REGULATION OF HEAT PRODUCTION BY LARGE MOTHS

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INTRODUCTION

Moths produce large increases in their body temperatures by contraction of wing muscles (Dotterweich, 1928; Sotavalta, 1954; Dorsett, 1962; and others). This is a metabolically expensive process (Krogh & Zeuthen 1941; Sotavalta, 1954). Many moths have an insulating 'fur' which retains the heat they produce (Church, 1960). Further, the 'warm-up' process or 'shivering' may involve a special neuromuscular mechanism (Kammer, 1965).

Using a behavioural approach we were able to show that the sphinx moth, *Celerio lineata*, regulates its body temperature rather precisely during periods of spontaneous activity (Adams & Heath, 1964a), and that moths only loosely tethered maintain their body temperatures during flight within a narrow range (34–38° C.) against air temperatures from 10° to 30° C. (Heath & Adams, 1965). When the air temperature is above 30° C. the moths land periodically and cool off. The present study is an attempt to estimate the metabolic cost of maintenance of a high body temperature by moths.

The metabolic rate among insects is high during flight. It varies from 20 l.O_2/kg.hr. in Drosophila (Chadwick & Gilmour, 1940) and 76 l. O_2/kg.hr. in the desert locust (Weis-Fogh, 1952) to 100 l. O_2/kg.hr. in bees and butterflies (Prosser, 1961). Some of this energy is changed to heat. Even the moderate metabolic rates reported in the locust may cause an incidental temperature rise in the thorax of 6° C. (Church, 1960). The dense 'fur' of moths or bees decreases the rate of heat loss and may result in larger gradients between thorax and ambient air (Church, 1960). A flying insect without control of its heat production would have a constant temperature excess determined by its heat production and its thermal conductance, but it would not be able to regulate its body temperature to a constant level. This is the case in the migratory locust, flown in the laboratory (Church, 1960).

The cost of 'warm-up' preparatory to flight has received little attention. Krogh & Zeuthen (1941) calculated the cost of 'warm-up' in *Vanessa atalanta* at 8–30 l. O_2/kg.hr., and *Geotrupes* at 26 l. CO_2/kg.hr., but they did not obtain direct measurements of the cost of maintaining an elevated body temperature. Church (1960) studied the thermal conductance of insect 'fur' by implanting a hot-wire electrode in the thorax of a dead moth and measuring the temperature difference between thorax and an ambient air stream of known velocity. From the current supplied to the electrode he was able to calculate rates of heat loss and hence the heat production

required to maintain a given difference in temperature. He found 1·94 cal./min. in still air produced a temperature difference of 25° C. in *Sphinx hyastri*.

The behaviour of warming sphinx moths has been described by Dotterweich (1928) and Dorsett (1962). The events in *Celerio lineata* are sufficiently similar to make a full description unnecessary. The changes in thoracic temperature accompanying thermogenic behaviour of a restrained moth are shown in Fig. 1. The behaviour is quite striking and can be seen easily through the walls of a respirometer.

In this study we measured thoracic temperature and obtained cooling curves which permit calculation of the heat production requisite for thermoregulation. We also obtained oxygen consumption rates for animals during quiescence and thermogenic behaviour; these can be expressed as heat production. The two methods yield similar values.
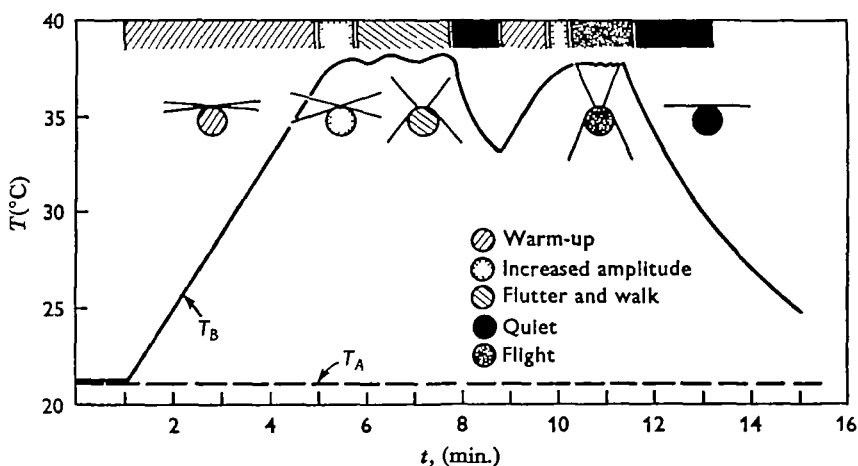

Fig. 1. Thermogenic behaviour of a sphinx moth. The activities and wing movements are related to heat production. T_B, Thoracic temperature; T_A, ambient temperature.

MATERIAL AND METHOD

Experimental animals. Adult sphinx moths, *Celerio lineata*, were obtained in the field during the spring and summer. The giant silkmoths, *Rothschildia jacobae*, were obtained as pupae and emerged in captivity.

Temperature measurements. Both thermistor and thermocouple implants were made along the thoracic mid-line just anterior to the scutellum. The thermistor probes have been described (Adams & Heath, 1964a). The thermocouple probe was made of iron constantan wire (0·2 mm. diameter). The probe leads were 1 m. long and permanently glued to the thorax of the insect. Both thermistors and thermocouple junctions resided between the flight muscles at a depth of 1–2 mm. Thermistor resistance was determined by a bridge circuit and recorded on a pen-writing oscillograph. Thermocouple junctions were connected to a recording potentiometer. Thermistors and thermocouples were calibrated against a thermometer calibrated by the United States National Bureau of Standards. Insects were discarded if the implant appeared to interfere with flight. Similar techniques were used to place thermistors in the mid-abdominal region. Implanted moths were tethered by the probe leads but otherwise

unconfined. The probe lead was attached to a vertical cloth which formed a resting place for torpid moths.

Oxygen consumption. A volumetric microrespirometer was used to measure O_2 consumption of torpid, warming and active moths. The respirometers were placed in a temperature-controlled water bath ($\pm 1°$ C.). The R.Q. was determined with the apparatus described by Scholander *et al.* (1952). The respirometer was opened and allowed to equilibrate with the atmosphere every 15–20 min. on runs with inactive animals or after bouts of activity. During the experimental period the moths were observed continuously through the walls of the respirometer chamber.

<div align="center">RESULTS</div>

Rate of heating. Moths 'warm up' prior to flight by a rapid low-amplitude contraction of the flight muscles. The rate of increase of thoracic temperature was measured directly from temperature recordings. During 'warm-up' the rate of increase is constant until the moth reaches the temperature levels required for activity. Then the warming rate decreases, and the temperature may even fall slightly as flight or movement begins. The significance of the thoracic temperature at cessation of warming has been discussed elsewhere (Adams & Heath, 1964a). Fifteen *Celerio lineata* warmed at a rate of 4·06° C./min. (range 3·1–5·2) at ambient temperatures of 15–24° C. The rate of heating showed a regression of 0·09° C./min. for each 1° C. decrease of ambient temperature. Further analysis of these data showed the rate of heating to be independent of ambient temperature ($P < 0.05$). Below 13° C. *C. lineata* is impossible to arouse, although it may increase the thoracic temperature 1–3° C. before ceasing wing vibrations. If the moth has already warmed to activity levels (34·5–38° C.) and then is placed at a new temperature of 13° C. it is able to prevent its body temperature from falling (Heath & Adams, 1965).

Four individuals of *Rothschildia jacobae* also showed rates of warming independent of ambient temperatures. But their rate, 2·5° C./min., was slower than that of the sphinx moth.

Abdominal temperature during activity. Although the thorax warms rapidly during activity, the abdomen remains at or near ambient temperature throughout the activity cycle. Fig. 2, a representative recording, shows that the abdominal temperature begins to rise at the termination of the 'warm-up' period. The rate of rise is irregular and the maximum increase is only 2–3° C. For this reason computations of oxygen consumption and heat production of active animals are based upon thoracic weight.

Oxygen consumption of torpid moths. The metabolic rate of sphinx moths kept at ambient temperatures from 26° to 36° C. are shown in Fig. 3. These data were obtained from animals which displayed no motion throughout the interval of measurement, and they reasonably represent minimal values. The rate of oxygen consumption increases with increasing temperature with a Q_{10} of 2·27. The wide range of metabolic rates results from summing the activities of individuals of different sizes. Oxygen consumption depends upon the weight of the animal and it is lower per gram of tissue in large animals than in small ones (Fig. 4). The degree of dependence of oxygen consumption on weight varies with temperature and is greater at low than at higher temperatures.

Oxygen consumption of active moths. Torpid moths (*Celerio*) were stimulated into pre-flight 'warm-up' by vigorously shaking the respirometer. Oxygen consumption was measured at 30 sec. intervals throughout the 'warm-up' period (Fig. 5). The oxygen consumption of moths at various intervals during 'warm-up' are shown in Fig. 6. Since heating rate is so uniform, the duration of the 'warm-up' period could be used to
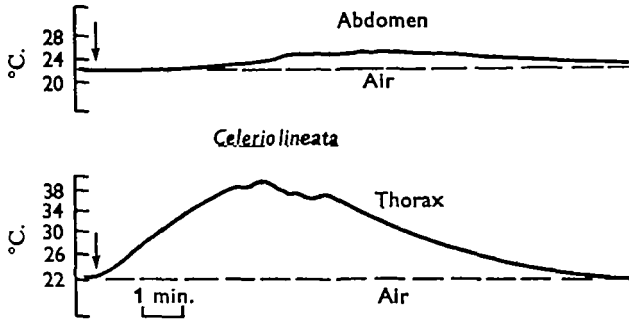

Fig. 2. Temperatures of the abdomen and thorax during activity. Differences of 10° C. or more develop during active periods.
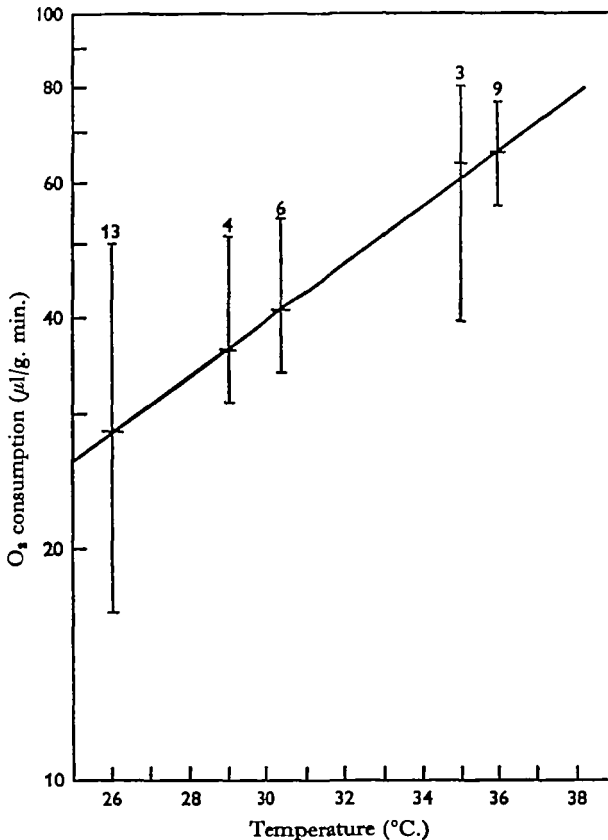

Fig. 3. Temperature dependence of oxygen consumption by torpid moths. Vertical line, range; crossbar, mean; 'number' is number of individuals measured. Values given are mean (*N* = 4–6) oxygen consumption of each individual.

estimate the difference in temperature between the moth and the chamber (1 min. = 4° C. rise). The metabolic rate was calculated using only the weight of the thorax. The greater the temperature difference achieved, the greater the metabolic cost of continued warming. Moths in respirometers kept at water-bath temperatures above 35° C. showed no pre-flight 'warm-up'. Assuming a 4° C/min. warming rate the moths ceased warming at body temperatures of 37·5–38° C. independent of ambient temperature. These values for heating time compare favourably with those reported for unconfined moths (Heath & Adams, 1965). Following the 'warm-up' period the moth often continued consuming oxygen at a higher rate than that of torpid moths but much below that during 'warm-up'. During these 'post-warm-up' periods the moths flapped their wings through a wider arc than during pre-flight 'warm-up'. They often tumbled about in the respirometers. An unconfined moth would take flight at this point in the activity cycle, and maintain a relatively constant body temperature.
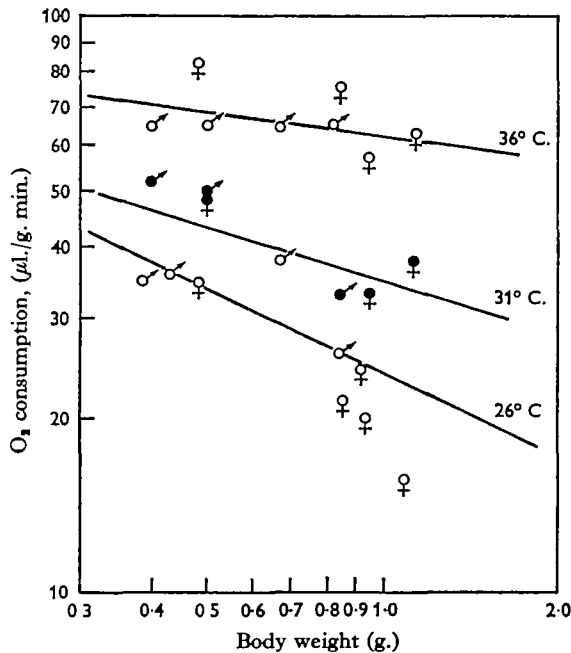

Fig. 4. Weight dependence of oxygen consumption by torpid moths at three temperatures. Points are mean oxygen consumption of each individual (N = 4–6). Lines are linear regressions and largely serve to connect measurements at each temperature.

Oxygen consumption was measured at intervals of 30 sec. to 1 min. immediately following the 'warm-up' period (Fig. 7). Several restrictions were placed upon the data obtained. First, the moth had to show uniformly high levels of activity in the respirometer throughout the interval of measurement. Second, only measurements obtained during the first 2 min. of activity following 'warm-up' were used because the high usage of oxygen during 'warm-up' and ensuing activity could seriously deplete the oxygen concentration in the respirometers. Third, activity was operationally defined to include only intense activity of the flight muscles. The thoracic weight was used to calculate the rate of oxygen consumption per gram.

Oxygen consumption during activity increases linearly with decreasing temperature (Fig. 7). A line connecting oxygen consumption at 26° C. and 30·5°C. extrapolates to zero at 37·5° C., the regulated temperature of active moths. The conclusion that *Celerio lineata* increases its metabolic rate with decreasing temperature so as to regulate its body temperature is inescapable.

Respiratory quotient. The respiratory quotient of *Celerio lineata* ranged from 0·75 to 1·00 (*N* = 12). Active animals averaged 0·79; inactive animals averaged 0·83. No significance can be attached to this difference. These values are comparable to those obtained by Zebe (1954).
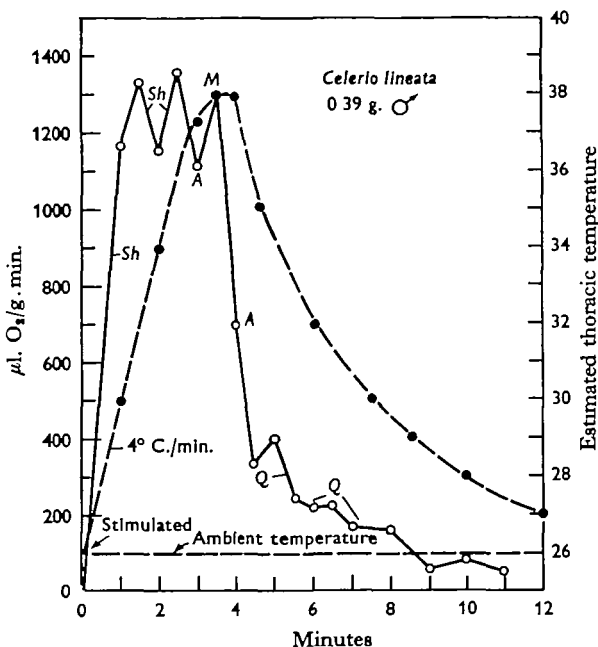

Fig. 5. Oxygen consumption and estimated thoracic temperature of a sphinx moth through a cycle of warming, activity and cooling. The activity of the moth in the respirometer is shown as *Sh* (warm-up), *A* (active), *Q* (quiet = cooling), and *M* (mixed activities). Body temperature is estimated from these as *Sh* = rise of 4 °C./min.; A, maintaining temperature; *M*, mixed 'warm-up' and active behaviour, a decreasing rate of warming; *Q*, cooling. The cooling curve is that of moth of a similar size.

Calculated metabolic rate. After a period of intense activity the moths become quiescent and their body temperatures drop exponentially to ambient levels. Since the heat appears to be generated by the flight muscles, which are inactive during cooling, our assumption is that no significant heat production occurs during cooling, which is therefore a Newtonian process. Since an animal maintaining a constant temperature balances its heat production against its heat loss, it is possible to use the cooling curve of the animal to estimate the heat production required to maintain a constant body temperature. More explicitly, rate of heat loss (dH/dt) equals rate of heat production, when body temperature is held constant. Newton's Law of cooling states that

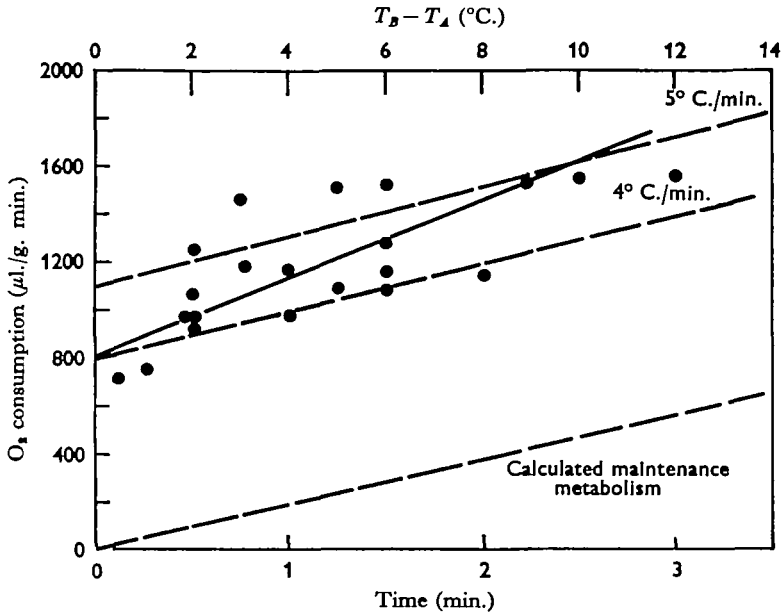$$dH/dt = AC(T_B - T_A),\qquad\qquad(1)$$

Fig. 6. Oxygen consumption of *Celerico lineata* during 'warm-up'. The consumption rate increases with duration of 'warm-up' period. The solid line is a least-square regression of oxygen consumption on time. The differences between thoracic temperature and ambient temperature (T_B-T_A) is estimated from the warming rate of $4°$ C./min. Dashed lines are calculated from the cooling curve of a 0·39 g. male moth (thorax 0·25 g.). The interval between the maintenance and $4°$ C./min. or $5°$ C./min. represents the cost of warming a 0·39 g. male moth.
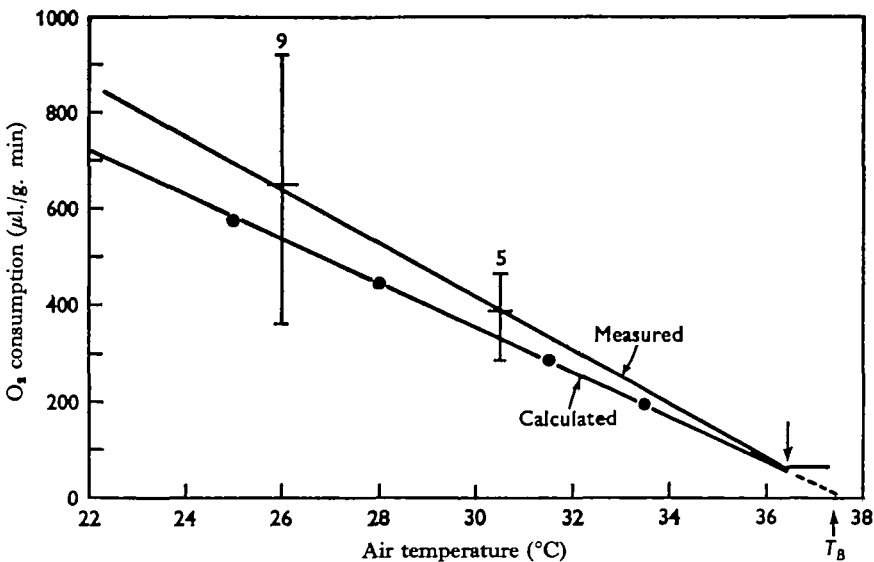

Fig. 7. Oxygen consumption of moths during periods of uniform activity following 'warm-up'. The rate increases with decreasing ambient temperature. Range (vertical line), mean (crossbar) and number of animals are given. The 'measured' line connecting mean oxygen consumptions extrapolates to zero at an air temperature of 37·5–38° C. which corresponds to body temperature during activity (T_B). The arrow at 36·5° C. is the intercept of active and torpid metabolism and represents the minimal metabolic rate. The calculated line is based upon the cooling curve of a 0·39 g. male *Celerio* (thorax 0·25 g.).

where A is area cooled, C is thermal conductance, T_B is body temperature, and T_A is ambient temperature. The amount of body temperature change (dT_B) may be measured from the cooling curve for given values of ($T_A - T_B$) and a given time interval (dt). In practice, ($T_A - T_B$) is taken at the centre of the time interval used. To compute heat loss the weight of the cooling tissue (thoracic weight) must be known. Heat loss for any given value of dT_B is given by

$$dH/dt = WS\,dT_B/dt,\qquad\qquad (2)$$

where W is thoracic weight (g.) and S is specific heat (cal. g.$^{-1}$ °C.$^{-1}$). Assuming a specific heat for insect tissue of 0·8 (Krogh & Zeuthen, 1941), we calculate for a 0·25 g. *Celerio* thorax, at a temperature difference of 9·5° C. ($T_B - T_A$): $dH/dt = 0.25$ g. $\times$ 0·8 cal./g. $\times$ 2·8° C./min. = 0·56 cal./min.

Further, assuming a caloric equivalent of oxygen at 4·8 cal./ml., then the oxygen consumption at a temperature difference of 9·5° C. is 0·117 ml./min., or 0·448 ml./g..min. Similarly, one obtains 0·199 ml./g..min for a difference of 4° C., 0·288 ml./g..min for a difference of 6° C., and 0·566 ml./g..min for a difference of 12·5° C. In Fig. 7 these computations are compared with measured values of oxygen consumption. In Fig. 6 a similar comparison is made for moths during warming. Calculated values for O_2 consumption are about 85 % of observed values. Observed values may be high due to some oxygen being used to provide kinetic energy of wing movement, which would be transferred to the walls of the vessel as heat. Furthermore, the calculations are based upon observations of cooling rates in still air and thus represent minimal values; an actively flying animal, in a moving airstream, will lose more heat by conduction.

An acceptable value for heat production can be computed from the cooling curves, for moths of known size. These calculations may be extended to encompass an entire activity cycle, with reasonable assurance of correctness.

Metabolic cost of activity for a lifetime. If the metabolic cost of a single cycle of activity can be computed, so can the cost of activity in an adult lifetime. For this a moth should be implanted with a thermistor or thermocouple and its body temperature recorded until it dies. If this is carefully done, an implanted moth will live as long as a non-implanted moth. To compute the cost of activity, we assume again a caloric equivalent of oxygen of 4·8, and a specific heat of 0·8. The rate of cooling can be measured directly from the recorded temperature. Because death is the end-point of the experiment, the fresh thoracic weight of the individual cannot be obtained directly. Instead, the whole body weight is used. But computing the cost of each cycle of activity is tedious. Since there is simple proportionality between caloric output per minute and the temperature difference per minute, the area under a temperature–time curve is roughly proportional to heat production. We need only assume that the extra heat used to increase body temperature at the beginning of an activity cycle will appear as the area under the cooling curve at the end of the cycle.

For any given chart paper there will be a conversion factor to convert temperature–time units (degrees × min) to caloric units (cal./cm.²). Then it is only necessary to measure the area under the curve with a planimeter and convert the sum of all the activity cycles to calories.

Silk moths (*R. jacobae*) do not feed in the adult stage so these were used to test the approach outlined above. Since the amount of activity and the cost of a given period of

activity vary with temperature, the moths were kept in constant-temperature chambers throughout the experiment. Two moths were started at each of five constant-temperature levels. Some of the records were interrupted by failure of a chamber to maintain a constant temperature for long periods, by probe failures, or temperature-recorder failures. One individual at each of four temperatures was followed throughout its lifetime without incident (two males at 17° and 29° C. and two females at 21° and 25° C.) In spite of the small sample the results are interesting and instructive. Fig. 8 is an example of the records obtained.
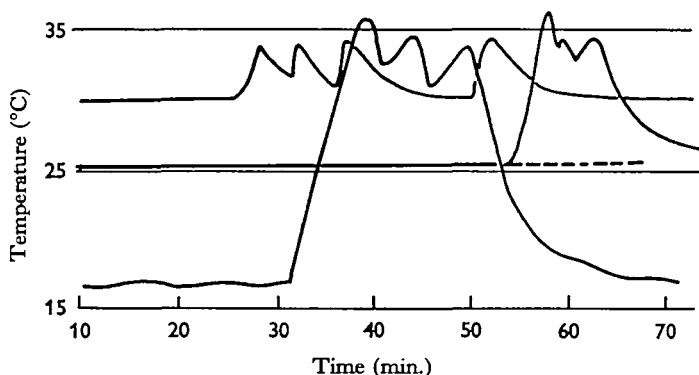

Fig. 8. 'Warm-up' and activity in three *Rothschildia jacobae* kept at 17°, 25° and 29° C. All animals warmed to about the same temperature levels. The active period is operationally defined as the interval from the beginning of 'warm-up' to the beginning of a cooling curve that extends to ambient temperature. Thus the animal at 29° C. shows two periods of activity; the others show only one each.

Each record was analysed for the period of spontaneous activity, the number of active periods, the heating rate, maximum and minimum temperatures during the activity periods, and the area under the temperature–time curve. The latter was converted to calories by using the cooling curve of the animal to estimate heat production during activity. Fig. 9 summarizes these data. The average activity period ranged from 20 to 30 min. but was depressed to less than 20 min. with the moth kept at 17° C. However, the number of active periods increases markedly with temperature ($Q_{10} = 8\cdot3$). The rate of heating is uniform for individuals kept above 20° C. but slightly depressed for the animal at 17° C. The total caloric output increases with temperature ($Q_{10} = 2\cdot2$). The thoracic temperature is maintained uniformly between 32° and 36° C. One female moth did not reach the same temperature levels as the others. This is reflected in the lower figure for total calories she used. Additional data are shown for a male kept at 23° C. but whose recording was interrupted.

Although the moth at 29° C. had more periods of activity than the other moths, its total lifetime, active plus inactive time, was less than a week, while the animal kept at 17° C. lived nearly 2 weeks. A greater share of the energy store of the moth at 17° C. was probably used as maintenance energy in torpor. If degradation of 1 g. of fat produces 9500 cal., the energy expenditure of the moth of 310 cal. at 29° C. requires only 32 mg. of fat. Gilbert & Schneiderman (1961) found moths of the related species, *R. forbesi* and *R. orizabae*, had 29% (1·690 g.) and 32% (0·416 g.) body weight respectively as extractable lipid in males and 3·7% (0·186 g.) in a female *R. orizabae*.

Using these figures we estimate that no more than 10 % of the lipid reserve is used for heat production in a 1 g. male *R. jacobae*, but females may use as much as 50 % of their reserve for heat production.
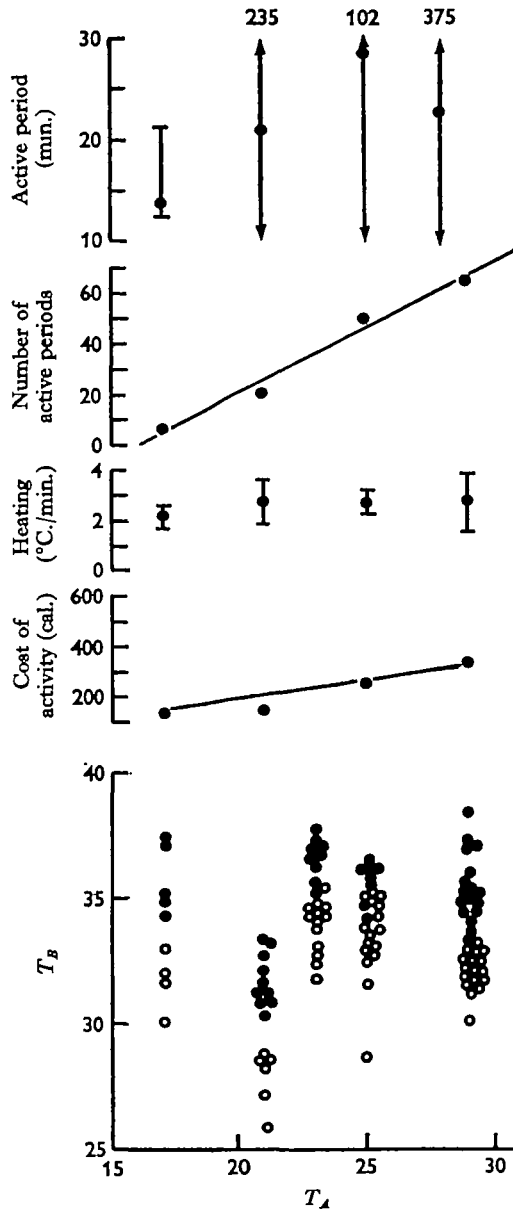

Fig. 9. Summary of thermogenic activities and temperature regulation of four *R. jacobae*. Top graph: ●, mean active period; numeral and bar, range. Some periods lasted less than 10 min. Second graph: ●, total number of active periods; the line, fitted by eye, has a Q_{10} of 8·3. Third graph: ●, mean; vertical bar, range. Fourth graph: ●, total estimated energy expenditure for thermoregulation; the line, fitted by eye, has a Q_{10} of 2·2. Bottom graph: maximum (●) and minimum (○) thoracic temperatures during active periods. Not all temperatures are shown, but the highest and lowest values and representative intermediates are included. The animals kept at 17°, 23° and 29° C, are males; the ones at 21° C. and 25° C. are females. The low temperatures of the animal kept at 21° C. are reflected in the lower value of total calories expended.

DISCUSSION

Moths can regulate heat production to maintain relatively constant thoracic temperatures when active. The cost of this regulation is high, but it is only a fraction of the cost of flight. Some heat produced by flight is conserved, so that temperature regulation is partly incidental to activity.

Adjustment of the metabolic rate to offset heat loss also occurs during the 'warm-up' for flight. A moth maintains a constant rate of rise of internal temperature through the 'warm-up' period. The constancy of the rate of temperature increase becomes progressively more expensive as the difference in temperature between thorax and environment increases. The metabolic rate increases sufficiently to offset the increasing cost of 'warm-up'.

The regulatory process of moths is strikingly similar to that of birds and mammals, yet it differs in two fundamental features: in the duration of the period of regulation and in the range of tolerated variation of body temperature.

Spontaneously active moths may maintain their body temperature at high levels for periods ranging from several minutes to 2 hr. or more. During this time the moths fly, feed, and seek mates. At other times they are torpid. Among birds and mammals the body temperature is usually kept high throughout life with only a slight depression accompanying sleep. A few birds and mammals undergo seasonal hypothermia (hibernators) or daily hypothermia (bats and humming birds), but even among daily 'hibernators' the active and warm period exceeds 8 hr./day (Pearson, 1960).

Active white-lined sphinx moths maintain their body temperature between 34·8° and 38° C. (Adams & Heath, 1964a) and *R. jacobae* between 32° and 36° C. Moths seem indifferent to temperature changes within this range. Although birds and mammals may tolerate changes of this magnitude during bursts of activity or under stress, they normally maintain the body temperature in a more restricted range.

These differences may be related to the difference in size between homeothermic vertebrates and moths. If only the temperature of the thorax, and perhaps the head, of a moth are regulated, then a moth's effective size is a full order of magnitude smaller than that of the smallest bird or mammal. Changes in body temperature occur so rapidly that a closer control of internal temperature is not feasible.

At high ambient temperatures the temperature excess produced in the flight muscles may require moths to stop flight and cool off. However, similar restrictions apply to birds and mammals. Under severe stress some moths, like their vertebrate counterparts, may employ evaporative mechanisms to hasten cooling (Adams & Heath, 1964b).

Warm moths radiate detectably in the infra-red. Callahan (1965) has discovered sense organs on moths capable of detecting infra-red radiation at wavelengths (7–13 μ) radiated by a warm moth. The atmosphere is transparent in this region. He suggests that thermal radiation may be detected by moths and used in conjunction with pheromones as an aggregating signal. Moths are often few in number and widely scattered in a given area. Species are highly seasonal and often fly only a few hours each night. The small metabolic store of male moths coupled with their large energy requirements favour development of multiple mechanisms to facilitate discovery of receptive females. Recognition may be facilitated by the characteristic wave length

corresponding to the regulated internal temperature. Our observations lend support to his view. Female Lepidoptera in general, and probably *Rothschildia jacobae*, have much smaller stores of fat than males (Gilbert & Schneiderman, 1961). Their energy stores are too small to permit extensive flights. However, our observations suggest that they 'warm up' as often as males and use perhaps 50 % of their energy stores for heat production. This seemingly wasteful use of energy may generate an infra-red signal which helps males to find mates.

Temperature regulation by moths occurs when conditions are suitable for activity. In this sense, the process is a behavioural one, and it requires a behaviourist's approach. Much of the work on heat production of insects has been done without this consideration. The sequence of behaviour elicited from a moth disturbed during its day-time retreat is different from that of a moth during its usual period of activity at night (Adams & Heath, 1964a). For this reason animals stimulated to activity during the day may not show the fine adjustments of body temperature and behaviour recorded from spontaneously active and chronically implanted moths. However, it is simply not possible to provide suitable conditions to the moth on a flight mill or in a respirometer. Under such conditions one must be aware of the artifacts introduced. For example, an insect on a flight mill is forced to fly without the option of landing or moving into a shaded situation to lose the excess heat developed. Sotavalta (1954) found he could force honeybees to extremely high body temperatures (44·5° C.) on a round-about in ambient temperatures at 36° and 37° C. He points out that the high values obtained in the laboratory may never occur in nature. Indeed, we doubt whether bees would voluntarily fly at all at such high temperatures. Similarly, the behaviour of individuals in a respirometer must be followed continuously to assure that a meaningful measurement will result.

SUMMARY

1. Moths 'warm-up' prior to flight at mean rates of 4·06° C./min. in *Celerio lineata* and 2·5° C./min. in *Rothschildia jacobae*. The abdominal temperature rises only 2–3° C. during activity.

2. Oxygen consumption of torpid sphinx moths increases by a factor of 2·27 as temperature changes from 26° to 36° C.

3. Oxygen consumption during 'warm-up' increases with duration of 'warm-up' from about 1000 μl./g. min during the initial 30 sec. to nearly 1600 μl./g. min. during the 3rd min. This increase compensates for increasing heat loss from the thorax during 'warm-up'.

4. When the moths are regulating thoracic temperature, oxygen consumption increases with decreasing air temperature from a mean of about 400 μl./g. min at 31° C. to about 650 μl./g. min. at 26° C

5. Values of O_2 consumption calculated from the cooling curve of *C. lineata* are about 85 % of the measured values of O_2 consumption.

6. The giant silk moth, *Rothschildia jacobae*, regulates thoracic temperature during activity between about 32° and 36° C. at ambient temperature from 17° to 29° C. Moths kept at high temperatures are active longer, have more periods of activity and expend more energy for thermoregulation than moths kept at low temperatures.

7. Large moths increase metabolism during active periods to offset heat loss and

thereby maintain a relatively constant internal temperature. In this regard they may be considered endothermic, like birds and mammals.

8. We estimate that male moths use 10 % of their stored fat for thermoregulation, while females may use 50 %.

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