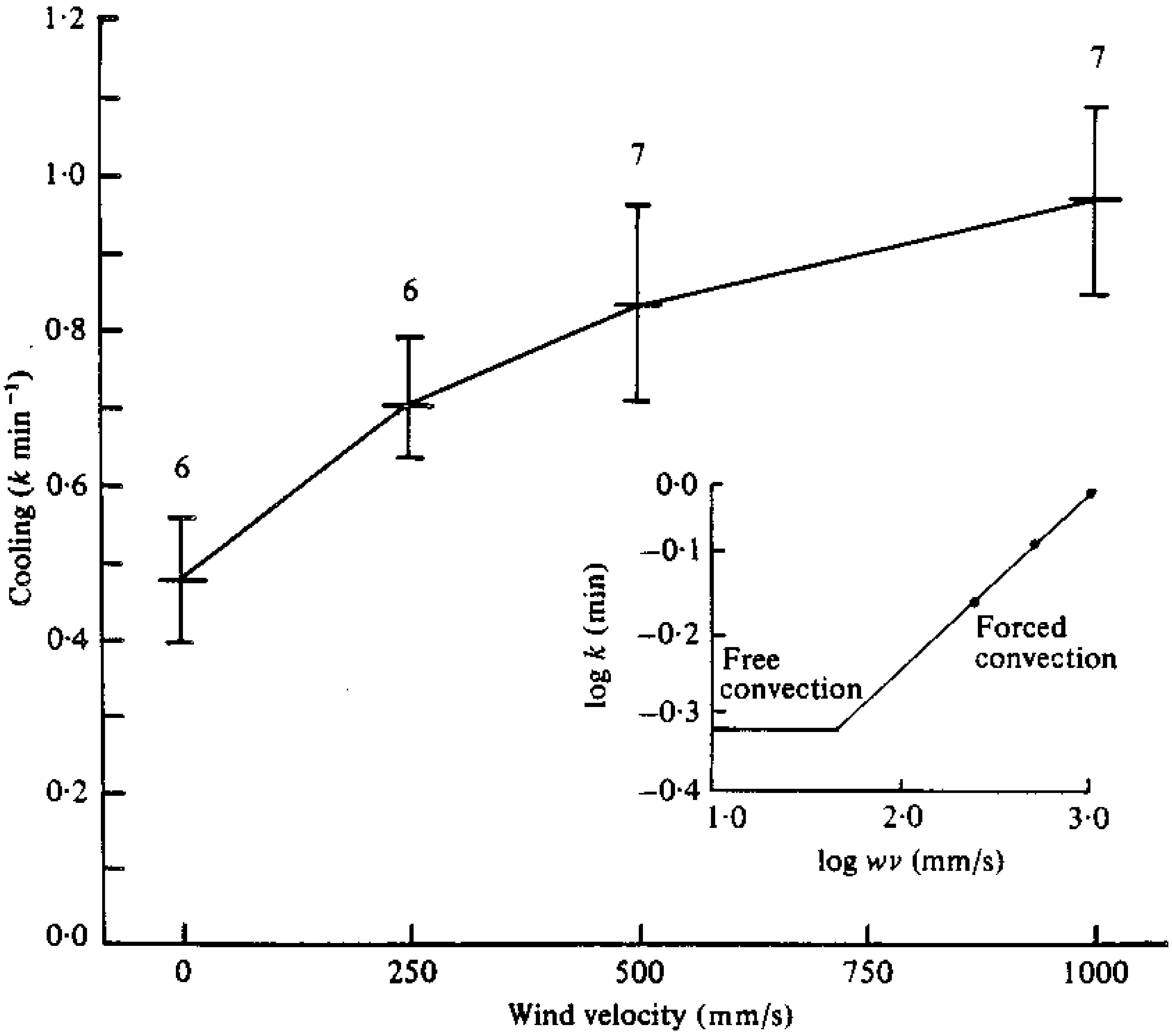

Fig. 5. Thoracic cooling constants ($\bar{x} \pm$ S.D.) of moths in relation to wind speed. Numbers indicate range. Insert: double log plot of mean thoracic cooling constant and wind velocity. The relation extrapolates to the heating rate in still air (i.e. no forced convection) at a wind speed of 45 mm/s.

and cooled at similar rates (heating constant = 0·57 $\text{min}^{-1} \pm 0·04$, $N = 3$; cooling constant = $0·55 \pm 0·05$, $N = 3$). Heating constants of moths recently killed in ethyl acetate was slightly lower than, but not significantly different from heating and cooling constants of living animals (0·48 $\text{min}^{-1} \pm 0·10$, $N = 6$, $T = -2·16$, $P > 0·05$). Differences in heating and cooling may have been influenced by body size, since the living animals used ($\bar{x} = 0·103$ g) were slightly smaller than the dead animals ($\bar{x} = 0·111$). Heating curves of the thoraxes of living and dead moths were linear on semi-logarithmic coordinates. The high correlation coefficients for linear regressions of heating and cooling curves ($r = 0·99$) for both living and dead moths indicate that heating is passive.

Thoracic scales had only a slight insulating effect in still air. Heating constants of dead moths with thoracic scales removed was 12% (range = 3–19%, $N = 5$) greater than for the same moths with thoracic scales intact (Fig. 4).

The thoracic cooling constants of dead moths are a curvilinear function of wind velocity. As in heating and cooling experiments for moths in still air, linear regressions of $\triangle T$ *v.* wind speed on semi-logarithmic coordinates were highly significant ($r = 0·99$). Cooling constants increased from 0·48 to 0·7 min^{-1} between 0 and 250 mm s^{-1}, and from 0·84 to 0·97 between 500 and 1000 mm s^{-1} (Fig. 5).

Convective heat transfer in insects is similar in still air and at low wind velocities,

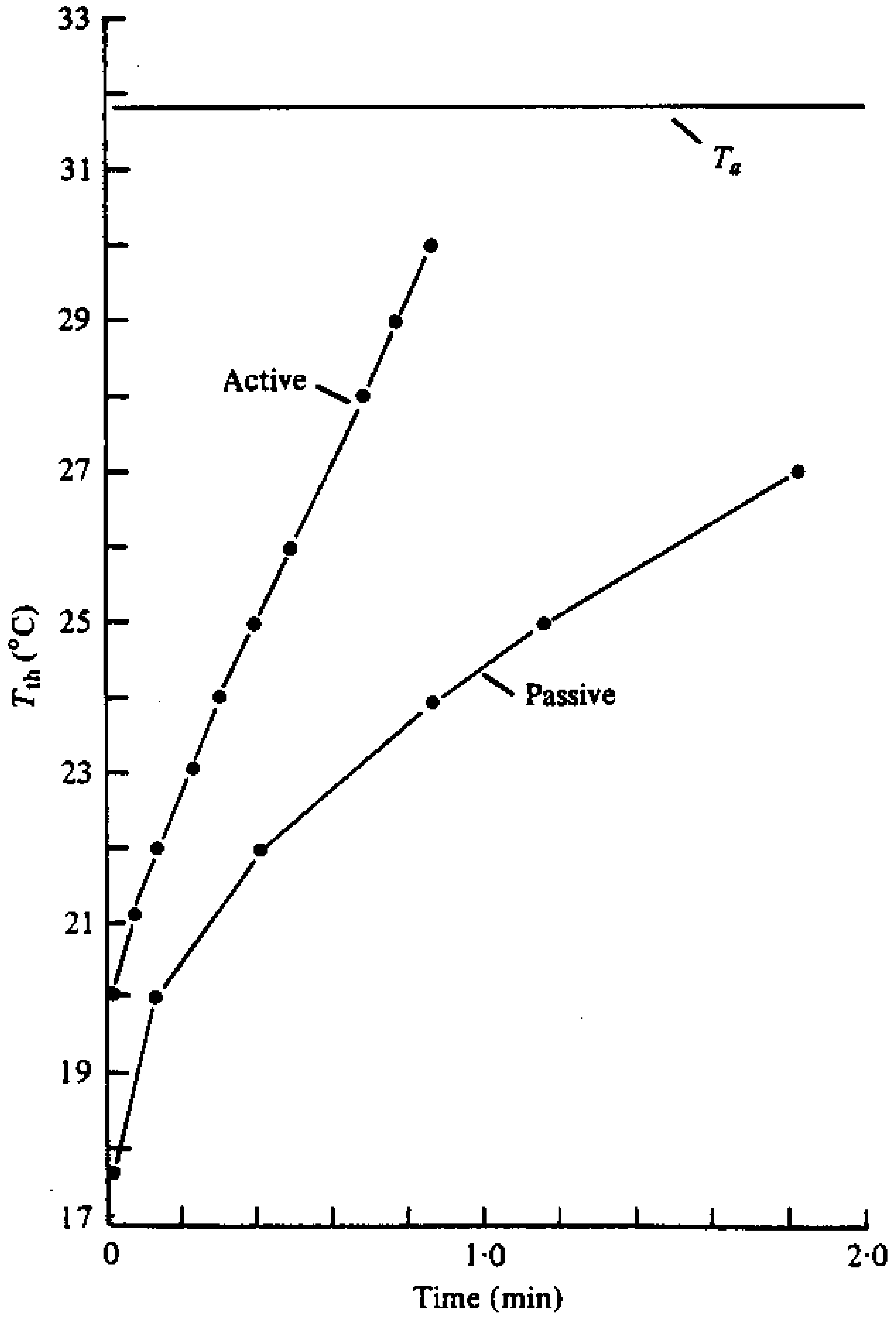

Fig. 6. Passive and active warming in 0·079 g gypsy moth. Thermocouple was in the same location for both experiments.

and occurs by free convection (Digby, 1955; Monteith, 1973). Above a certain wind speed the insulation is disrupted and forced convection is the major mode of heat exchange. On double log coordinates the mean thoracic cooling constant in moving air is linearly related to wind velocity ($r^2 = 0·99$, Fig. 5) and described by the equation:

$$\log K = 0·235 \log V - 0·717$$

where K is the cooling constant (min^{-1}) and V is the wind velocity (mm s^{-1}). The cooling constant extrapolates to the still air constant at a wind speed of approximately 45 mm s^{-1}.

Pre-flight warm up. At a T_a of 22 °C or more, flight by moths could be immediately elicited by touching them. Under these circumstances flight was continuous and controlled. At lower temperatures, however, touching the moths caused them to tumble about, often on their backs, for periods up to 30 s. In most cases, after a few seconds of tumbling, the moths would right themselves and vigorously flap their wings, while the legs remained firmly attached to the ground. Unlike warm-up previously described for moths (Dorsett, 1962; Heath & Adams, 1967; Kammer, 1970*b*; Heinrich & Bartholomew, 1971), butterflies (Kammer, 1970*a*) or skippers (Kammer, 1968), the gypsy moths seemed to be flying 'in place'. That is, the amplitude of the wing beats was usually at least 70°, and occasionally exceeded 90°.

This behaviour is undoubtedly pre-flight warm-up, since it was only seen at low temperature (17–22 °C) and only prior to take off. Fig. 6 shows heating curves for the same 0·079 g moth. In one case heating was passive while in the other case heating was facilitated by endogenous heat production and conspicuous 'medium amplitude' wing beats. In passive heating the rate of temperature increase declines as T_{th} approaches T_a. In contrast, the moth that heats both passively and actively maintains a linear increase in T_{th}, suggesting an increased rate of heat production as T_{th} increases.

DISCUSSION

Morphology and power input. Mass-specific power input of gypsy moths is low compared with values for other insects of similar mass (Kammer & Heinrich, 1978). Within several families of moths, mass-specific P_i is inversely related to body mass (Bartholomew & Casey, 1978). P_i in gypsy moths is only 40% of the P_i predicted for a sphinx moth of similar mass (Bartholomew & Casey, 1978) and about 36% of the measured P_i of the lasiocampid moth, *Malacosoma americanum*, a moth having similar body mass (Casey, 1979). Differences in P_i of moths at any given mass are to be expected because there can be substantial differences in wing length and area (Greenewalt, 1962) that will directly affect power requirements (see, for example, Weis-Fogh, 1973) and, therefore, the power input. Differences between the gypsy moth and the lasiocampid moth are undoubtably related to their respective wing loadings (Casey, 1979). Morphological differences leading to different P_i's for animals of similar mass have been demonstrated for different species of sphingid moths (Casey, 1976*b*) and for sphingid and saturniid moths (Bartholomew & Casey, 1978). In both studies the species having the highest wing loading also had the highest P_i during flight.

Wing-stroke frequency and power input. The interrelationship between n and P_i is particularly interesting because the moths are capable of flight over a 20 °C range of T_{th}, and much evidence indicates that metabolism by the flight muscles in moths is directly related to T_{th} (see Kammer & Heinrich, 1978). Gypsy moths are capable of controlled flight at several wing-stroke frequencies that are temperature-dependent (Fig. 1). Thermal dependence of n during flight has been reported in non-thermoregulating insects having myogenic rhythms (Sotavolta, 1947) and neurogenic rhythms (Kammer, 1970*a*) but their relation to power input in unclear. In gypsy moths, since P_i is relatively constant at all T_a's there must be an increased P_i per wing stroke as T_a decreases. Since there is only a modest change in n with T_a (Fig. 1) the magnitude of the change in P_i/stroke is low (0·93 mW/stroke at T_a = 18·5–0·76 mW/stroke at T_a = 35). A qualitatively similar inverse relationship between P_i/stroke and T_a is suggested for Monarch butterflies (Kammer, 1970*a*). Lepidopterans can vary the power input of the flight motor both by changing the number of active motor units and by changing the amount of double firing of each unit (Kammer, 1970*b*). In locusts, double firing can result in two to three times the work output of an ordinary twitch (Wilson & Weis-Fogh, 1962; Neville & Weis-Fogh, 1963). Associated changes

Table 2. *Mass-specific* (WKg^{-1}) *and total* (mW) *heat balance of* 0·10 *g flying gypsy moth at* T_a = 22 °*C and* 50 % *relative humidity*

(Numbers in parenthesis indicate the percent of total heat production estimated from metabolic measurements.)

	Mass-specific ($W\ kg^{-1}$)		Total (mW)
Power input	224		22·4
Heat production	179		17·9
Thoracic heat loss	138	(77)	13·8
Respiratory heat loss	12	(6)	1·2
Total heat loss	150	(83)	15·0

in the wing movements of lepidopterans by changes in wing twisting and amplitude to compensate for changes in n are unclear and should be studied.

It is obvious that the moths cannot continually compensate for reduction of n as T_a decreases by increasing P_i/stroke. The occurrence of warm-up behaviour at T_a's below 22 °C suggests that a minimum T_{th} of about 22 °C (Fig. 3), corresponding to a minimum wing-stroke frequency of about 25 s^{-1} (Fig. 1) is necessary for flight. However, warm-up behaviour is probably not useful when T_a is 15 °C or less because under the conditions of measurement the moths could only maintain T_{th} about 7 °C above T_a during flight. It is probable that under normal circumstances in the field, thoracic temperatures would be even more similar to air temperatures (see below). In the field, at T_a's between 10 and 15 °C male gypsy moths were either unwilling or unable to initiate warm-up, even after continual prodding.

Thoracic temperature and heat exchange. Data from the present study can be used to calculate the total heat loss of flying gypsy moths. Since T_{th} is not regulated, total power input can be divided into three components (after Weis-Fogh, 1964):

$$P_i = P_{a+i} + P_{th} + P_w$$

where P_{a+i} = aerodynamic and inertial power output, P_{th} = heat loss from the surface of the thorax and P_w = heat loss from the respiratory tract by evaporation of water. The mechanical efficiency of flight muscles is assumed to be 0·2 (Weis-Fogh, 1973) so that P_{a+i} = 20 % of P_i; total heat production becomes 80 % of P_i.

Respiratory heat loss. Assuming that air inspired at ambient temperature is saturated at T_{th} while in the thorax, the rate of respiratory heat loss can be calculated. For example, at T_a = 22 °C and relative humidity of 50 %, the inspired air contains 10·2 mg H_2O/l. At T_{th} = 28·6 (Fig. 1) saturated expired air contains 29·5 mg H_2O/l. Therefore warming and wetting of tidal air in the thorax adds 19·3 mg H_2O/l. Assuming an O_2 extraction efficiency of 5 % (Weis-Fogh, 1967), at a metabolic rate of 45 ml O_2 $(g.h)^{-1}$, a flying gypsy moth will ventilate at 900 ml $(g.h)^{-1}$. Total water evaporated (19·3 mg H_2O/l × 0·9 l $(g.h)^{-1}$) is 17·4 mg H_2O $(g.h)^{-1}$ and total heat loss (2·42 J/mg evaporated) is 11·7 W kg^{-1}. This amounts to only about 6 % of the total heat production (Table 2). If ventilation is determined by O_2 demand, since oxygen consumption is similar at different air temperatures, respiratory heat loss should be a minor avenue of heat exchange at all temperatures.

Thoracic heat loss. Passive heat loss from the surface of the thorax occurs largely by radiation and convection. Heat loss by evaporation from the cuticle or by conduction to other parts of the body represents an insignificant fraction of the total heat production (Church, 1960). In the laboratory, data from thoracic cooling curves may be used to calculate rates of thoracic heat loss during flight, if the appropriate wind speed is known (Bakken, 1976; Casey, 1976*b*). Under the conditions of measurement there should be no significant radiant heat input to the moths. Gypsy moths flying in a closed chamber have no significant forward speed. Therefore the only air movement across the thorax is due to the induced velocity of air passing through the wing disc. The induced velocity of a 0·1 g gypsy moth during hovering flight, based on momentum theory of helicopter aerodynamics (Pennycuick, 1968; equation 3), is 63 cm s^{-1}. The cooling constant at this wind speed (equation 1) is 0·873 min^{-1}. Thoracic conductance is 49·9 W (kg. °C)$^{-1}$ and thoracic heat loss (thoracic conductance times the thoracic temperature excess and the thorax mass) is 13·8 mW, about 77% of the heat production (Table 2). If the temperature of the head (mass $\simeq$ 8 mg) = T_{th} and heat loss is similar to that of the thorax, an additional 2·76 mW (15·4%) is accounted for.

The close correspondence between measured heat production and calculated heat loss (Table 2) indicates that measurement of thoracic temperature in small moths of low wing loading can be used to estimate the metabolic heat production. A similar approach has been successfully employed by Weis-Fogh (1964) for locusts (*Schistocera gregaria*) attached to a flight balance, flying in a wind-tunnel. This is of great interest, because data on the metabolism of insects during forward flight are scarce (Kammer & Heinrich, 1978). If the moth flies at a speed of 2 m s^{-1}, thoracic heat loss should be about 30% greater than it is during 'near hovering flight' (Fig. 5). In addition, heat loss via radiation to the night sky should be greater than the heat loss due to radiation in the present study (Church, 1960). Finally, metabolic heat production while flying at normal cruising speeds should be lower than measured in this study (see Pennycuick, 1969; Rayner, 1979), which would further reduce the difference between thoracic temperature and air temperature. Consequently, the steady-state $\triangle T$ of moths flying at normal cruising speeds should be within a few degrees of the air temperature, less than half the $\triangle T$'s measured in the present study.

Although thoracic conductance of moths is inversely related to body mass, the lack of thermoregulation by *L. dispar* is probably not due to excessively high rates of heat loss *per se*. Most insects having a body mass of 100 mg have generally similar thoracic conductance. For example, the thoracic conductance of a gypsy moth is only about 15% greater than predicted for a 100 mg sphinx moth (Bartholomew & Epting, 1975) and about 20% less than that of a tabanid fly (May, 1978). The relatively minor effect of pile in reducing the thoracic heat loss (Fig. 4) is a consequence of the overriding effect of surface-to-volume ratio as body size decreases (Digby, 1955). While rates of heat loss are determined by size, rates of heat production are a by-product of the power requirements that are determined by the aerodynamic configuration (Weis-Fogh, 1973). Interspecific differences of thoracic heat loss are minor compared with differences in P_i. Despite high rates of thoracic heat loss, a wide range of T_{th} is shown by different insects. At T_{th} = 22 °C the lasiocampid moth, *Malacosoma americanum*, maintains T_{th} at 41·5 °C – about 13·5 °C higher than that of the gypsy moth (Casey, 1979). Although similar in mass, the moths differ in shape. Thoracic temperatures and corresponding rates of heat production correlate with flight morphology, particularly wing loading.

Thermoregulation during flight is unnecessary for gypsy moths as a consequence of their morphology. The two major functions for thermoregulation during continuous flight are to ensure that the flight motor produces sufficient power for controlled flight, and to prevent thoracic overheating (Heinrich, 1974). As a consequence of their morphology, power generation by the flight motor of gypsy moths is sufficient to meet the relatively low power requirements for flight over a wide range (22–42 °C) of muscle temperatures. As the moths are usually nocturnal, they will not normally experience significant exogenous heating during flight. Relatively low rates of endogenous heat production, coupled with thoracic conductance, makes it unlikely that the moths would overheat even on warm summer evenings.

This work was supported by NSF grant PCM77-16450 and by the New Jersey State Experiment Station (Project no. 754). I thank H. Mozolic and B. Joos for technical assistance, R. Chanese, New Jersey Department of Agriculture, for providing the moth pupae, and Dr R. Foreman, Botany Department, Rutgers University, for permission to collect moths in the Hutchinson Memorial Forest.

REFERENCES

Bakken, G. S. (1976). A heat transfer analysis of animals: Unifying concepts and the application of metabolism chamber data to field ecology. *J. Theor. Biol.* **60**, 337–384.

Bartholomew, G. A. & Casey, T. M. (1978). Oxygen consumption of moths during rest, pre-flight warm-up, and flight in relation to body size and wing morphology. *J. exp. Biol.* **76**, 11–25.

Bartholomew, G. A. & Epting, R. J. (1975). Allometry of post-flight cooling rates in moths: a comparison with vertebrate homeotherms. *J. exp. Biol.* **63**, 603–613.

Bartholomew, G. A. & Heinrich, B. (1973). A field study of flight temperatures in moths in relation to body weight and wing loading. J. *exp. Biol.* **58**, 123–135.

Casey, T. M. (1976*a*). Flight energetics of sphinx moths: power input during hovering flight. *J. exp. Biol.* **65**, 529–543.

Casey, T. M. (1976*b*). Flight energetics in sphinx moths: heat production and heat loss in *Hyles lineata* during free flight. *J. exp. Biol.* **64**, 545–560.

Casey, T. M. (1979). Flight energetics of gypsy moths and tent caterpillars – similar mass but different shapes. *Amer. Zool.* **19** (3), 898.

Church, N. S. (1960). Heat loss and the body temperature of flying insects. II. Heat conductance within the body and its loss by radiation and convection. *J. exp. Biol.* **37**, 186–212.

Digby, P. S. B. (1955). Factors affecting the temperature excess of insects in sunshine. *J. exp. Biol.* **32**, 279–298.

Dorsett, D. A. (1962). Preparation for flight in hawk-moths. *J. exp. Biol.* **39**, 571–588.

Greenewalt, C. H. (1962). Dimensional relationships in flying animals. *Smithson misc. Collns* **144** (2), 1–46.

Heath, J. E. & Adams, P. A. (1965). Temperature regulation in the sphinx moth during flight. *Nature, Lond.* **205**, 309–310.

Heath, J. E. & Adams, P. A. (1967). Regulation of heat production by large moths. *J. exp. Biol.* **47**, 22–23.

Heinrich, B. (1970). Thoracic temperature stabilization by blood circulation in a free-flying moth. *Science, N.Y.* **186**, 580–582.

Heinrich, B. (1971*a*). Temperature regulation in the sphinx moth, *Manduca sexta*. I. Flight energetics and body temperature during free and tethered flight. *J. exp. Biol.* **43**, 141–152.

Heinrich, R. B. (1971*b*). Temperature regulation in the sphinx moth, *Manduca sexta*. II. Regulation of heat loss by control of blood circulation. *J. exp. Biol.* **43**, 153–166.

Heinrich, R. B. (1974). Thermoregulation in insects. *Science, N.Y.* **185**, 747–756.

Kammer, A. E. (1968). Motor patterns during flight warm-up in lepidoptera. *J. exp. Biol.* **48**, 89–109.

Kammer, A. E. (1970*a*). Thoracic temperature, shivering and flight in the Monarch butterfly, *Danaus plexippus* (L). *Z. Vergl. Physiol.* **68**, 334–344.

Kammer, A. E. (1970*b*). A comparative study of motor patterns during preflight warm-up in hawkmoths. *Z. Vergl. Physiol.* **70**, 45–56.

Kammer, A. E. & Heinrich, B. (1978). Insect flight metabolism. *Adv. Ins. Physiol.* **13**, 133–228.

May, M. L. (1976). Warming rates as a function of body size in periodic endotherms. *J. comp. Physiol.* **111**, 55–70.

Monteith, J. L. (1973). *Principles of Environmental Physics.* London: E. Arnold.

Neville, A. C. & Weis-Fogh, T. (1963). The effects of temperature on locust flight muscle. *J. exp. Biol.* **40**, 111–121.

Pennycuick, C. J. (1968). Power requirements for horizontal flight in the pigeon. *J. exp. Biol.* **49**, 527–555.

Pennycuick, C. J. (1969). The mechanics of bird migration. *Ibis* **111**, 525–556.

Rayner, J. M. V. (1979). A new approach to animal flight mechanics. *J. exp. Biol.* **80**, 17–54.

Sotavolta, O. (1947). The flight-tone (wing stroke frequency) of insects. *Acta ent. Fenn.* **4**, 1–117.

Weis-Fogh, T. (1964). Biology and physics of locust flight. VIII. Lift and metabolic rate of flying locusts. *J. exp. Biol.* **41**, 257–271.

Weis-Fogh, T. (1967). Respiration and tracheal ventilation in locusts and other flying insects. *J. exp. Biol.* **47**, 561–587.

Weis-Fogh, T. (1973). Quick estimates of flight fitness in hovering animals, including novel mechanisms for lift generation. *J. exp. Biol.* **53**, 169–230.

Wilson, D. M. & Weis-Fogh, T. (1962). Patterned activity of co-ordinated motor units, studied in flying locusts. *J. exp. Biol.* **39**, 643–667.