ENERGETICS AND THERMOREGULATION OF MALACOSOMA AMERICANUM (LEPIDOPTERA: LASIOCAMPIDAE) DURING HOVERING FLIGHT[1]

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Oxygen consumption of the eastern tent caterpillar moth, *Malacosoma americanum* (mean body mass = 88 mg), during free hovering flight was independent of ambient temperature from 17 to 30 C and averaged 126 ml of O_2 $(g \cdot h)^{-1}$. Mean wing stroke frequency was also unaffected by T_a and varied between 56 and 58 (s^{-1}). Thoracic temperature varied between 34 and 41 C between T_a's of 10–30 C. Thoracic conductance of intact (dead) moths in still air is similar to predicted values and increased by 75% between air flows of 0 and 2.0 m $\cdot$ s^{-1}. Thoracic insulation significantly retarded thoracic cooling and this effect was more pronounced at high than at low wind speeds. High levels of heat production compared with other moths of similar mass are a consequence of higher power requirements resulting from relatively small wings operating at high stroke frequencies. High T_{th} is necessary for the initiation of flight. During flight at moderate and high T_a, heat loss is regulated to prevent thoracic overheating.

INTRODUCTION

It is well known that specific heat loss is inversely related to body size, because as size decreases, the surface to volume ratio increases (Digby 1955; Bartholomew and Epting 1975; May 1976). The heat production during flight is not a function of body size per se, but rather is a by-product of the power requirements which are determined by the aerodynamic configuration (Weis-Fogh 1973). Consequently, heat production can vary markedly within a given size range depending upon the size and shape of the wings. Unless heat loss is facilitated by physiological mechanisms (Heinrich 1970, 1975), the combination of passive thoracic heat loss and production will determine the equilibrium body temperature. In moths of different families, wing loading is directly related to body

size (Greenewalt 1962; Bartholomew and Heinrich 1973). Therefore, as size decreases, rates of heat loss increase while power requirements decrease. The combination of these factors suggests that very small moths should fly at relatively low thoracic temperatures (T_{th}). In moths of 200 mg or less from several families, T_{th} during flight averaged less than 6 C above air temperature (Bartholomew and Heinrich 1973).

Few data are available on the flight energetics of Lasiocampid moths. Moths of this family are of particular interest because, except for sphinx moths, their T_{th}'s during flight are higher than other Lepidoptera (Bartholomew and Heinrich 1973). In addition, unlike sphingids, several Lasiocampid species, such as *Artace* spp., are less than 100 mg in size and their T_{th}'s during flight are much greater than those of other species of similar body mass (Bartholomew and Heinrich 1973; Bartholomew and Casey 1978). The adult of the eastern tent caterpillar, *Malacosoma americanum*, is similar in body size and wing morphology to *Artace* spp. and is a common pest species in the Northeastern

United States. The purpose of the present study is to provide a detailed examination of the energetics, wing stroke frequency, thoracic temperature, and thermal balance of this species during free, hovering flight over a range of ambient temperatures.

MATERIAL AND METHODS

Adult male moths were collected in the Hutcheson Memorial Forest, Somerset County, New Jersey, by attracting them to a 15-W ultraviolet lamp hanging on a white sheet supported by a tree limb. The moths were placed in plastic 35-mm film canisters for transport to the laboratory. All experiments were performed within 24 h of capture.

The moths flew inside an air-tight glass jar (volume 875 ml). The moths flew vigorously and continuously, without need of prodding, for durations up to 15 min. In all cases, true hovering flight occurred, that is, the stroke plane was nearly horizontal while the body was nearly vertical (see Weis-Fogh 1973). Flight performance of the moths did not appear to be inhibited by confining them within the flight chamber.

Thoracic temperature of moths immediately after flights of at least 2 min was measured to the nearest 0.1 C using a 44-gauge copper-constantan thermocouple threaded into a 26-gauge hypodermic probe attached to a Bailey Instruments laboratory thermometer. The moths were held by the distal portion of the forewings, and the probe was stabbed into the center of the thorax.

Oxygen consumption was measured by taking 60-ml samples of air from the flight chamber immediately after a flight through a three-way stopcock cemented to the lid of the jar. Flight duration was measured by a stopwatch. The air sample was injected at 55ml/min via infusion pump through a dessicant into a Beckman E-2 rapid response oxygen analyzer. Oxygen consumption was calculated according to the formula derived by Bennett, Dawson, and Bartholomew (1975). Rate of oxygen consumption was converted to rates of energy expenditure assuming 1 ml O_2 = 20.09 J.

Wing stroke frequency (n) was measured by holding a directional microphone at the mouth of the jar during a flight. The microphone was attached to a Sony A400 cassette tape recorder. After the experiment, the tape recorder was connected to a storage oscilloscope set at sweep duration of 200–500 ms. Wing strokes were counted either directly from the stored trace or the sweep duration was decreased and the period between wing strokes was measured to the nearest 0.1 mm with calipers.

Body mass and mass of thorax were measured to the nearest milligram on a top-loading balance. Head mass and wing mass were measured to the nearest 0.2 mg on a Mettler balance. Linear dimensions were measured to the nearest 0.1 mm with calipers. Wing areas were measured by taping the wings in natural flight position onto a piece of paper and tracing their outline with a planimeter. Fur depths were measured using a calibrated ocular on a dissecting microscope.

COOLING CURVES

Minimum thoracic conductance was estimated from cooling curves of thoraxes of dead moths. A small area of fur was removed from the dorsal thorax with microforceps and a hole was punched through the cuticle using a microsurgical probe. Forty-four-gauge (.002 inches in diameter) copper-constantan thermocouples were implanted into the center of the thorax. The thoracic pile was so extensive that it easily covered the denuded section after the thermocouple was implanted. Therefore, it is unlikely that the implantation procedures caused the cooling rates to be elevated significantly. Thoracic temperature was recorded at 6- or 10-s intervals by attaching the output of a laboratory thermometer to a multichannel recording digital multimeter. In some experiments, T_{th} was continuously measured on a servo-channel (150 mm full scale) of a polygraph. Ambient tempera-

ture was also monitored during the experiments.

Cooling curves were measured in a small wind tunnel constructed by attaching a squirrel-cage blower to a Plexiglas cylinder (diameter 15.4 cm, length 85 cm). Interposed between the test area and the blower were soda straws (20.3 cm long) which served to linearize the air flow. Wind speed was controlled by a variac attached to the blower and by gauze patches placed over the mouth of the blower.

The moths were attached to small wooden splints (1 mm × 1.5 mm) using a small drop of quick-drying liquid glue. The splints (6 cm long) were embedded in modeling clay positioned at the end of a long (80 cm) glass rod. The rods, in turn, were attached to a rubber stopper clamped to a ring stand.

In a typical experiment the moths were heated outside the tunnel using a microscope lamp. Simultaneously, wind speed in the center of the tunnel was measured using a heated thermopile air meter, inserted through a hole cut in the Plexiglas. When T_{th} of the moth reached approximately 45 C, the air probe was removed from the tunnel and the ring stand with glass rod, clay, splint, and moth was moved so that the moth could be placed in the wind tunnel at the exact spot where wind speed was just measured.

Thoracic cooling constants were calculated as 2.303 times the slope of the semilog plot of log $(T_{th} - T_a)$ vs. time. Cooling constants of the thorax (min^{-1}) were converted to thoracic conductance (mW/g/°C) assuming a specific heat of 3.43 J/g/°C. Thoracic insulation was removed by lightly rubbing the thorax with laboratory tissue.

RESULTS

MORPHOLOGY

The body is short and stubby (total length = 1.5 cm). The thorax is approximately 0.5 cm long and 0.5 cm wide, and is heavily furred (fig. 1). The insulation (mean depth = 2.0 mm) is arranged perpendicular to the surface of the thorax.

The legs are heavily insulated down to the tarsal joints. The abdomen, approximately 1 cm in length, tapers toward the posterior and is also furred on both the dorsal and ventral surface. However, unlike the thoracic insulation, the scales of the abdomen are less dense and their long axes are parallel to the surface of the abdomen.

Morphometric parameters are summarized in table 1. Thoracic mass with head, legs, and wings removed is 40% of the body mass. In comparison to other moths of similar mass (Bartholomew and Heinrich 1973), the mean wing loading of the tent caterpillar (37 mg/cm^2) is relatively high.

ENERGY METABOLISM AND FLIGHT PERFORMANCE

The flight of *Malacosoma americanum* was unaffected by ambient temperature between 10 and 30 C. In the field the moths were capable of vigorous controlled flight at T_a = 10 C. Both rapid forward flight and hovering were routinely observed. In the laboratory the moths flew equally well at 17 C and 30 C. Mean rates of mass specific oxygen consumption were about 125 ml O_2 $(g \cdot h)^{-1}$. Although the flight metabolism was variable at any given T_a (e.g., SD at T_a of 23 C = 19.4, fig. 2), $\dot{V}O_2$ was not dependent on ambient temperature. At ambient temperatures of 17–30 C, mean wing stroke frequencies (n) of the moths varied from 56.5 to 58.5 beats/s (fig. 2). The n for *M. americanum* are generally similar to the predicted value (about 60 s^{-1}) for insects in group 2 (see Greenewalt 1962, fig. 12) based on wing length.

Metabolic parameters for *M. americanum* are summarized in table 2. Since $\dot{V}O_2$ and n do not vary significantly with ambient temperature (fig. 2), all data are averaged. Mean n = 58.3 (± 2.2 SD, no. = 17) and mean $\dot{V}O_2$ = 126.4 ml O_2 $(g \cdot h)^{-1}$ (±24.2, no. = 20).

On a mass-specific basis, rates of oxygen consumption of *M. americanum* during hovering flight are greater than those for
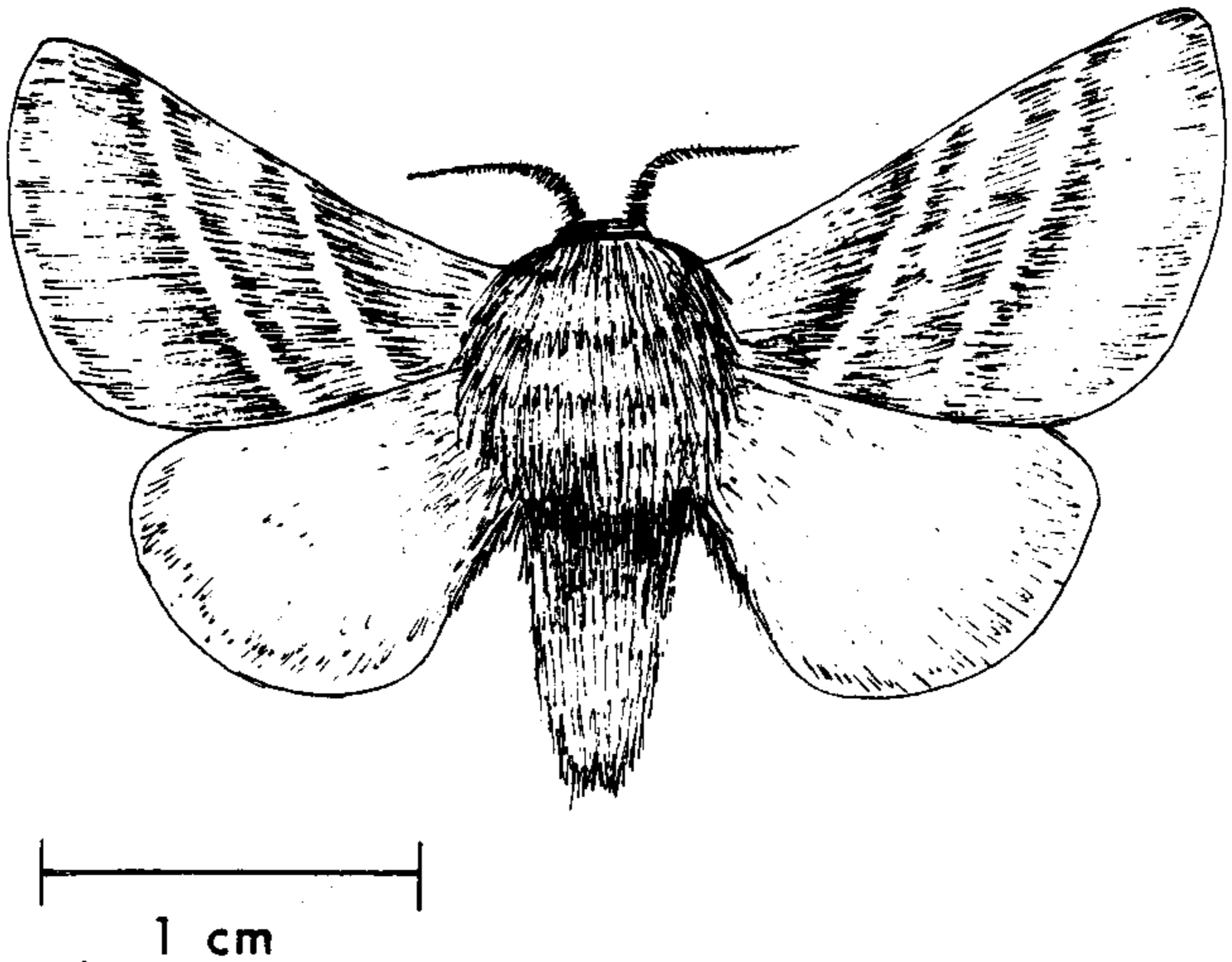
FIG. 1.—The tent caterpillar moth, *Malacosoma americanum* (note insulation on the thorax)

TABLE 1

MORPHOMETRICS OF MALE "MALACOSOMA AMERICANUM" MOTHS

	x	SD	Range	No.
Body mass (mg)	88.8	21.8	55–134	18
Thoracic mass (mg)	38.5	8.7	23–59	18
Wing mass (mg)[a]	5.0	.47	4.2–6.4	10
Wing length (mm)	14.6	1.7	12–17	10
Wing area (cm²)[a]	2.36	.46	1.33–2.70	14

[a]All wings.

TABLE 2

METABOLIC PARAMETERS FOR "MALACOSOMA AMERICANUM" DURING
FREE HOVERING FLIGHT

	O_2 Consumption	Energy Expended
Total metabolism	11.0 ml O_2/h	61.4 mW
Specific metabolism	125 ml O_2/g_{bw}/h	698 mW/g
Thorax-specific metabolism	285 ml O_2/g_{th}/h	1594 mW/g_{th}
Stroke work	.053 μl O_2/stroke	1.06 mJ/stroke
Thorax-specific stroke work	1.37 μl O_2/g_{th}/stroke	2.75 mJ/g_{th}/stroke

most hovering insects. However, these rates are generally similar to those of *Artace* spp., a lasiocampid moth having similar body mass and morphology. Moreover, predicted values for $\dot{V}O_2$ of a 90-mg sphinx moth (Bartholomew and Casey 1978) are 127 ml O_2 $(g \cdot h)^{-1}$, less than 1% different from measured values for *M. americanum*. Other data (table 2) also suggest that metabolic rates of hovering *M. americanum* are not extraordinary. Stroke work amounts to 0.053 μl of O_2 (1.06 mJ/stroke). Based on thoracic mass, the energy expenditure of the flight motor is 1.37 μl O_2 $(g_{th}/stroke)^{-1}$, similar to the values obtained for locusts and slightly lower than those of sphinx moths (see Kammer and Heinrich 1978).

THORACIC TEMPERATURE

Despite their small size, the thoracic temperature of these moths during flight exceeded ambient temperature by as much as 24 C. In the field, $(T_a \approx 10$ C) T_{th} varied between 32 and 36 C. In the laboratory, mean T_{th} of moths flying inside the respirometer increased from 37 C ($\pm$ 1.8 SD, no. = 10) at $T_a = 17$ C to 41.7 C ($\pm$ 1.6, no. = 9) at 23 C (fig. 3). At $T_a = 30$ C, however, the mean T_{th} (41.8 C, no. = 9) did not differ significantly from T_{th} at 23 C. Flight performance and energy expenditure did not differ between T_a's of 23 and 30 C (fig. 2). Therefore, the moths must be regulating their rate of heat loss since $T_{th} - T_a$ (the driving force for passive thoracic heat loss) is lower at the high T_a.

The thoracic temperature of quiescent moths approximated the ambient temperature. Moths were incapable of flight at these low temperatures. At all T_a's in-

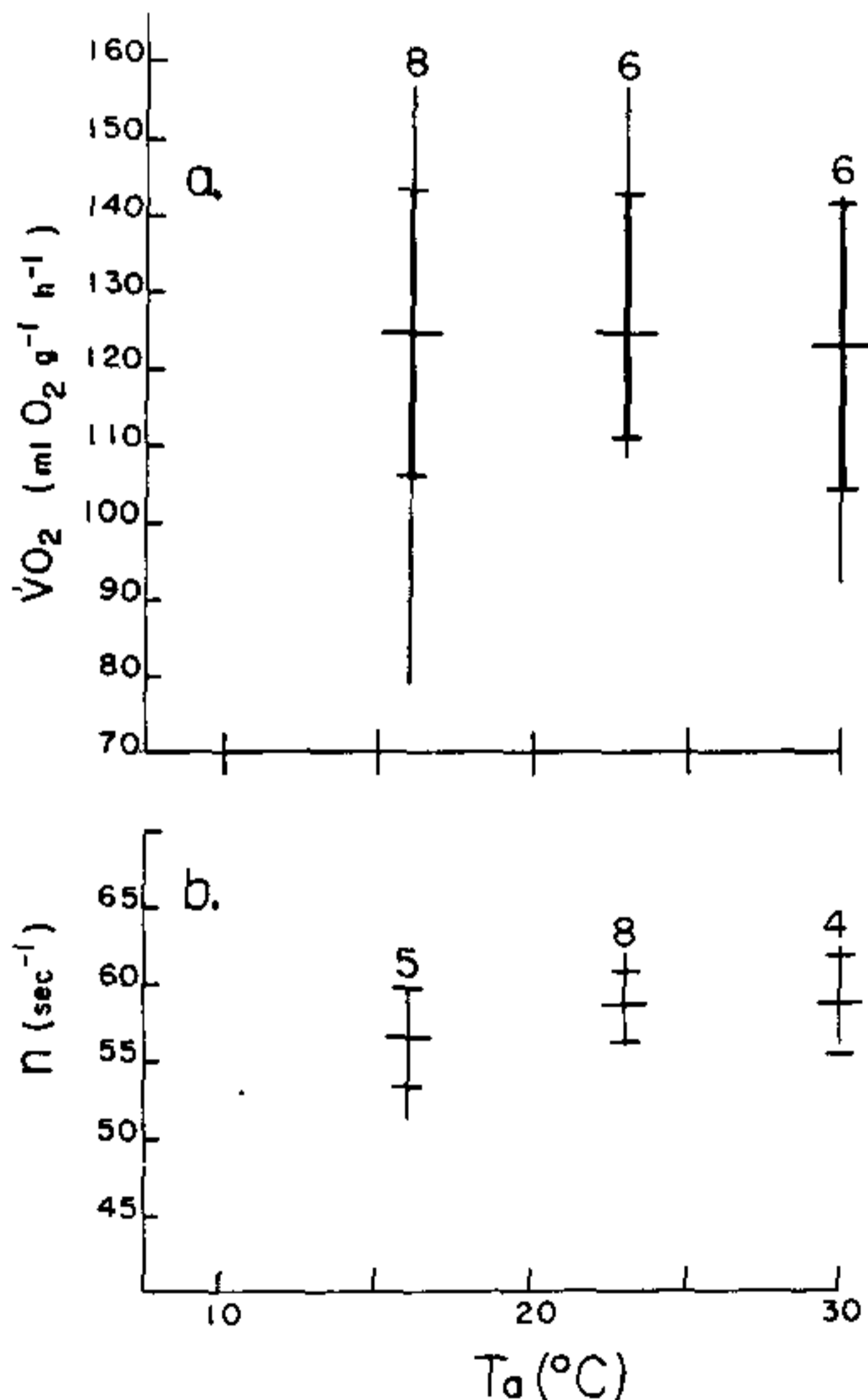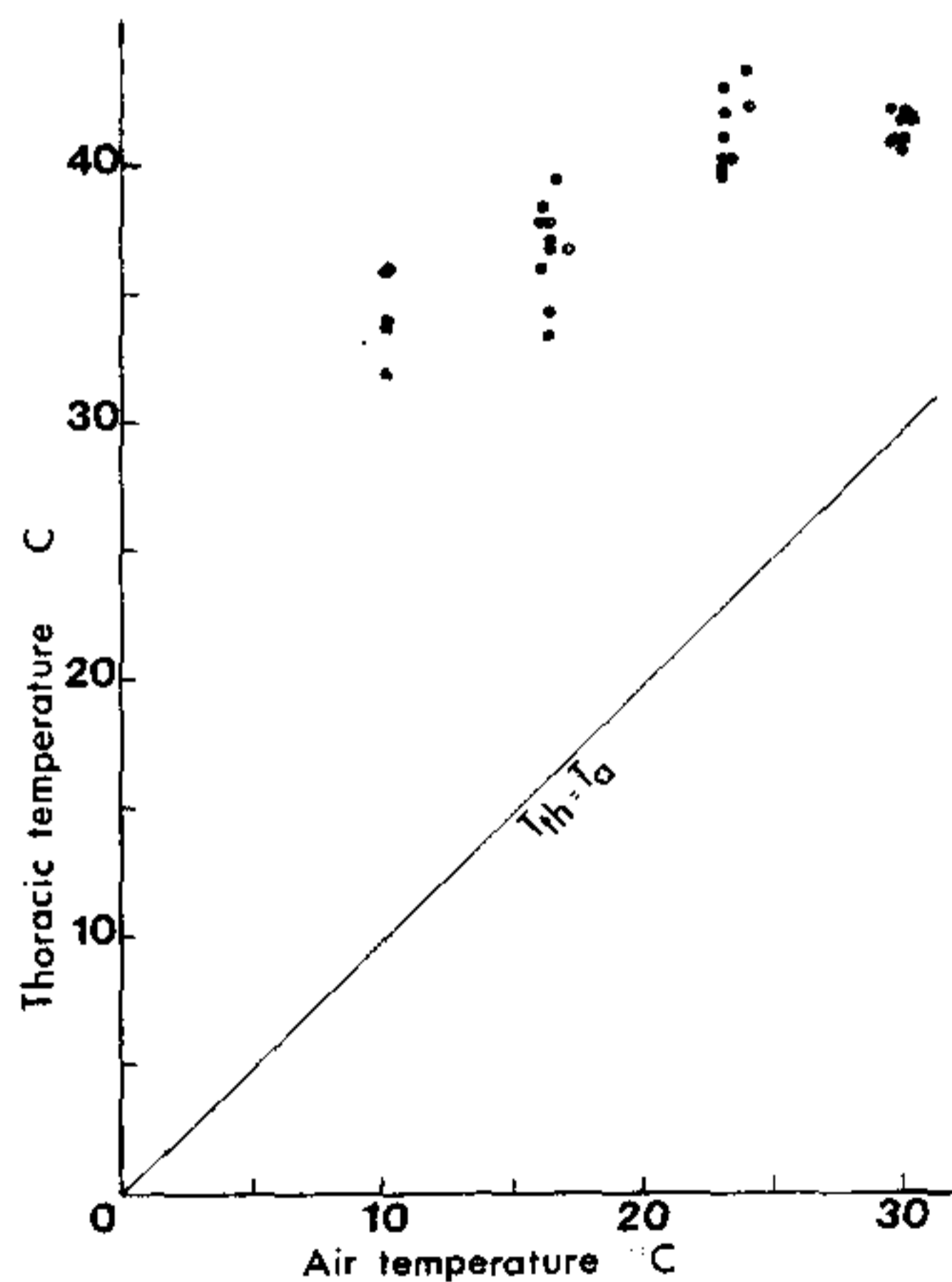
FIG. 2.—The relation of (a) oxygen consumption and (b) wing stroke frequency to air temperature; thick vertical bars indicate ±SD, thin vertical bars indicate range, horizontal bars represent the means ± standard deviation, and numbers indicate sample size.

FIG. 3.—Thoracic temperature of moths in relation to air temperature. Each point represents a separate individual. Data at $T_a = 10$ C were obtained in the field; all other data were collected in the laboratory.

vestigated, prior to flight the moths initiated a preflight warm-up routine in which the wings were held above the body. "Shivering" movements corresponding to synchronous contraction of upstroke and downstroke muscles were visible as small amplitude movements of the wings. Preflight warm-up behavior of *M. americanum* was qualitatively similar to preflight warm-up behavior of sphingid moths (Dorsett 1962).

THORACIC COOLING

Thoracic cooling curves of dead moths were linear when plotted on semilogarithmic coordinates (fig. 4). Correlation coefficients for linear regressions for each individual cooling curve were highly significant ($r^2 \geqslant .98$). In still air, the mean thoracic cooling constant of moths was 0.55 min^{-1}. Thoracic conductance in still air amounts to 31.4 mW/g_{th}/°C (table 3). This value represents the minimum thoracic conductance since the moths are dead, thereby negating increased rates of heat loss by transport of blood to the abdomen (Heinrich 1970). Moreover, conductance of moths in flight will be greater than the minimum conductance due to air movements which increases heat loss by forced convection.

In moving air, thoracic cooling constants increased in relation to the wind speed (fig. 4). Between still air and 0.35 m/s, the thoracic cooling constant increased by about 41% (fig. 5). The cooling constants of moths whose thoracic insulation was intact showed only slight increases at wind speeds above 0.75 m/s.

The thoracic insulation had a significant effect on the cooling constant. In still air, thoracic cooling constants of moths with thoracic scales removed was 0.72 min^{-1} ($\pm$ 0.06 SD, no. = 5), about 30% greater than for moths with intact insulation. This difference is significant at the 5% level. As wind speed increased, the effect of thoracic insulation on the cooling rate of moths becomes even more pronounced (fig. 5). At wind speed of 2.0 m/sec (well within the possible flight speed of *M. americanum*) moths with thoracic insulation removed exhibited cooling constants of 1.84 min^{-1}, about 100% greater than those of intact animals at the same wind speed (fig. 5).

DISCUSSION

METABOLISM, MORPHOLOGY, AND FLIGHT PERFORMANCE

While body weight is an important determinant of flight metabolism in moths (Casey 1976*b*; Bartholomew and Casey 1978), within a given size range the morphology of moths varies widely
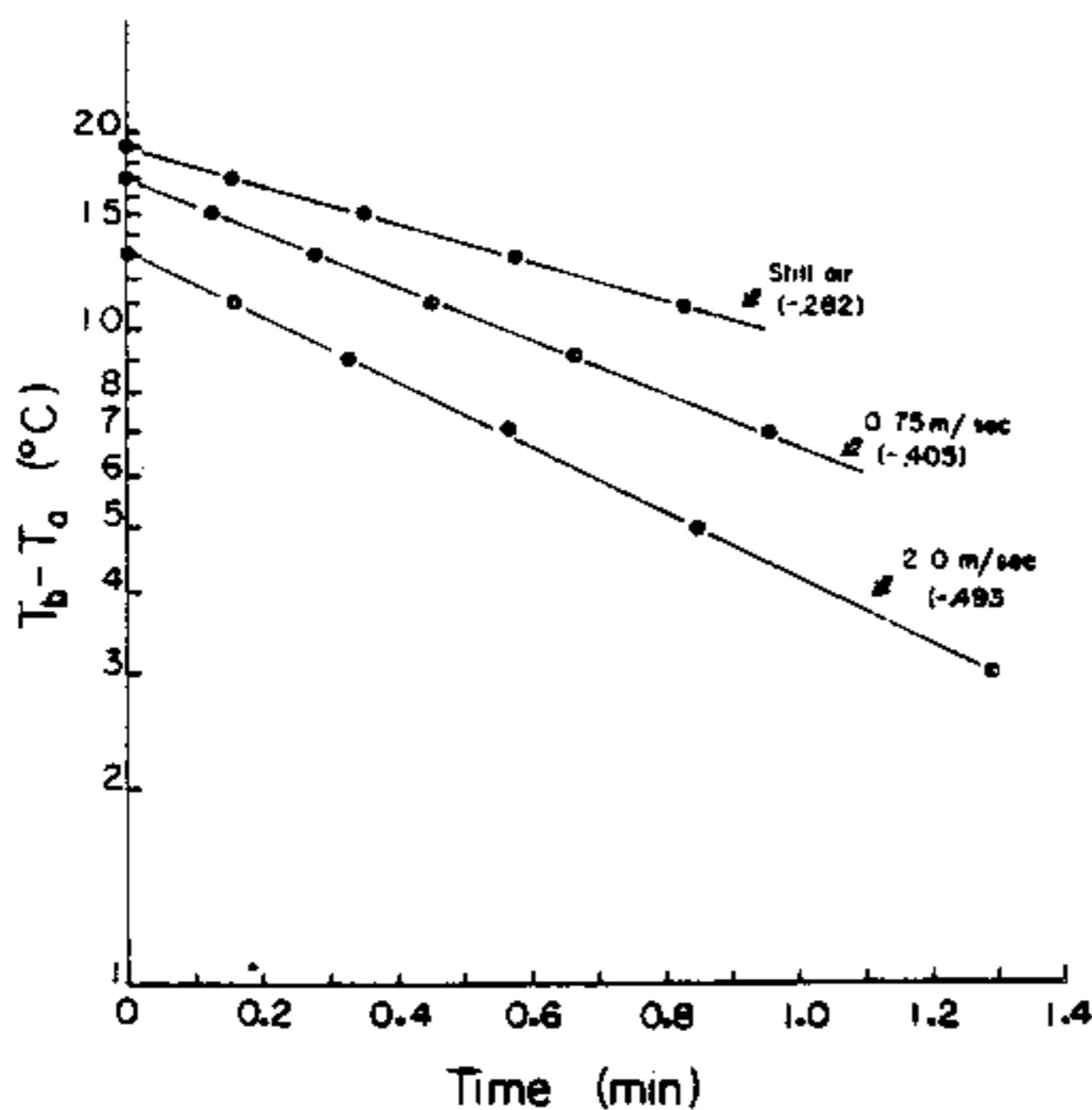

FIG. 4.—Cooling curves of 0.088-g moth in still air, 0.75 m/s wind and 2.0 m/s wind. Numbers in parentheses represent the slopes of the lines obtained by linear regression.

TABLE 3

THORACIC CONDUCTANCE OF "MALACOSOMA AMERICANUM" WITH AND WITHOUT THORACIC INSULATION IN RELATION TO WIND SPEED (1W/kg·°C = 1.163 Kcal/kg·h·°C)

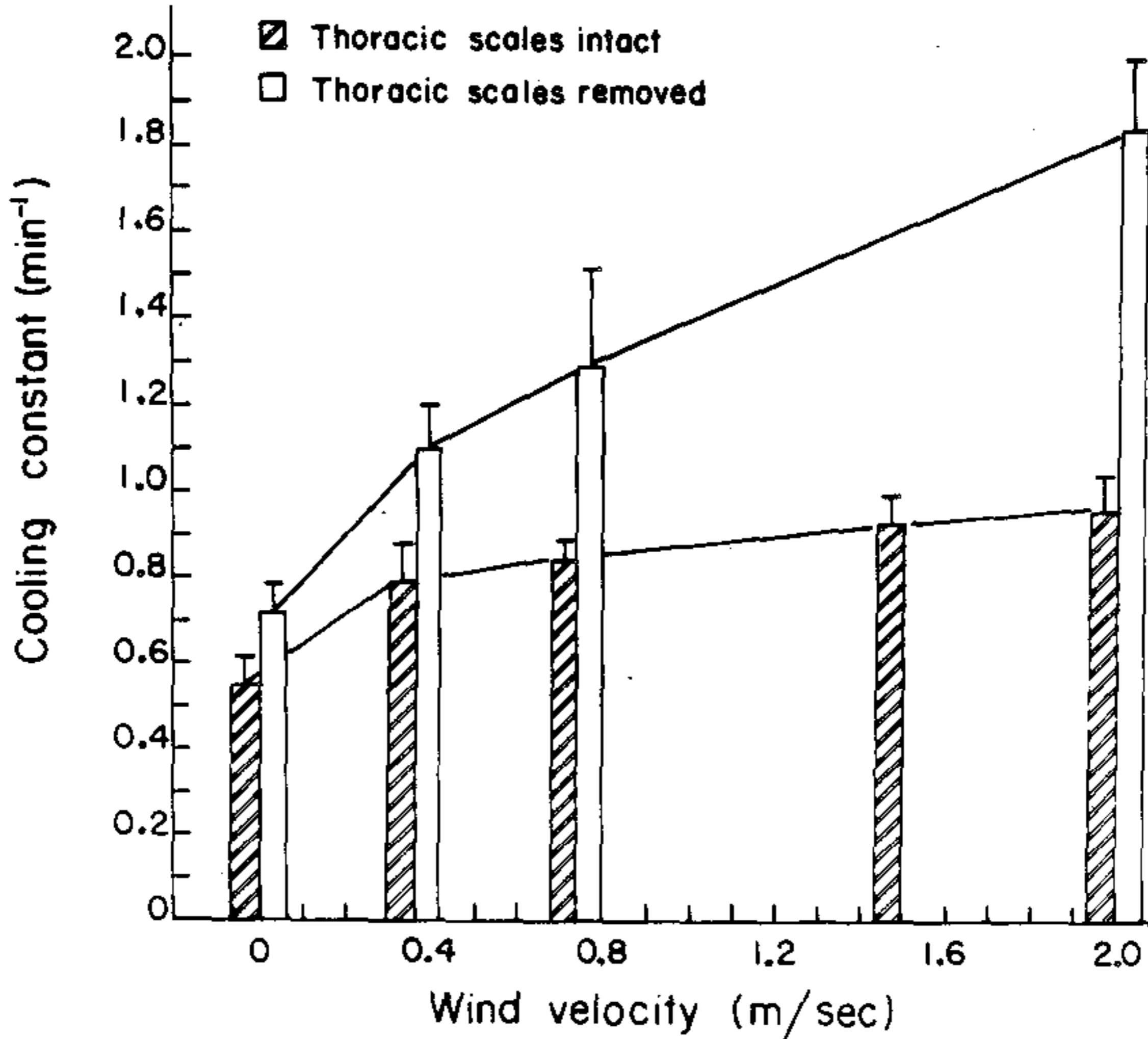| Wind Velocity (m/s)	Intact Animals (W/kg·°C)	Insulation Removed (W/kg·°C)
0	31.4	41.0
.35	45.0	62.9
.75	48.0	73.3
1.50	52.9	...
2.0	55.0	105.6

FIG. 5.—Thoracic cooling of intact moths (hatched bars, no. = 5) and moths whose thoracic insulation was removed (white bars, no. = 4) at several wind speeds. Mean values are connected and standard deviation is indicated by the lines projecting from the bars.

(Greenewalt 1962; Bartholomew and Heinrich 1973). A comparison of the flight energetics of the tent caterpillar moth with those of the gypsy moth (Casey 1980) is particularly interesting because these species are similar in weight but differ substantially in wing morphology (table 4).

Rates of oxygen consumption during flight were independent of air temperature for both species. However, mean rate of oxygen consumption of *Malacosoma americanum* is approximately 2.6 times greater than that of *Lymantria dispar*. Mean thoracic weights of the two species were 42% and 40% of the total body weights, yielding metabolic rates of 1,591 mW/g_{th} for *M. americanum* vs. 551 mW/g_{th} for *L. dispar*. Differences in rates of heat production are clearly correlated with morphological differences of the two species (table 4). The major difference be-

tween the two species is their wing area. The total wing area of *L. dispar* is 2.3 times greater than the wing area of *M. americanum*. Measured *n* of *M. americanum* at T_a = 20–25 C is more than twice that of *L. dispar*. However, metabolism per wing stroke is similar for the two species (table 4).

The lift generated by the two species must be similar, because lift must balance the weight. The wing shape is undoubtedly a major determinant of the power requirements. Other things being equal, a large wing produces greater lift per stroke than a small wing, and consequently operates at lower wing-stroke frequencies.

In addition to a reduction of aerodynamic power requirements, a reduced *n* will also result in a substantial reduction in wing inertia. For sphinx moths in this size range, inertial power requirements are at least four times greater

TABLE 4

COMPARISON OF MORPHOMETRIC, ENERGETIC, AND THERMAL PARAMETERS
FOR THE GYPSY MOTH ("LYMANTHRIA DISPAR") AND THE TENT CATERPIL-
LAR MOTH ("MALACOSOMA AMERICANUM"), MOTHS OF SIMILAR SIZE BUT
DIFFERENT SHAPES

	Lymantria dispar	*Malacosoma americanum*
Body mass (g)	.101	.088
Thorax mass (g)	.041	.036
Wing length (cm)	2.00	1.45
Wing area (cm²)	5.39	2.36
Wing load (N/m²)	.195	.396
Energy metabolism (mW)	22.6	60.0
Metabolism/thorax (mW/g)	551	1591
Thorax temperature (°C)	28	41.5
Wing-stroke frequency (s⁻¹)	27	58
Stroke work (mJ/stroke)	.94	1.06

SOURCE.—Data for *L. dispar* are from Casey (1980).

than aerodynamic requirements (Casey 1981). Because the larger wings of the gypsy moth move more slowly and need to be accelerated and decelerated less often per unit time than those of *M. americanum*, the inertial power requirements of the former should be substantially less than those of the latter. Mechanical data are needed to evaluate this hypothesis.

Not enough information is available for *M. americanum* to make detailed statements about its flight mechanics, but several points are of interest. Although the moth appears to exhibit normal hovering with no clap-and-fling mechanism (Weis-Fogh 1973), further kinematic analyses are necessary to prove this. Unsteady aerodynamics are likely to be important during hovering since lift coefficients calculated by using a triangular-wing-shape factor and the method of Weis-Fogh (1973) are in excess of 2.0. If wing shape is not terribly important in determining the induced power (Ellington 1980), the momentum jet estimate of induced power output amounts to 8.7 mW/g, about 6.2% of the mechanical power output assuming that flight muscle has a mechanical efficiency of 0.2. Given the size and shape of the wings and the low maximum lift/drag ratio of lepidopterans (Nachtigall 1976), profile power requirements may

significantly exceed induced power requirements. However, even if profile power output is twice the induced power output, the total aerodynamic power output during hovering (the sum of induced and profile power) amounts to only 19% of the mechanical power available for flight. The remainder presumably is lost as a result of acceleration and deceleration of the wing at the extremes of the stroke (see Weis-Fogh 1972, 1973; Casey 1981).

Major differences in flight performance of insects 100 mg or less are related directly to wing size and shape and to differences in the physiology of the flight motor. Within the macrolepidoptera and other synchronous fliers, increases in the size of the wings allows for a reduction in wing stroke frequency and energy metabolism. The disadvantage of this strategy is equally obvious since large wings reduce the speed and maneuverability during flight. The Hymenoptera and the Diptera epitomize the alternative adaptation, namely, small wings operating at high stroke frequencies made possible by the development of myogenic rhythms and fibrillar muscles. As a result, wing stroke frequencies considerably in excess of 100 s⁻¹ are common among bees and flies (Sotavalta 1947). Compared with moths and butterflies, the Hymenoptera

and Diptera are more accomplished fliers, not only in terms of flight speed, but also in the range of speeds and control which they exhibit on the wing. In addition, unlike moths (Casey -1981), metabolic and mechanical data for Hymenoptera and Diptera argue for the presence of an elastic system to counteract the inertial power requirements, thereby reducing a potentially significant power drain (Weis-Fogh 1973). This may explain the fact that hovering flight of *M. americanum* is more expensive than that of the bumblebee, despite the higher aerodynamic power requirements of the latter (Weis-Fogh 1973; Heinrich 1975).

THERMOREGULATION

Thermoregulation during flight depends on a balance between the rates of heat loss and heat production. Minimum rates of heat loss depend primarily on body size. The similarity of thoracic conductance of *M. americanum* to predicted values for sphingid and saturniid moths (Bartholomew and Epting 1975) and to tabanid flies and gypsy moths (May 1976; Casey 1980) indicates that the tent caterpillar moth is not unusual with respect to its rates of thoracic heat loss. Therefore, the major difference in the capacity for thermoregulation in contrast to other moths of similar body weight must be differences in heat production. The heavy thoracic insulation has a greater effect on retarding the rate of heat loss at high wind speeds than at low ones (fig. 5), indicating its major role in reducing forced convection. Thoracic heat loss during forward flight will be much greater than during hovering due to high wind speeds (induced wind velocity of hovering moths is only 50–75 cm/s), while heat production during forward flight will be lower than in hovering (Pennycuick 1969). Since the flight morphology of *M. americanum* allows them to fly at relatively high speeds, the thoracic insulation may be more significant for maintenance of high T_{th} during forward flight than during hovering.

The high cost of flight for *M. ameri-* *canum* requires a relatively high thoracic flight temperature before flight can be initiated. Unlike geometrids and lymantriids, which are capable of immediate flight at a variety of air temperatures, *M. americanum* must utilize a preflight warm-up behavior, and between T_a's of 14 and 28 C, initiates flight at 37–39 C (Casey, Buser, and Hegel 1981). A moth which is capable of generating a thoracic temperature excess of 25 C at low T_a will overheat at higher T_a's without active thermoregulatory mechanisms. Since energy metabolism is independent of T_a (fig. 2a) and thoracic temperature during flight does not parallel the isothermal line (fig. 3), thermoregulation must occur by regulation of heat loss (Heinrich 1971; Casey 1976a).

Minimum rates of heat production during flight are related to shape as well as size, since shape will have an important effect on power requirements and these, in turn, determine the energy metabolism during flight (table 4). In large insects, such as sphingid and saturniid moths, significant differences in energy metabolism have been measured for moths of a given body mass (Casey 1976b; Bartholomew and Casey 1978), but their rates of passive thoracic cooling are sufficiently low that both families of moths must thermoregulate at moderate to high T_a's to prevent overheating (Bartholomew and Heinrich 1973). In smaller insects, unless the energy demand associated with flight cost is high, rates of passive heat loss are sufficiently high to prevent the maintenance of high, relatively constant temperatures during flight over a range of T_a. However, if power requirements are low, the muscles are capable of generating sufficient energy at low and variable T_{th} so that thermoregulation in unnecessary (Kammer 1970; Casey 1980). In the moths, a whole spectrum of thermal conformation and thermoregulation is exhibited (Bartholomew and Heinrich 1973). The noctuids, for example, many of which overlap the 100–200-mg size class, are intermediate in their wing loading compared with *M. americanum* and *L. dispar,* show

conspicuous preflight. warm-up (Sotavalta 1954), and maintain thoracic temperature well below that of *M. americanum*. Unlike *L. dispar*, T_{th} is regulated during flight (Bartholomew and Heinrich 1973). If still smaller-sized moths are considered, it is unlikely that rates of heat production could continue to parallel the rates of heat loss as size decreases due to limits in the ability of striated muscle to generate energy (Weis-Fogh and Alexander

1976). Furthermore, since wing loading of moths tends to decrease as body mass decreases, heat production as a by-product of the flight effort should not increase to match rates of heat loss in most small moths. The alternative, that excess heat is produced for thermoregulation over and above that necessary to meet power requirements, has not been demonstrated in flying insects.

LITERATURE CITED

BARTHOLOMEW, G. A., and T. M. CASEY. 1978. Oxygen consumption of moths during rest, preflight warm-up, and flight in relation to body size and wing morphology. J. Exp. Biol. 76:11–25.

BARTHOLOMEW, G. A.. and R. J. EPTING. 1975. Allometry of post-flight cooling rates in moths: a comparison with vertebrate homeotherms. J. Exp. Biol. 63:603–613.

BARTHOLOMEW. G. A., and B. HEINRICH. 1973. A field study of flight temperatures in moths in relation to body weight and wing loading. J. Exp. Biol. 58:123–135.

BENNETT, A. F., W. R. DAWSON, and G. A. BARTHOLOMEW. 1975. Effects of activity on aerobic and anaerobic metabolism in the Galapagos marine iguana. J. Comp. Physiol. 100:317–329.

CASEY, T. M. 1976a. Flight energetics in sphinx moths: power input during hovering flight. J. Exp. Biol. 64:529–543.

———. 1976b. Flight energetics in sphinx moths: heat production and heat loss in *Hyles lineata* during free flight. J. Exp. Biol. 64:545–560.

———. 1980. Flight energetics and heat exchange of gypsy moths in relation to air temperature. J. Exp. Biol. 88:133–145.

———. 1981. A comparison of mechanical and metabolic estimates of flight cost of hovering sphinx moths. J. Exp. Biol. (in press).

CASEY, T. M., C. S. BUSER, and J. HEGEL. 1981. Physiology and energetics of pre-flight warm-up in the Eastern tent caterpillar moth (*Malacosoma americanum*). J. Exp. Biol. (in press).

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 hawkmoths. J. Exp. Biol. 39:571–588.

ELLINGTON, C. P. 1980. Vortices and hovering flight. *In* W. NACHTIGALL, ed. Proceedings of the conference on unsteady effects of oscillating animal wings. Saarbrucken, West Germany.

GREENEWALT, C. H. 1962. Dimensional relationships for flying animals. Smithsonian Misc. Collections 144(2):1–46.

HEINRICH, B. 1970. Thoracic temperature stabiliza-

tion by blood circulation in a free flying moth. Science 168:580–581.

———. 1971. Temperature regulations of the sphinx moth, *Manduca sexta*. II. Regulation of heat loss by control of blood circulation. J. Exp. Biol. 54:153–166.

———. 1975. Thermoregulation in bumblebees. II. Energetics of warm-up and free flight. J. Comp. Physiol. 96:155–166.

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

KAMMER, A. E., and B HEINRICH. 1978. Insect flight metabolism. Advance. Insect Physiol. 13: 133–288.

MAY, M. L. 1976. Warming rates as a function of body size in periodic endotherms. J. Comp. Physiol. 111:55–70.

NACHTIGALL, W. 1976. Wing movements and the generation of aerodynamic forces by some medium sized insects. *In* R. G. RAINEY, ed. Insect flight. Symposium of the Royal Entomological Society Vol. 7. Blackwell Scientific, London.

PENNYCUICK, C. J. 1969. The mechanics of bird migration. Ibis 111:525–556.

SOTAVALTA, O. 1947. The flight-tone (wing stroke frequency) of insects. Acta. Entomol. Fenn. 4:115.

———. 1954. The essential factor regulating the wing stroke frequency of insects in wing mutilation and loading experiments and in experiments at subatmospheric pressure. Ann. Zool Soc. "Vamano" 12, no. 2:1–66.

WEIS-FOGH, T. 1972. Energetics of hovering flight in hummingbirds and Drosophila. J. Exp. Biol. 56:79–104.

———. 1973. Quick estimates of flight fitness in hovering animals including novel mechanisms for lift production. J. Exp. Biol. 59:79–104.

WEIS-FOGH, T., and R. McN. ALEXANDER. 1976. The sustained power output obtainable from striated muscle. Pages 511–526 *in* T. J. PEDLEY, ed. Scale effects in animal locomotion. Academic Press, New York.