

ALLOMETRY OF POST-FLIGHT COOLING RATES IN MOTHS: A COMPARISON WITH VERTEBRATE HOMEOTHERMS

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SUMMARY

1. The rates of post-flight cooling in 25 saturniid moths of 8 genera ranging in weight from 81 to 2650 mg were measured and compared with cooling rates in sphingids, birds and mammals.
2. The initial and terminal cooling rates of the saturniids did not differ significantly.
3. Large saturniids have relatively smaller thoraxes than small ones.
4. In saturniids the rate of post-flight cooling is inversely related both to thoracic volume and total weight.
5. Cooling rate is less dependent on thoracic volume in saturniids than in sphingids.
6. Weight-specific conductance calculated on the basis of total weight, shows that moths are not as well insulated as birds or mammals. However, when considered on the basis of thoracic weight, the weight-specific conductance of saturniids and sphingids closely approximates that predicted by the regression of weight-specific conductance on total body weight in birds and mammals.
7. Since the insulation of saturniids and sphingids is no more effective for animals of their size than is that of birds and mammals, their high body temperatures during activity appear to depend primarily on high levels of heat production.

INTRODUCTION

No homeothermic vertebrates weigh less than 2-3 g. Moreover, except for shrews, most mammals and birds weighing less than 5 g are heterothermic and maintain high and regulated body temperatures only when they are active or when food is available in excess (see Bartholomew, 1972 for review). During periods of inactivity heterotherms have the capacity to allow body temperature to fall to within a degree or so of ambient temperature. The term heterothermy is ordinarily used with reference to hummingbirds, small bats, and small rodents. However, it also is applicable to those insects which maintain high and regulated body temperatures, when active, despite the fact that some of them weigh much less than a gram (see Heinrich, 1974 for a detailed review). Among these heterothermic insects are moths of the families Sphingidae and Saturniidae. Sphingids and saturniids differ in several physiological

and morphological attributes that affect insect body temperatures; for example, relative size of the thorax and abdomen, wing loading, scalation, and feeding habits.

For endothermic animals to regulate body temperature, rates of heat production and heat loss must be balanced. Rates of heat loss of endotherms can be quantified in terms of cooling rates if the animals are dead or in a heterothermic state. The cooling rates of birds and mammals (Herreid & Kessel, 1967) when allometrically scaled show the same inverse proportionality as does the scaling of rates of heat production below the zone of thermal neutrality (Lasiewski, Weathers & Bernstein, 1967). Both heat loss and heat production below the zone of thermal neutrality can be expressed as weight-specific thermal conductance, $\text{cal (g h } ^\circ\text{C)}^{-1}$, where $^\circ\text{C}$ refers to the difference between body temperature and ambient temperature (a quantity that is often called the 'temperature excess' by students of insects).

Analysis of post-flight cooling rates in sphingids indicates that their weight-specific thermal conductance scaled against body weight shows the same slope as that of birds and mammals (Bartholomew & Epting, 1975). This indicates that the attainment of elevated and regulated flight temperatures by sphingids is primarily dependent on the high level of heat production by flight muscles rather than on especially reduced rates of heat loss.

Information on post-flight cooling in saturniids is limited to the cecropia moth *Hyalophora cecropia* (Oosthuizen, 1939; Heath & Adams, 1967; Hanegan & Heath, 1970; Bartholomew & Casey, 1973). Comparative data on body temperatures in both sphingids and saturniids during flight is available for many Central American species (Bartholomew & Heinrich, 1973). The present study examines the rates of post-flight cooling of saturniids ranging in weight from 81 to 2650 mg under controlled conditions of air temperature and air movement, and compares the allometry of their cooling rates with that of sphingids, birds and mammals.

MATERIALS AND METHODS

The experimental work was carried out at the Tropical Training and Research Center of the Inter-American Institute of Agricultural Sciences of the Organization of American States in Turrialba, Costa Rica. The Center is 9° north of the equator at an elevation of 600 m and receives heavy rainfall at all times of the year.

The moths were captured at a light and handled as previously described for sphingids (Bartholomew & Epting, 1975). Each moth was anaesthetized, and a 40 gauge copper-constantan thermocouple was implanted in its thorax. Some of the smaller individuals initiated pre-flight warm-up as soon as the effects of the anesthesia wore off, but most of the moths remained quiescent until stimulated by gently touching them or blowing on them. The larger individuals aroused most readily in the late afternoon or early evening. Temperatures were measured to the nearest 0.1°C with a Microprobe thermometer (Bailey Instruments, Saddlebrook, New Jersey, U.S.A.).

Thoracic temperatures were recorded during warm-up and post-flight cooling in still air (ambient temperature $24\text{--}26^\circ\text{C}$). Each moth was then killed and weighed to the nearest mg. After our return to the University of California the moths were relaxed and pinned with the fore- and hind-wings overlapped in approximately the

Table 1. Summary of morphometric and physiological data related to post-flight cooling of the saturniid moths measured in the present study

	Weight (mg)	Thoracic volume mm ³	Initial temperature (°C)	Cooling rate (°C min ⁻¹ °C ⁻¹)		
				Initial	Terminal	Entire
Subfamily Hemileucinae						
<i>Automeris bamus</i>	2350	346.4	34.2	0.168	0.131	0.138
	2400	452.4	36.0	0.203	0.191	0.196
	748	268.6	33.8	0.235	0.226	0.230
	464	331.3	35.2	0.355	0.269	0.290
<i>A. celata</i>	409	212.0	38.9	0.385	0.267	0.283
<i>A. metzli</i>	2080	254.5	35.0	0.147	0.129	0.134
<i>A. sugana</i>	238	62.8	—	—	—	—
	288	87.5	35.7	0.355	0.262	0.283
<i>Dirphia flora</i>	435	165.9	32.5	0.309	0.177	0.196
<i>Hylesia</i> sp.	189	62.8	32.8	0.824	0.654	0.666
	183	87.5	37.0	0.472	0.378	0.408
	232	38.9	—	—	—	—
	152	28.3	35.0	0.470	0.274	0.341
	383	33.7	35.0	0.456	0.302	0.334
	420	56.5	29.8	0.304	0.304	0.304
	107	38.5	34.6	0.583	0.311	0.380
	59	—	—	—	—	—
	116	24.7	34.8	0.728	0.408	0.468
	81	14.7	33.6	0.748	0.387	0.442
<i>Molippa sabina</i>	1301	763.4	40.7	0.426	0.152	0.191
Subfamily Saturniinae						
<i>Copaxa</i> sp.	446	298.6	36.2	0.297	0.256	0.269
	407	111.3	32.7	0.152	0.115	0.122
	322	—	—	—	—	—
	505	190.1	38.4	0.375	0.299	0.313
	363	147.3	—	—	—	—
<i>Rothschildia</i> sp. A	545	254.5	34.8	0.265	0.189	0.200
<i>Rothschildia</i> sp. B	1654	282.0	31.2	0.143	0.134	0.136
Subfamily Rhesocytinae						
<i>Machaerosema norax</i>	1679	225.7	35.5	0.191	0.161	0.170
	2650	254.5	36.0	0.237	0.175	0.193
	1736	254.5	35.7	0.182	0.127	0.140

position used during flight. Each animal was photographed and wing area was measured with a planimeter on natural-size prints. The length and diameter of the thorax of each dried specimen were measured to the nearest 0.1 mm with calipers.

Data were processed at the UCLA Computer Center. Identifications were made by Julian P. Donahue of the Entomology Section of the Natural History Museum of Los Angeles County, where the moths are now on deposit.

RESULTS

After arousal, the moths warmed rapidly and tried to take off as soon as they approached flight temperature. Saturniids do not hover, and the cage was too small for free flight by any but the smallest individuals. Most of the animals flopped and tumbled about for a variable period (a few seconds to several minutes) before coming

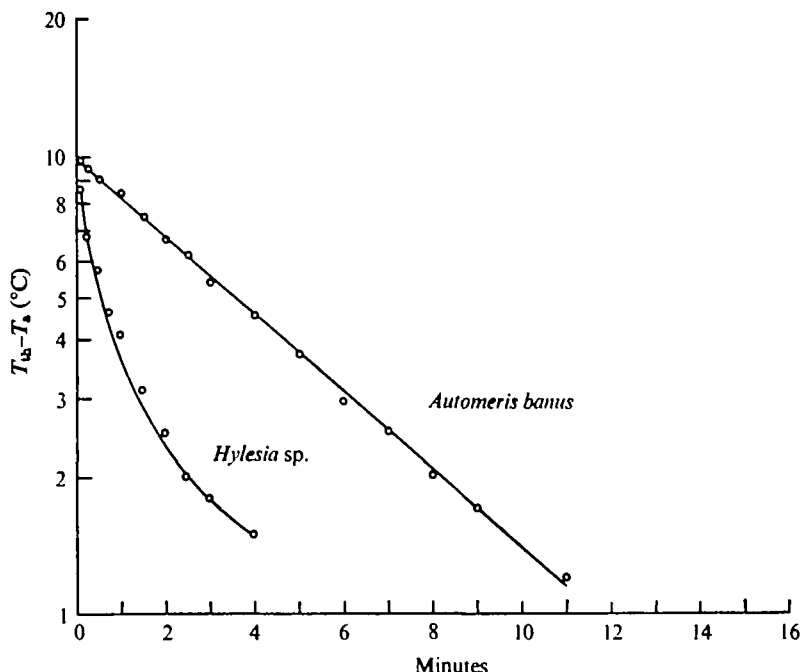


Fig. 1. The course of thoracic temperature during post-flight cooling in two species of saturniids. The *Hylesia*, weight 116 mg, showed the greatest difference observed between initial and terminal cooling rates. The *Automeris*, weight 2400 mg, showed no difference between initial and terminal cooling rates.

to rest and starting to cool down. We observed no effects of duration of attempted flight on the rate of cooling. Data similar to those in Fig. 1 were obtained for 25 moths of 8 genera belonging to 3 subfamilies (Table 1).

Changes in rates of cooling

When ambient temperature is constant, the temperature of a passively-cooling object of homogeneous structure decreases exponentially and, therefore, describes a straight line when plotted on a semilogarithmic grid. When plotted thus, the cooling rates of only two of the saturniids are adequately described by straight lines. In all other cases the cooling rates were steeper initially than terminally (Fig. 1 and Table 1). From this we infer that in most cases cooling was physiologically-facilitated, initially, and passive, terminally. For the saturniid sample as a whole these differences were less pronounced than in sphingids (Bartholomew & Epting, 1975). For purposes of analysis and comparison we shall consider only the rates of cooling during the terminal 5 °C, all of which are linear when plotted semilogarithmically.

Effects of size on cooling rate

In saturniids the log-transformed values of terminal cooling rates decreased linearly with the log-transformed values of total body weight with a slope of -0.32 (Fig. 2). Most of the heat generated by the flight muscles of saturniids (Hanegan & Heath, 1970; Bartholomew & Casey, 1973; Hanegan, 1973) and sphingids (Heinrich

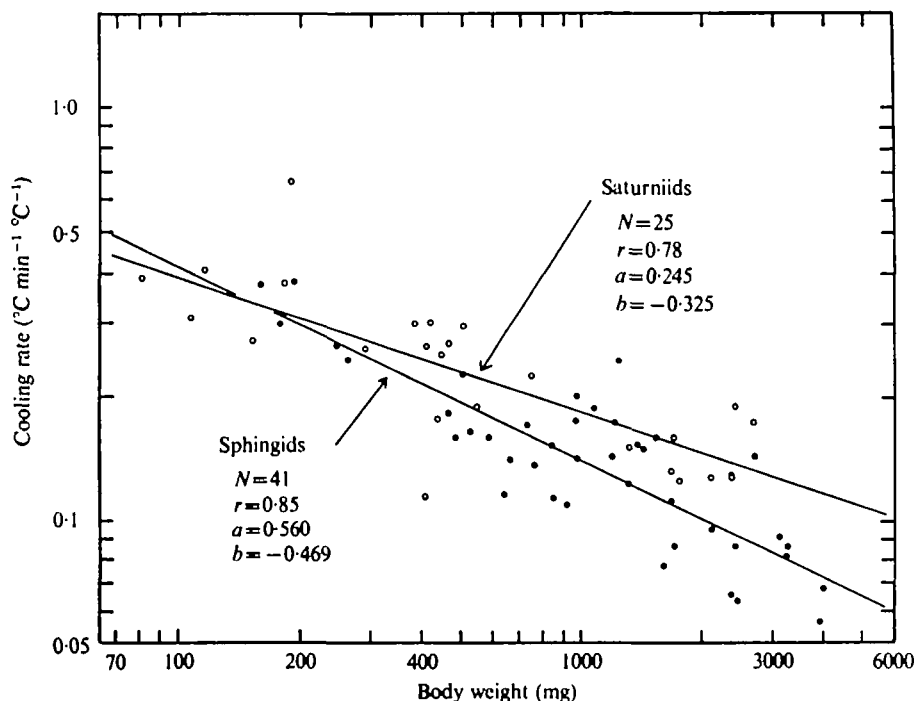


Fig. 2. Linear regressions of the log-transformed values of terminal cooling rate and body weight in saturniids and sphingids. The data for sphingids are taken from Bartholomew & Epting (1975).

1970) is retained in the thorax while the abdomen remains at or near ambient temperature. Therefore, when considering the effects of size on rates of heat loss, it is appropriate to deal with the weight of the thorax rather than that of the total body. Since we could not determine the thoracic weights of the individuals on which we measured cooling rates without destroying them, we have used the calculated volume of their thoraxes as an index to thoracic weight. We treated the thorax as a cylinder and calculated its volume from measurements of length and diameter. The slope of the regression of the log-transformed values of thorax volume and body weight is approximately 0.8 (Fig. 3), which indicates that big saturniids have relatively smaller thoraxes than little ones. The terminal cooling rates were inversely related to thorax volume; the slope of the log-transformed values of terminal cooling rate on thoracic volume for saturniids was approximately -0.28 (Fig. 4).

We also captured and dissected a few saturniids and sphingids to obtain the weight of the thorax (not including appendages) as well as total body weight (Table 2). The regression of the proportional weight of the thorax against total weight was not significant in either family, $P > 0.10$. This finding agrees with our regression of thoracic volumes on body weight for sphingids (Fig. 3), which predicts that the proportional weight of the thorax should be independent of total body weight. The regression of thoracic volume on body weight for saturniids, however, predicts that larger saturniids should have a smaller proportion of body weight as thorax. The failure to find a significant regression of the proportional weight of the thorax against

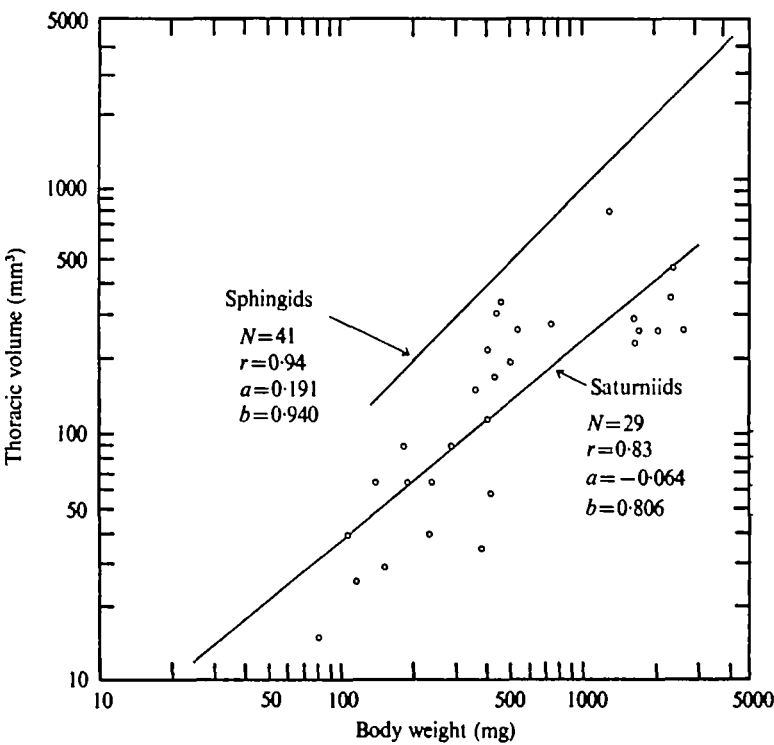


Fig. 3. Linear regressions of the log-transformed values of thoracic volume and body weight. The line for sphingids is taken from Bartholomew & Epting (1975).

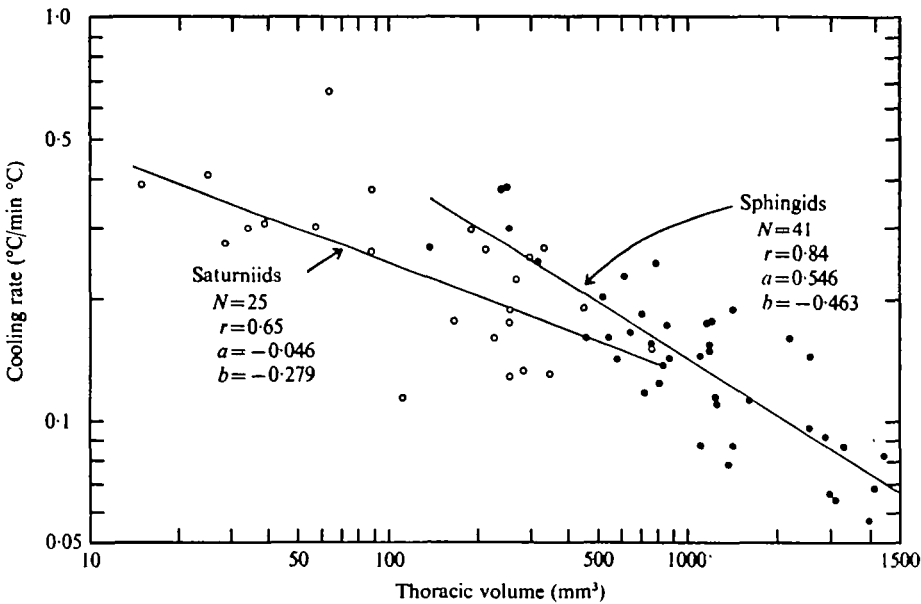


Fig. 4. Linear regressions of the log-transformed values of terminal cooling rate and thoracic volume.

Table 2. Thoracic and body weights in some saturniids and sphingids

	Total wt (mg)	Thoracic wt (mg)	Thorax/total (%)
Saturniidae			
<i>Automeris</i> sp.	392	168	42.9
<i>Hylesia</i> sp.	63	26	41.3
	209	60	28.7
	611	219	35.8
<i>Copaxa</i> sp.	357	122	34.2
	456	158	34.6
<i>Machaerosema norax</i>	1752	477	27.2
$\bar{X} \pm \text{s.e.}$	—	—	34.96 \pm 0.022
Sphingidae			
<i>Amplifypterus</i> sp.	816	318	39.0
	982	392	39.9
	1339	368	27.5
	531	218	41.0
<i>Cautethia spuria</i>	192	76	39.6
<i>Epistor ocypte</i>	487	275	56.5
	609	304	49.9
<i>Erinnyis ello</i>	1281	556	43.4
	1852	750	40.5
	1474	662	44.9
<i>Xylophanes thyelia</i>	304	158	52.0
	427	155	36.3
<i>Xylophanes belti</i>	1000	441	44.1
$\bar{X} \pm \text{s.e.}$	—	—	42.66 \pm 0.020

body weight for saturniids may be due to small sample size. Further data on thoracic volume and thoracic weights are necessary to clarify this point.

DISCUSSION

Effects of body proportions and insulation

The patterns of post-flight cooling in saturniids although fundamentally similar to those of sphingids (Bartholomew & Epting, 1975) show differences that can be related to body proportions, insulation, and heat transfer to the abdomen.

When the terminal cooling rates are plotted against thoracic volume rather than against body weight, the effects of the differences in body proportions of sphingids and saturniids are eliminated. Because of the difference in body proportions (Fig. 3) in the two families, Fig. 2 overestimates the dependence of cooling on size in saturniids but not in sphingids. A comparison of the slopes of the log-transformed values of terminal cooling rates on thoracic volumes shows that cooling rate is less dependent on thoracic volume in saturniids than in sphingids (Fig. 4).

The positions of the regression lines in Fig. 4 show that in our samples, saturniids generally cool more slowly than sphingids, and are therefore, better insulated. Although quantitative data are lacking, saturniids have conspicuously long scales. Church (1960) showed that scales of moths have a pronounced effect on the retention of heat in the thorax. These two facts are consistent with our observation that even

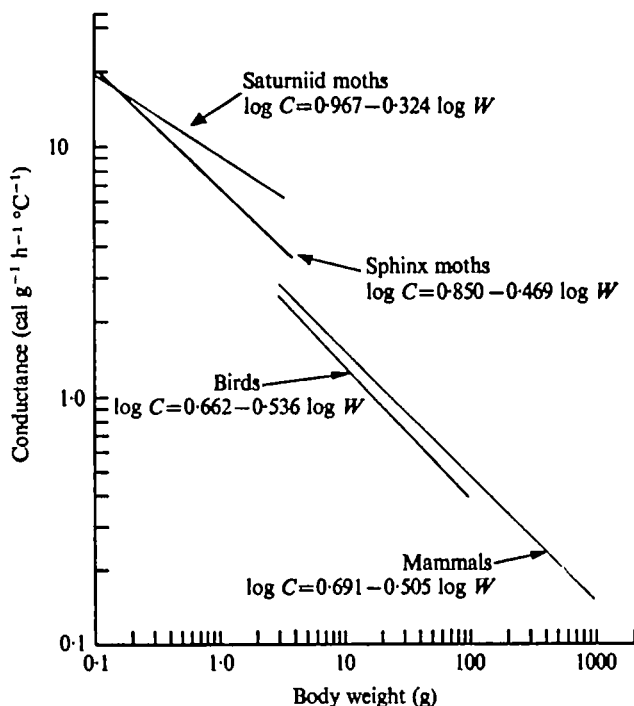


Fig. 5. Linear regressions of the log-transformed values of weight-specific thermal conductance and body weight. The lines for birds and placental mammals are from Herreid & Kessel (1967). For convenience of comparison the data for the two families of moths have been converted to $\text{cal g}^{-1} \text{h}^{-1} \text{°C}^{-1}$ using the value of $0.83 \text{ cal g}^{-1} \text{°C}^{-1}$ for the specific heat of their tissues.

a very small (59 mg) saturniid (*Hylesia* sp.) was capable of elevating thoracic temperature 10° above air temperature.

In sphingids we found that cooling rates were significantly greater initially than terminally and interpreted this as evidence for facilitated transfer of heat to the abdomen during the period immediately after cessation of flight (Bartholomew & Epting, 1975). In our sample of saturniids the difference between initial and terminal cooling rates were less pronounced. More extensive sampling of saturniids will be necessary to confirm this difference between the two taxa. However, if real it may be correlated with the fact that saturniids as a group have somewhat lower flight temperatures than sphingids (Bartholomew & Heinrich, 1973) and fly only a few times during their life cycle. This difference does not affect the discussion which follows because the analyses are based entirely on terminal cooling rates.

Thermal conductance in moths, birds, and mammals

As previously noted (Bartholomew & Epting, 1975) the weight-specific conductance of sphingids has the same slope as that of birds and mammals, but is 60% greater in the range in which the weights of sphingids and homeothermic vertebrates overlap. Because of the high weight-specific conductance (based on total weight) of sphingids, we concluded that their elevated body temperatures result primarily from high rates of heat production and are only secondarily dependent on effectiveness of insulation.

The weight-specific conductance of saturniids is even higher than that of sphingids (Fig. 5). Therefore, if we think in terms of total body weight, the same conclusion is also justified for saturniids. However, as noted by Heinrich & Bartholomew (1971) with warm-up rates in a variety of taxa, body weight is an unsatisfactory parameter for evaluating the achievement of elevated body temperature in heterothermic insects. This is due to the fact that heat generation occurs in the flight muscles and nearly all the heat is retained in the thorax while the abdomen typically remains at or near air temperature (Heinrich, 1974). No such simple compartmentalization occurs in bird and mammals. The fraction of the total body that heterothermic and homeothermic vertebrates maintain at core temperature obviously varies with body size, body proportions, and the difference between core and ambient temperatures.

The lines for vertebrates in Fig. 5 encompass the complex partitioning of heat exchanges involved in the maintenance of uniform core temperatures because they are based on measurements of oxygen consumption as well as on cooling rates; moreover, they closely approximate a similar regression for birds calculated by Lasiewski, *et al.* (1967) that is based exclusively on oxygen consumption. However, the lines for saturniids and sphingids ignore the obvious partitioning of the body into two thermal components, the endothermic thorax and the abdomen. From the data in Table 2 and Figs. 3 and 5 it is possible to take this partitioning into account and to estimate the dependence of thermal conductance on thoracic weight rather than total body weight. Our data on thorax weight and volume in sphingids strongly indicate that the relative size of thorax is independent of total weight. The data on thoracic weight and volume in saturniids do not agree on this point probably because of the small sample of thoracic weights. In the absence of information about the specific gravity of the thorax in saturniids, we will use the slope of the regression of thorax volume on total weight in both families of moths for further analysis.

Herreid & Kessel (1967) found that the regressions of conductance on weight in birds and mammals do not differ significantly. Therefore, for purposes of comparison we have averaged the slopes and intercepts for the bird and mammal regressions and have used the new line to represent all endothermic amniotes.

In our sample of saturniids (Table 2) most of the body weights cluster near 0.4 g, and thoracic weights average about 35 % of total body weight. To derive the regression of weight-specific conductance on thoracic weight in saturniids it is necessary to transform both slope and intercept for the changes in thorax volume with increasing size. This slope was transformed by converting the scaling constant for weight-specific conductance (-0.324) to a scaling constant for total conductance (0.676) and then dividing this quantity by the scaling constant for thoracic weight (1.165). The thoracic weight scaling constant was calculated using the scaling constants for conductance versus thoracic volume (-0.279) and conductance versus body weight (-0.325) from Figs. 2 and 4. When the former is exponentiated to 1.0, the value for the scaling constant of thoracic weight is 1.165. The intercept was then shifted so that the new regression passes through the thoracic weight corresponding to a moth with a total body weight of 0.4 g. In sphingids thoracic weight averages 42 % of body weight and there is no dependence of the proportional volume of the thorax on body weight. Consequently, it is only necessary to translate the regression line so that it

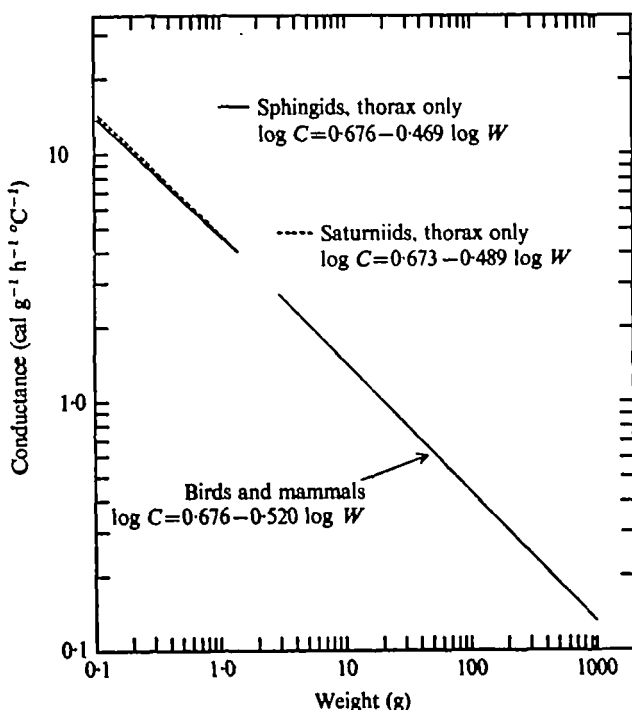


Fig. 6. Linear regressions of the log-transformed values of weight-specific conductance and weight. The line for vertebrates is the average of the lines for birds and mammals in Fig. 5 (see text). The lines for the moths are based on calculated thoracic weights (see text).

passes through the thoracic weight corresponding to some arbitrary body weight, in this case, 1 g.

When these transformations are made the new regression lines for the moths correspond closely to the line for vertebrates. The weight-relative conductances of the thoraxes of sphingids and saturniids are essentially predicted by the regression line for vertebrates (Fig. 6). Consequently, the achieved levels of heat production in either of these moth families need not be as high as predicted on the basis of the weight-relative conductance of their entire bodies.

The similarity of the heterothermy of large insects with that of small birds and small mammals is a remarkable instance of evolutionary convergence. Despite the profound differences in morphology and physiological organization of insects and vertebrates, those members of both groups that depend on internally generated heat for the production of elevated and regulated body temperatures have had to satisfy the same physical constraint: the balancing of the rates of heat loss with rates of heat production. Thus, it is noteworthy that the rates of heat loss of sphingids and saturniids show the same allometric scaling as that of birds and mammals. From this we infer that the insulation of these moths is no more effective for animals of their size than is that of birds and mammals. Thus, the high body temperatures of saturniids and sphingids during activity appear to depend primarily on high levels of heat production – a function for which the flight muscles of insects are uniquely well equipped because of their extremely high metabolic rates.

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REFERENCES

- BARTHOLOMEW, G. A. (1972). Aspects of timing and periodicity of heterothermy. In *Hibernation and Hypothermia, Perspectives and Challenges* (ed. F. E. South *et al.*), pp. 663-80. Amsterdam: Elsevier Publishing Co.
- BARTHOLOMEW, G. A. & CASEY, T. M. (1973). Effects of ambient temperature on warm-up in the moth. *Hyalophora cecropia*. *J. exp. Biol.* **58**, 503-7.
- BARTHOLOMEW, G. A. & EPTING, R. J. (1975). Rates of post-flight cooling in sphinx moths. In *Perspectives of Biophysical Ecology, Ecological Studies*, vol. 12 (ed. D. M. Gates and R. B. Schmerl), pp. 405-15. New York: Springer-Verlag.
- 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**, 123-35.
- CHURCH, N. S. (1960). Heat loss and the body temperatures of flying insects. II. Heat conduction within the body and its loss by radiation and convection. *J. exp. Biol.* **37**, 186-212.
- HANEGAN, J. L. (1973). Control of heart rate in cecropia moths; response to thermal stimulation. *J. exp. Biol.* **59**, 67-76.
- HANEGAN, J. L. & HEATH, J. E. (1970). Mechanisms for the control of body temperature in the moth. *Hyalophora cecropia*. *J. exp. Biol.* **53**, 349-62.
- HEATH, J. E. & ADAMS, P. A. (1967). Regulation of heat production by large moths. *J. exp. Biol.* **47**, 21-33.
- HEINRICH, B. (1970). Thoracic temperature stabilization by blood circulation in a free-flying moth. *Science* **168**, 580-2.
- HEINRICH, B. (1974). Thermoregulation in endothermic insects. *Science* **185**, 747-56.
- HEINRICH, B. & BARTHOLOMEW, G. A. (1971). An analysis of pre-flight warm-up in the sphinx moth. *Manduca sexta*. *J. exp. Biol.* **55**, 223-39.
- HERREID, C. F. & KESSEL, B. (1967). Thermal conductance in birds and mammals. *Comp. Biochem. Physiol.* **21**, 405-14.
- LASIEWSKI, R. C., WEATHERS, W. W. & BERNSTEIN, M. H. (1967). Physiological responses of the giant hummingbird, *Patagona gigas*. *Comp. Biochem. Physiol.* **23**, 797-813.
- OOSTHUIZEN, M. J. (1939). The body temperature of *Samia cecropia* Linn. (Lepidoptera, Saturniidae) as influenced by muscular activity. *J. ent. Soc. sth Afr.* **2**, 63-73.