

BODY WEIGHT AND THE ENERGETICS OF TEMPERATURE REGULATION

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INTRODUCTION

The recent rebirth of interest in the 200-year-old field of homoiothermic energetics may be dated from three papers published in 1950 by Scholander, Irving and colleagues. These papers furnished many data and a theoretical analysis of the energetics of temperature regulation in tropical and arctic birds and mammals. A massive body of data has since become available through the efforts of many workers. Unfortunately, there has been little effort to extend Scholander and Irving's model (which was based on Newton's law of cooling) to meet the challenge of new data. One of the peculiarities of this model is that it is presented in a weight-independent form, although two of its parameters, basal rate of metabolism and thermal conductance, are well-known to be weight-dependent.

In this paper the influence of weight on the energetics of homoiotherms will be re-examined; special attention will be given to the applicability of Newton's law of cooling.

NEWTON'S LAW OF COOLING

Since Newton's law of cooling will be the analytical basis for the discussion in this paper, it is first necessary to understand what it says and to know the limitations that are imposed upon it. As originally formulated Newton's law states that the rate at which the temperature of a body falls is proportional to the difference in temperature between the body and the environment: $dT_b/dt = \phi(T_b - T_a)$, where ϕ is a cooling constant (see the Table of Symbols for all definitions and units). But a fall in temperature can be related to a loss of heat, since $\Delta T_b = \Delta Q/s.W$. Therefore,

$$\begin{aligned} dQ/dt &= s.W.\phi(T_b - T_a) \\ &= C(T_b - T_a) \end{aligned} \quad (1)$$

which is the form of Newton's law to be used in this paper.

Equation (1) indicates that the net heat loss from an object warmer than its surroundings is proportional to the temperature differential between the object and its environment. A proportionality constant C (usually referred to as thermal conductance, but maybe more properly called the coefficient of heat transfer) is defined such that $C(T_b - T_a)$ is equal to the rate of heat loss (not C , as erroneously stated by me, 1966*a, b*). If an animal regulates its temperature perfectly, T_b is constant and the rate of metabolism equals $C(T_b - T_a)$ when there is no thermal source for regulation other than metabolism.

Two aspects of this relationship must be kept always in mind: (1) $C(T_b - T_a)$ is an approximation of the summed heat loss by a warm animal to a cool environment, and (2) there are biological limits placed on this approximation. Each of these conditions must be examined briefly to avoid any misunderstandings.

Newton's law of cooling is an approximation to the sum of the amounts of heat lost by radiation, convection, conduction, and evaporation, respectively

$$M = \epsilon \sigma A_1 (T_b^4 - T_a^4) + h A_2 (T_b - T_a) + k A_3 (T_b - T_a) + L A_4 w. \quad (2)$$

One might therefore argue that it would be best to represent the rate of metabolism of an endotherm by equation (2). There are two reasons why this is not usually done. (1) It is an unnecessarily complex statement as shown by the rather simple linear relationship usually existing between the rate of metabolism and the temperature differential (e.g. Tucker, 1965), if for no other reason than that the biological variability of intact animals is sufficiently great to obscure the mathematical intricacies of the theoretically rigorous statement. (2) Equation (2) is difficult to apply because of the variable nature of the effective surface areas in each term and because of the complexities of the convective constant. Although Newton's law is a rough approximation of heat loss, the uncertainties in the application of equation (2) are sufficient to deny it a practical advantage in spite of its theoretical security.

Newton's law of cooling can be derived from equation (2). Note that $(T_b^4 - T_a^4)$ is approximately equal to $4T_a^3(T_b - T_a)$ when $T_b - T_a$ is small, as is the case in biological systems. Therefore,

$$\begin{aligned} M &= (\epsilon \sigma A_1 4T_a^3 + h A_2 + k A_3) (T_b - T_a) + L A_4 w \\ &= c_1 (T_b - T_a) + L A_4 w. \end{aligned} \quad (3)$$

(When temperature is incorporated into the term for radiation as either T^3 or T^4 , it must be in $^{\circ}\text{K}$, but when a temperature differential is used either $^{\circ}\text{C}$ or $^{\circ}\text{K}$ may be used.) Equation (3) is applicable over all biologically relevant temperatures. It has two terms, one for heat loss based on a temperature differential and the other for evaporative heat loss. Biologically meaningful measurements of both oxygen consumption (metabolism) and evaporative water loss are difficult to make simultaneously (Lasiewski, Acosta & Bernstein, 1966). There is value, then, in a still simpler formulation when it is not practicable to measure evaporative water loss. This simplification can be made because the amount of heat lost by the evaporation of water at moderate to low environmental temperatures is a small, rather constant fraction of the total heat loss (e.g. Schmidt-Nielsen *et al.* 1965; Calder & Schmidt-Nielsen, 1967). Equation (3) therefore may be rewritten

$$M = (c_1 + c_2) (T_b - T_a) = C(T_b - T_a) \quad (4)$$

which, again, is Newton's law of cooling.

Newton's law of cooling, as represented in equations (1) and (4), resembles the Fourier equation for heat exchange with two exceptions. (1) A core temperature is used in Newton's law, which is justified by being easier to measure and by the fact that most of the temperature gradient between an endotherm and its environment exists between the surface and the environment (Porter & Gates, 1969), so that a surface temperature can be replaced by a core temperature with little error, except in animals that are both large and naked. (2) The surface area is not generally used in Newton's

law. The units for thermal conductance in this paper are cal/g-h °C (or equivalent). It has been argued that these units are not appropriate because heat loss occurs per unit of surface area, not per unit of weight. There is no question that the surface area is an important parameter of heat loss, but it is nearly impossible to measure the effective area, since it may be modified by postural changes and by changes in conductivity brought about by local vasoconstriction and vasodilation. Faced with this difficulty some observers advocate that surface area measurements be replaced by (constant) $W^{0.67}$. But surely it is better to use the simpler weight-specific units for conductance than to calculate a pseudo surface-specific conductance.

There are biological limits to the application of Newton's law. It is an appropriate expression only at cooler ambient temperatures, since the evaporative heat loss (which does not depend upon a temperature differential) becomes the predominate means of heat dissipation at higher temperatures. Another complication derives from the behaviour of C . As the ambient temperatures fall from moderate values, C gradually decreases to a minimal value. Any further fall in T_a requires an increase in heat production by the animal to maintain a constant body temperature. The ambient temperature above which changes in C are the major means of thermal adjustment to a varying T_a and below which changes in M predominate is called the lower limit of thermoneutrality (T_l). If the separation between the temperatures at which changes in C or M are used is sharp, the curve of metabolism on T_a below T_l has a slope equal to C and extrapolates to T_b when $M = 0$. But if an animal does not rigidly distinguish between 'physical' and 'chemical' regulation, C will decrease and M will increase with a fall in ambient temperature. As a result the slope of the curve of M on T_a below T_l is not equal to C and the curve extrapolates to a temperature greater than T_b when $M = 0$. Contrary to the opinion of some authors, this result does not invalidate the application of Newton's law to the heat exchange of homoiotherms, since this law is simply a mathematical approximation of the physics of heat exchange and *per se* does not incorporate any biological features, except for the dependence upon non-evaporative heat loss.

The two major criticisms of Newton's law, then, are that it is either physically too simple or that it is biologically inappropriate. But as long as the Newtonian simplification is used within its proper limits, e.g. at ambient temperatures below the mid-point of thermoneutrality, its great mathematical convenience can be profitably employed.

THE ENERGETICS OF MAMMALIAN THERMOREGULATION

Homoiotherms accommodate their energetics to unique environments mainly through a modification of thermal conductance and the basal rate of metabolism, M_b (McNab, 1966*b*). Since both parameters vary as a function of weight, species that differ greatly in weight may be compared if M_b and C are expressed relative to the values expected by weight from some 'standard', such as the curves of Kleiber (1960) for M_b and Herreid and Kessel (1967) for C . This transformation demonstrates that much of the observed variation in the level of T_b is due to relative variation in the basal rate and thermal conductance. The reason for this influence may be seen from rearranging Newton's law: $T_b = M/C + T_a$. Thus, T_b increases with an increase in the ratio M/C , which becomes M_b/C , when evaluated at the lower limit of thermoneutrality.

What is the physical basis for the influence of M_b/C on T_b ? This ratio is a measure of the temperature differential between a homoiotherm and the environment at the lower limit of thermoneutrality. Although temperature determines the rate of chemical reaction, the rate of chemical reaction may also determine the temperature of the system. Consider a furnace having a steady-state temperature distribution and consuming coal at a fixed rate. If the amount of coal fed to the furnace is increased, the rate of combustion will increase (assuming no other limiting factors) and the temperature of the furnace will rise to a new steady-state distribution, the level of which is

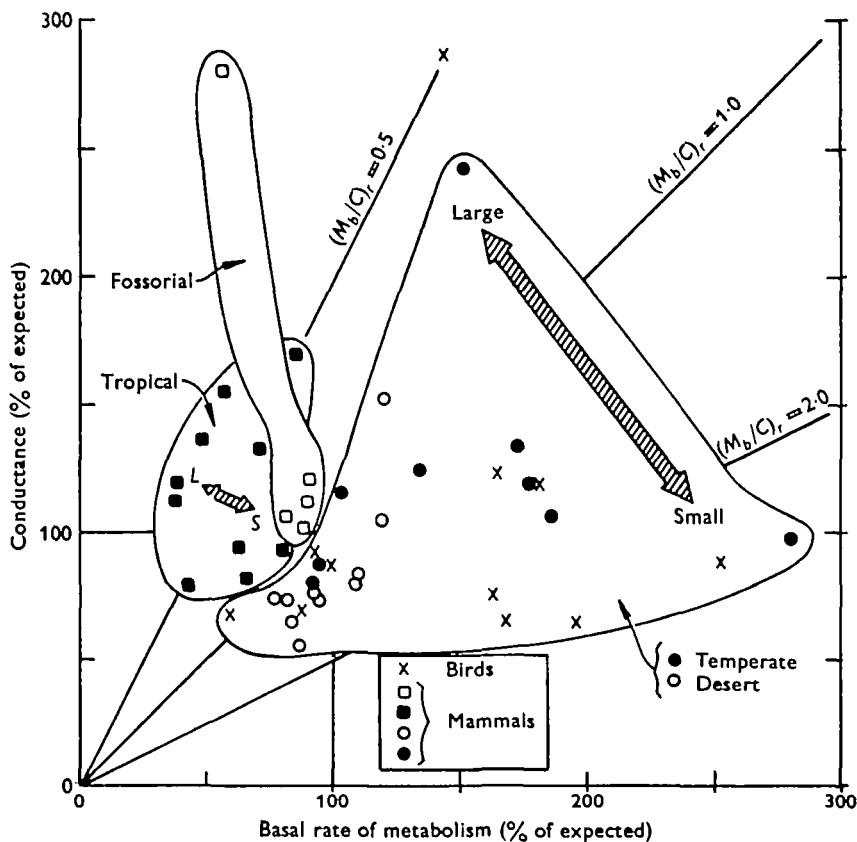


Fig. 1. Thermal conductance in mammals and birds as a function of the basal rate of metabolism (data from Tables 1 and 3). Each parameter is expressed as a percentage of the values expected from weight in mammals (see the text).

dictated by the temperature differential needed to dissipate the heat produced by the furnace. Endotherms can be compared to small furnaces, their temperatures determined, in part, by the proportionality existing between the rate of heat production and the temperature differential.

The biological significance of variations in the ratio M_b/C may be seen in Fig. 1. Temperate species generally have higher basal rates of metabolism than expected from weight, but they have only a modest increase, if any, in conductance (unless they are very large). The ratio M_b/C in these species tends, then, to be higher than expected

from weight, a condition that leads to the high, precisely regulated body temperatures typical of species living in a thermally unstable environment. Temperate species that live in deserts have a low M_b (to minimize water exchange) and in compensation have a low conductance. Fossorial rodents have both low basal rates and high conductances to reduce the threat of overheating in closed burrows. Tropical mammals also have low basal rates and high conductances, but like fossorial mammals, can tolerate the resulting low body temperatures by living in environments characterized by thermal stability.

Recent data on tropical bats (McNab, 1969) have shown that body weight also influences the level of T_b (contrary to the conclusion of Morrison & Ryser, 1952, but

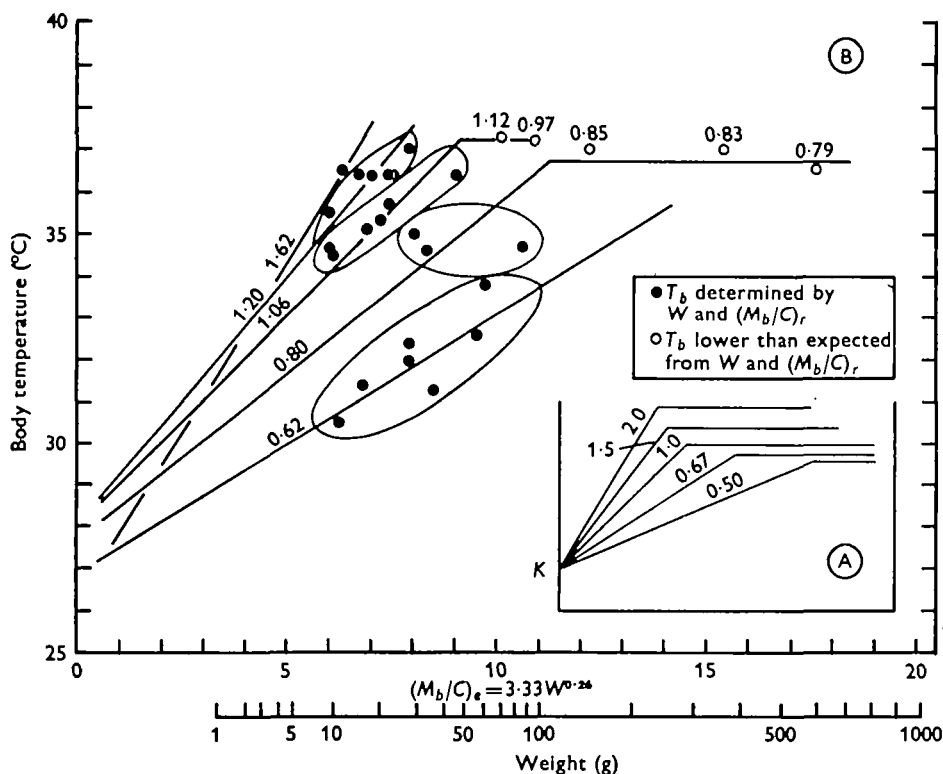


Fig. 2. A. The relation between T_b , $(M_b/C)_r$, and $(M_b/C)_e$ expected from equation (5). B. Body temperature in bats as a function of the ratios $(M_b/C)_r$ and $(M_b/C)_e$ (data from McNab, 1969). Values for $(M_b/C)_r$ indicated for each hollow point.

in agreement with Rodbard, 1950). If it is recalled that the absolute values of M_b and C are weight-dependent, the possibility arises that the level of body temperature is determined by the weight-dependent relationships of M_b and C , as well as the extent to which actual values conform to these expectations. Thus, the measured ratio M_b/C may be represented by the product $(M_b/C)_r(M_b/C)_e$, where the expected ratio $(M_b/C)_e = (3.4W^{-0.25})/(1.02W^{-0.51}) = 3.33W^{0.26}$ (McNab, 1966b; Herreid & Kessel, 1967) and the relative ratio $(M_b/C)_r$ is the dimensionless fraction: (measured ratio)/(expected ratio) = $(M_b/C)/(M_b/C)_e$. The relative ratio is identical to that described in previous analyses (McNab, 1966b, 1969).

Applying this analysis to Newton's law of cooling and rearranging

$$T_b = (M_b/C)_r (M_b/C)_e + K \tag{5a}$$

$$= 3.33 (M_b/C)_r W^{0.26} + K. \tag{5b}$$

If this suggestion for the weight-dependency of body temperature is correct, a plot of body temperature against $3.33W^{0.26}$ should give a family of linear curves, the slopes of which are equal to $(M_b/C)_r$ (see Fig. 2A). Such curves are plotted in Fig. 2B for bats and in Fig. 3 for other mammals. The expectation holds in both cases: T_b depends

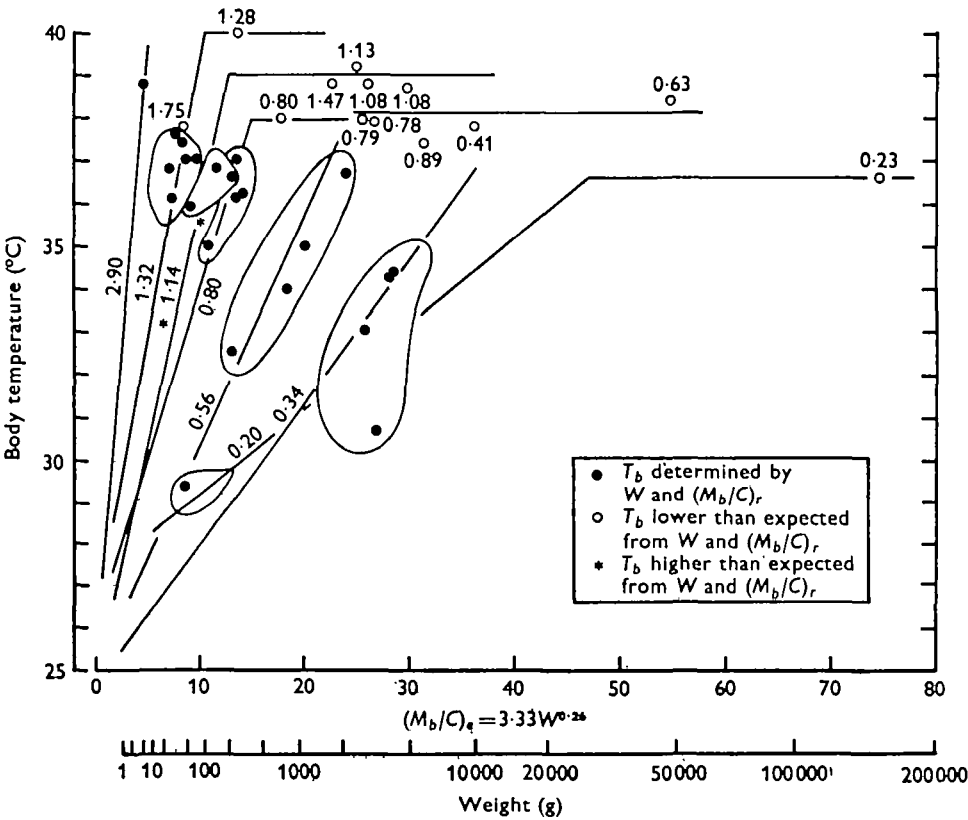


Fig. 3. Body temperature in mammals other than bats as a function of the ratios $(M_b/C)_r$ and $(M_b/C)_e$ (data from Table 1). Values for $(M_b/C)_r$ indicated for each hollow point.

upon the ratio $(M_b/C)_e$ up to 37 or 38 °C. (beyond which T_b is nearly constant). Moreover, body temperature varies with the ratio $(M_b/C)_r$ at a constant weight in a manner expected from equation (5). A similar dependency of T_b on M_b , C and W can be seen in the data of MacMillen & Nelson (1969) on marsupials. Equation (5), then, is simply Newton's law rewritten in a form that permits the influence of body weight on T_b to appear. The precision of regulation and the sensitivity of T_b to variations in T_a are also compatible with this analysis (McNab, 1969).

The weight at which body temperature shifts from being $(M_b/C)_e$ dependent to being $(M_b/C)_r$ independent may be called the 'critical' weight. This weight varies

with the ratio $(M_b/C)_r$ in a manner such that a high relative ratio may compensate for a small weight in the maintenance of a high temperature (Fig. 4). The equation for this relationship is

$$\begin{aligned}(M_b/C)_r &= 11.5(M_b/C)_e \\ &= 3.45W^{-0.28}\end{aligned}\quad (6)$$

whether obtained by extrapolating the curves in Figs. 2B and 3 to a common body temperature (38°C), or by taking the critical weights from the $(M_b/C)_r$ constant curves in these figures. A similar equation is obtained from equation (5a) by substituting $T_b = 38^\circ\text{C}$ and $T_l = 27^\circ\text{C}$ (the mean T_l for all mammals in Table 1).

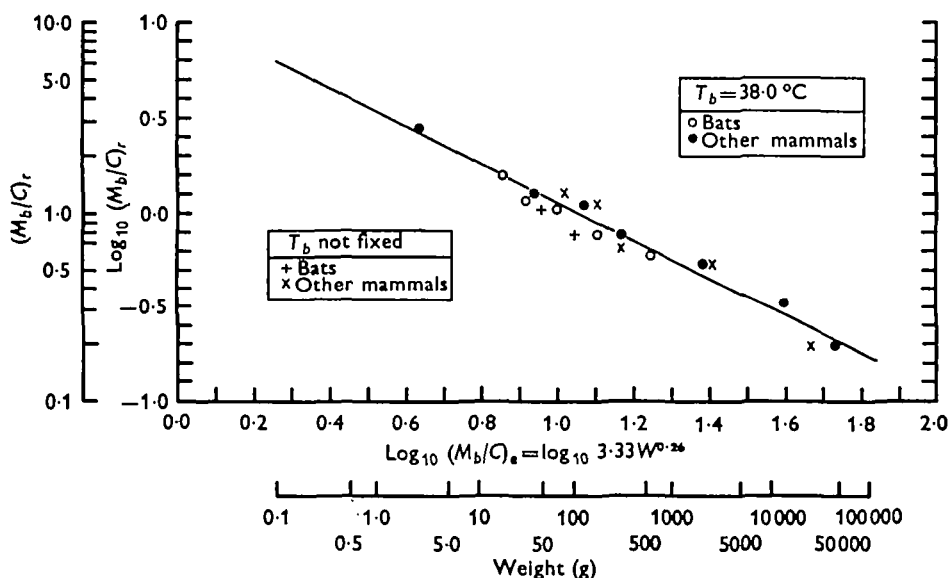


Fig. 4. The relation between $(M_b/C)_r$ and $(M_b/C)_e$ in mammals either at a fixed temperature or at the point beyond which T_b no longer depends upon $(M_b/C)_e$. The data were taken from Figs. 2 and 3.

A 'critical' weight results from the mathematical form of equation (5) and from the setting of a maximal T_b . Mammalian temperatures seem set near 38°C , all deviations being due either to a small weight or to deviations from the 'standard' curves of metabolism and conductance on weight.

A high, precisely regulated temperature, therefore, can be attained at any weight, provided that an appropriate energy expenditure, relative to conductance and weight, is made. The exact balance differs somewhat among mammals, but it has a consistent pattern: to regulate temperature precisely a species weighing 10 kg must have the ratio $(M_b/C)_r$ equal to or greater than 0.3, one weighing 500 g (in bats about 250 g) must have a ratio equal to 0.7, and one weighing 100 g (in bats 70 g) must have a ratio equal to 1.0.

A very small species must pay a high price for a high T_b . Morrison, Ryser & Dawe (1959) have shown that a common shrew, *Sorex cinereus*, even though weighing only 3.3 g, maintains a temperature of 39°C by having $(M_b/C)_r$ equal to about 2.9 (assuming

Table 1. *The energetics of mammals*

Species	Weight (g)	$(M_b/C)^*$	Basal metabolism		Conductance		T_b (°C)	T_{ill} (°C)	References [†]
			(c.c. O ₂ /g-h)	%†	(c.c. O ₂ /g-h °C)	%†			
<i>Tachyglossus aculeatus</i>	3000	26.7	0.22	48	0.026	137	30.7	22	Schmidt-Nielsen <i>et al.</i> (1966)
<i>Ornithorhynchus anatinus</i>	693	18.2	0.28	42	0.030	79	34.0	—	¶
<i>Marmosa muritorius</i>	13	6.5	1.44	80	0.26	93	33.2	27	¶c
<i>Didelphis marsupialis</i>	1000	20.1	0.52	85	0.054	169	35.0	25	¶
<i>Cercartus nanus</i>	70	10.1	0.85	72	0.14	118	35.6	31	¶
<i>Sorex cinereus</i>	3.3	4.6	7.0	280	0.54	98	38.8	23	Morrison <i>et al.</i> (1959)
<i>Aolus trivirgatus</i>	625	17.7	0.45	66	0.031	82	38.0	23	Morrison & Simões (1962)
<i>Cyclodes didactylus</i>	185	13.0	0.58	63	0.070	95	32.5	—	McNab, unpublished
<i>Bradypus</i> sp.	2600	25.7	0.18	38	0.024	120	33.0	—	¶
<i>Choloepus hoffmanni</i>	3770	28.3	0.16	37	0.018	113	34.4	—	¶
<i>Dasybus novemcinctus</i>	3700	28.2	0.25	57	0.027	155	34.5	—	¶
<i>Vulpes vulpes</i>	4440	29.6	0.55	134	0.018	124	38.7	8	Irving & Krog (1954), Irving <i>et al.</i> (1955)
<i>Canis familiaris</i>	6666	36.2	0.34	100	0.022	244	37.8	—	Hellstrom & Hammel (1967)
<i>Tamiasciurus hudsonicus</i>	229	13.5	1.50	172	0.086	134	40.0	20	Irving & Krog (1954), Irving <i>et al.</i> (1955)
<i>Geomys pinetis</i>	203	13.3	0.74	81	0.075	107	36.1	25	¶c
<i>Dipodomys merriami</i>	38	8.6	1.13	83	0.11	65	37.0	27	Carpenter (1966)
<i>D. agilis</i>	61	9.7	1.05	86	0.073	56	37.0	28	Carpenter (1966)
<i>Peromyscus eremicus</i>	22	7.4	1.48	94	0.16	74	36.1	30	¶c
<i>P. californicus</i>	46	9.0	1.03	81	0.11	74	35.9	28	¶c
<i>P. eremicus</i>	16	6.9	1.58	92	0.19	76	36.8	29	¶c
<i>P. maniculatus</i>	24	7.6	1.67	110	0.17	84	37.6	29	¶c
<i>P. truei</i>	33	8.3	1.53	109	0.14	80	37.4	27	¶c
<i>Neotoma lepida</i>	110	11.3	0.79	76	0.070	74	36.8	26	¶c
<i>N. fuscipes</i>	187	13.0	0.79	91	0.059	81	36.6	23	¶c
<i>Microtus montanus</i>	31	8.1	2.65	185	0.19	106	37.8	26	Packard (1968)
<i>Spalax leucodon</i>	208	13.4	0.79	89	0.068	101	37.0	25	¶c
<i>Tachyoryctes splendens</i>	234	13.8	0.79	90	0.073	112	36.2	27	¶c

Table 1 *cont.*

Species	Weight (g)	Basal metabolism		Conductance		T_b (°C)	T_{ill} (°C)	References¶
		(c.c. O ₂ /g-h)	%†	(c.c. O ₂ /g-h °C)	%‡			
<i>Erethizon dorsatum</i>	5530	31.3	103	0.015	116	37.4	7	Irving & Krog (1954), Irving <i>et al.</i> (1955)
<i>Heliothobius kapeti</i>	89	10.7	91	0.13	121	35.0	28	¶c
<i>Heterocephalus glaber</i>	39	8.6	56	0.45	281	29.4	—	¶c (T_b at $T_a = 20$ to 25 °C)
<i>Lepus americanus</i>	1581	22.6	178	0.029	121	39.8	10	Hart <i>et al.</i> (1965)
<i>L. alleni</i>	3000	26.7	120	0.029	153	37.9	20	Dawson & Schmidt-Nielsen (1966)
<i>L. californicus</i>	2300	24.9	119	0.021	105	39.2	14	Schmidt-Nielsen <i>et al.</i> (1965)
<i>Heterohyrax brucei</i>	2000	24.0	71	0.028	133	36.7	24	Taylor & Sale (1960)
<i>Procavia capensis</i>	2630	25.8	88	0.020	111	38.0	15	Taylor & Sale (1960)
<i>P. johnstoni</i>	2750	26.1	96	0.016	89	38.8	10	Taylor & Sale (1960)
<i>Sus scrofa</i>	48000	54.9	152	0.035	243	38.4	4	Irving (1956); Irving <i>et al.</i> (1955, 1956)
<i>Taurotragus oryx</i>	150000	74.6	141	0.016	615	36.6	24	Taylor & Lyman (1967)

* $(M_b/C)_a = 3.33W^{0.75}$.† M_b (%) = 100 mean/ $3.4W^{-0.75}$.‡ C (%) = 100 mean/ $1.02W^{-0.81}$.§ $(M_b/C)_r = M_b$ (%) / C (%).|| T_1 = lower limit of thermoneutrality.¶ Indicates that references are found in Table IV of McNab (1966); c indicates that values for M_b have been corrected to mean values.

that the mean minimal rate of metabolism measured in *Sorex* was equal to $1.4 M_b$, due to the specific dynamic action of protein metabolism). Small shrews are near the lower limit of weight for continuous homoiothermy. Animals of still smaller weights are theoretically capable of continuous homoiothermy, but apparently it is prohibitively expensive. For example, a mammal weighing 0.25 g requires a ratio $(M_b/C)_r$ equal to about 4.9 for T_b to be independent of weight. The intermittently endothermic sphinx moth (*Celerio*, thorax weight = 0.25 g) has $(M_b/C)_r$ equal to 0.6, only 12% of the expenditure needed for continuous homoiothermy (Heath & Adams, 1967). As a result this moth can thermoregulate only with the high heat production associated with wing movements; during quiescent periods the moth is poikilothermic.

In the evolution of a small weight, then, an endotherm has two alternatives: (1) to maintain the relative levels of M_b and C , as may well be dictated by its habits and its environment, and suffer a reduction in the level and precision of thermoregulation, or (2) maintain thermoregulation by means of a compensatory increase in the relative rate of metabolism, or a compensatory decrease in the relative conductance. It appears that the second 'choice' is utilized whenever energetically (that is, ecologically) feasible (e.g. McNab, 1969).

It is of interest at this point to examine the constant appearing in equation (5). First, let us consider the behaviour of K within a group of mammals, such as bats, rodents or edentates. Graphically, K , represents the level of T_b when $(M_b/C)_e = 0.0$. (Fig. 2A). It also represents the lower limit of thermoneutrality, T_l , since that is the environmental temperature at which the basal rate of metabolism intersects the curve whose slope is the minimal thermal conductance. One may ask how T_l is influenced by the ratio $(M_b/C)_r$ and by body weight. The effect depends upon whether or not body temperature is independent of weight. According to Newton's law, $T_l = T_b - M_b/C$. If body temperature depends upon weight, equation (5a) may be applied:

$$\begin{aligned} T_l &= (M_b/C)_r(M_b/C)_e + K - M_b/C \\ &= M_b/C + K - M_b/C \\ &= K, \end{aligned} \quad (7)$$

that is, the lower limit of thermoneutrality should be independent of weight and of the relative ratio $(M_b/C)_r$. If, however, T_b is dependent of weight, then from equation (5b)

$$T_l = T_b - 3.33(M_b/C)_r W^{0.28}; \quad (8)$$

T_l should decrease as each weight and $(M_b/C)_r$ increases.

Data on the lower limit of thermoneutrality in mammals (Table 1) are plotted in Fig. 5 as a function of weight. Clearly the variation in T_l , whether found among species or seasonally within species, conforms to the predictions of equations (7) and (8).

There is another source of variation inherent in K . It will be noticed in Figs. 2B and 3 that the curves below the 'critical' weight, although similar in form in the various groups of mammals, do not extrapolate to a common K ; K is higher in bats than in monotremes and edentates (Fig. 6a). And K is even higher in Australian marsupials. It should be re-emphasized that the analysis used above accounts for variations in the size of the temperature differential $T_b - K = T_b - T_l$ and will account for T_b

only when K is equal in all mammals. This is shown in Fig. 6B by the fact that much of the variation in T_b among the mammals in Fig. 6A disappears when the differential $T_b - T_l$ is used. In this case the differential approaches 0.0 as either $(M_b/C)_r$ or $(M_b/C)_e$ approaches 0.0. Therefore, the variation of K represents a variation in the

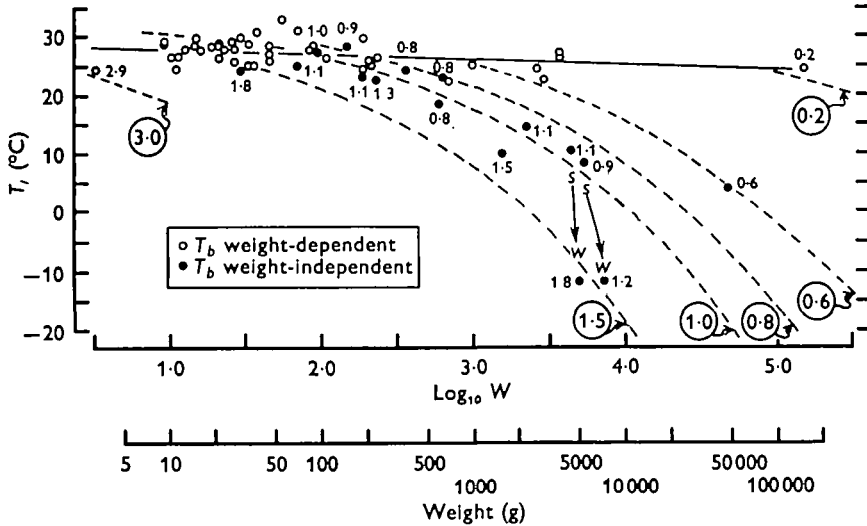


Fig. 5. The lower limit of thermoneutrality, T_l , in mammals as a function of body weight (data from Table 1). Numbers near solid points indicate values for $(M_b/C)_r$. Dotted curves expected from equation (8) for given values of $(M_b/C)_r$. S and W refer to summer and winter values, respectively.

Table 2. Variation in the set point of body temperature in bats as a function of food habits and distribution in South America

Species	z^* (°C)	Distribution			Food habits†	
		Trop.	Marginal	Temp.	Type	Range
<i>Rhinophylla pumilio</i>	7.2	×	—	—	Fruit	N?
<i>Desmodus rotundus</i>	6.6	×	×	—	Blood	B
<i>Glossophaga soricina</i>	6.5	×	—	—	Nectar, fruit	B
<i>Uroderma bilobatum</i>	6.4	×	—	—	Fruit	B?
<i>Noctilio labialis</i>	5.9	×	—	—	Insects	B
<i>Carollia perspicillata</i>	5.9	×	—	—	Fruit	B
<i>Molossus molossus</i>	5.9	×	×	—	Insects	B
<i>Eumops perotis</i>	5.7	×	—	—	Insects	B
<i>Phyllostomus discolor</i>	5.6	×	—	—	Fruit, meat	B
<i>Artibeus concolor</i>	5.6	×	—	—	Fruit	B?
<i>Noctilio leporinus</i>	5.2	×	×	—	Fish, insects	B?
<i>Vampyrops lineatus</i>	4.9	×	—	—	Fruit	B
<i>Tonatia bidens</i>	4.7	×	—	—	Meat	B
<i>Phyllostomus hastatus</i>	4.6	×	—	—	Meat, fruit	B
<i>Sturnira lilium</i>	4.5	×	×	—?	Fruit	B
<i>Artibeus jamaicensis</i>	4.2	×	×	—	Fruit	B
<i>Histiotus velatus</i>	4.2	?	×	×	Insects	B
<i>Anoura caudifer</i>	4.0	×	—	—	Nectar	N?
<i>Diphylla ecaudata</i>	3.9	×	—	—	Blood	N
<i>Diaemus youngi</i>	3.2	×	—	—	Blood	N

* $z = T_b - (M_b/C) - 22.2$.

† Range of foods used within a food type either broad (B) or narrow (N).

placement of the differential along a temperature axis and not in the ability of M_b/C to predict the size of the differential.

If there is significance in the variation of K , it should follow some meaningful pattern. The search for such a pattern is facilitated by substituting $T_0 + x$ for K , where T_0 is the lowest limit of thermoneutrality for any mammal whose T_b depends upon $(M_b/C)_e$ (here equal to 22.2°C in *Tachyglossus*), and x is the difference between the actual T_l for a particular species and T_0 . The range of x , then, is a measure of the

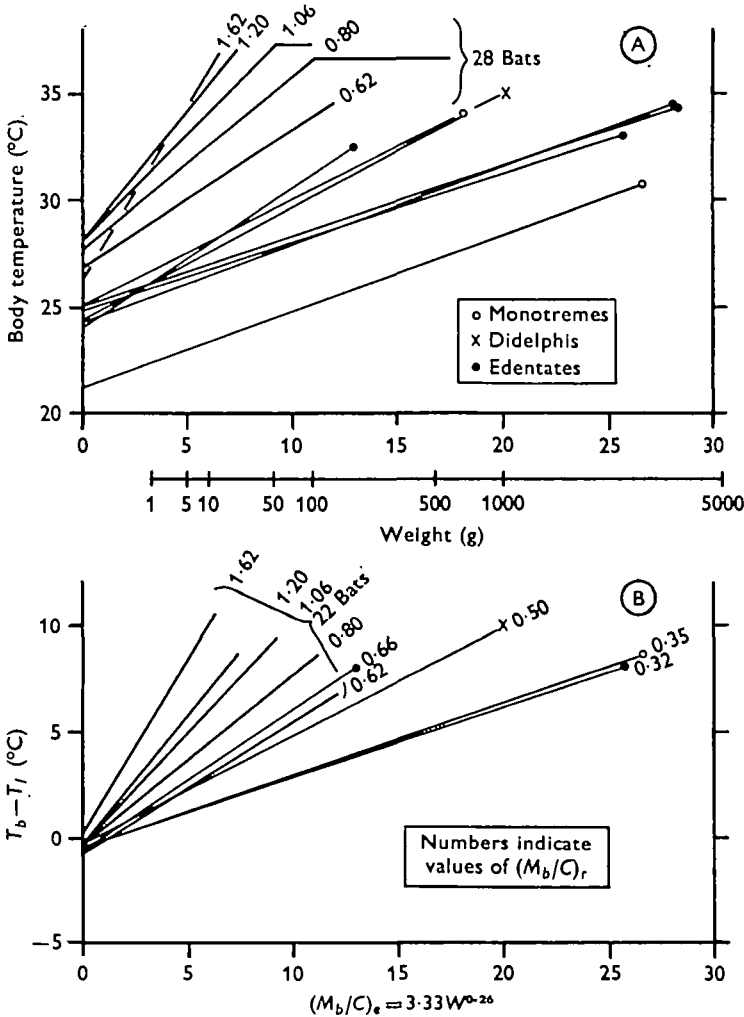


Fig. 6. A. Body temperature in selected mammals as a function of $(M_b/C)_r$ and $(M_b/C)_e$. B. The temperature differential between the body and the environment at the lower limit of thermoneutrality as a function of $(M_b/C)_r$ and $(M_b/C)_e$.

flexibility of the set point of body temperature independent of the influence of W , M_b , and C . Of two mammals having the same weight, basal rate of metabolism, and conductance, the species with the highest set point for temperature regulation, that is with the largest x , will have a higher rate of metabolism at all ambient temperatures below the lower limit of thermoneutrality of the warmer species. One may therefore

expect that mammals that live in cold climates or that have unusually narrow food habits might have small values for z , since this may be a means of reducing energy expenditure at a fixed weight without sacrificing the effectiveness of thermoregulation. These conclusions agree with the data on bats (Table 2). Furthermore, *Didelphis* has the lowest z for known marsupials, and it has moved farther into the temperate zone than any other marsupial; *Sorex* has a low z , which insures that its rate of metabolism is less than it would be for a mammal of its size with a large z ; and z is small in edentates and monotremes, tropical mammals with specialized food habits. Body temperature thus seems to be capable of some variation independent of M_b , C and W in a manner adaptive to the climate. It is not clear what sets the limits of variation in z .

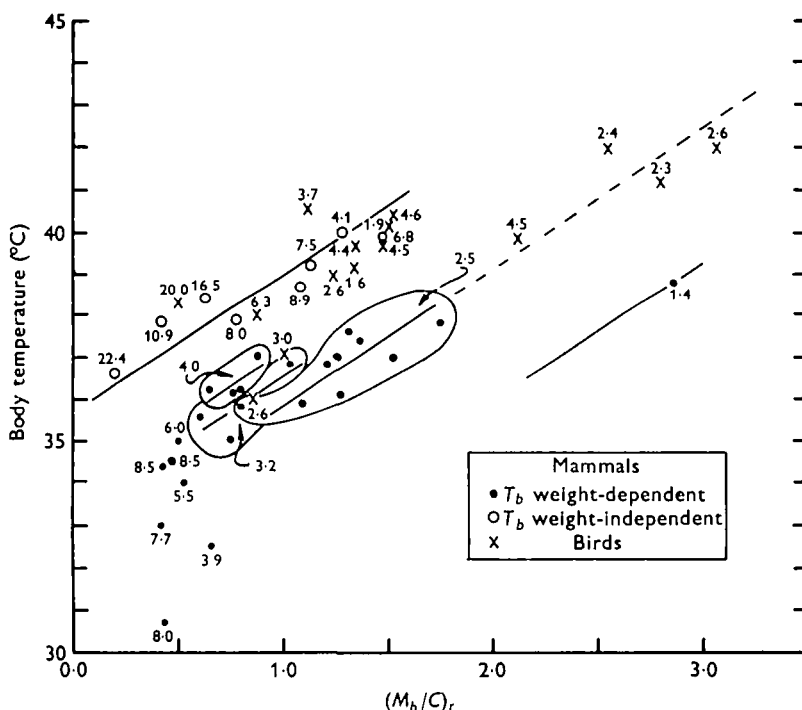


Fig. 7. The influence of $(M_b/C)_r$ on body temperature in mammals and birds (data from Tables 1 and 2). All values of $(M_b/C)_r$ for both birds and mammals use $(M_b/C)_s = 3.33W^{0.26}$ as a standard. Numbers on graph indicate $W^{0.26}$.

Beyond the 'critical' weight, body temperature is influenced by the ratio $(M_b/C)_r$. One can expect from equation (5b) that the slope of the curve of body temperature on the relative ratio would be equal to 3.33, irrespective of weight, since variation in $W^{0.26}$ is compensated for by variation in T_l . The same relationship between T_b and $(M_b/C)_r$ should also exist when T_b depends upon $(M_b/C)_e$, provided that weight and z are constant. Both of these expectations generally hold (Fig. 7), except at some low values for $(M_b/C)_r$, where there is variation in z .

Since a large weight can compensate for a low ratio $(M_b/C)_r$ in the maintenance of precise thermoregulation, large mammals tend to have lower ratios $(M_b/C)_r$ (Fig. 1) and therefore lower body temperatures than species of an intermediate size (Figs. 2B

and 3). This trend raises the possibility that the largest of mammals, the pachyderms and cetaceans, have even lower relative ratios and temperatures. One can conclude from Fig. 7 that T_b in mammals whose temperature is independent of $(M_b/C)_e$ should approach 35.7°C as $(M_b/C)_r$ approaches 0.0 and weight becomes infinitely large. Unfortunately, there are no adequate measurements of the energetics of large mammals; it is even difficult to obtain reliable measurements of their body temperatures.

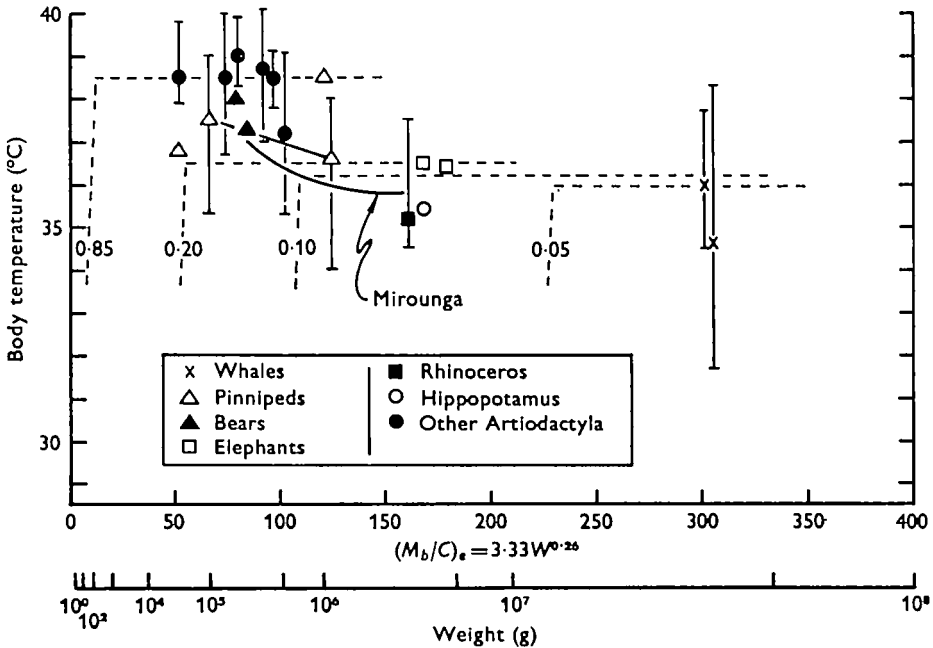
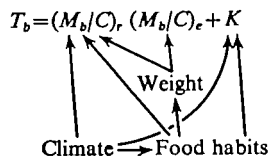


Fig. 8. Body temperatures in large mammals as a function of body weight. Dashed curves are for T_b when $(M_b/C)_r$ is constant. The data (mean \pm ranges) were taken from Allbrook *et al.* (1958), Bartholomew (1954), Benedict (1935), Bligh & Harthoorn (1965), Bligh *et al.* (1965), Buss & Wallner (1965), Irving & Krog (1954), Luck & Wright (1959), Morrison (1962), and Ray & Fay (1968).

The few data indicate a continuing decrease in temperature with an increase in weight, an asymptote in accord with the argument above occurring near 36°C (Fig. 8). The decrease in temperature with an increase in weight occurs intraspecifically both in the walrus (*Odobenus rosmarus*; Ray & Fay, 1968) and in the northern elephant seal (*Mirounga angustirostris*; Bartholomew, 1954).

It is clear from this discussion that the parameters T_b , T_l , M_b , C , and W have interrelations that are consistent with the Newtonian model of thermoregulation proposed by Scholander and Irving. It may also be tentatively concluded that the level of temperature regulation in mammals is determined in the following manner:



THE THERMOREGULATION OF BIRDS

Birds usually have higher resting temperatures than mammals; this has been explained as due to the high basal rates of metabolism and low thermal conductances of birds (McNab, 1966*a*). Two problems with this explanation have since arisen. One is that the higher level of metabolism in birds has been questioned by Lasiewski & Dawson (1967) and the lower conductances disputed by Herreid and Kessel (1967). Secondly, it remains to be determined what effect bringing weight into the analysis of mammalian temperatures has upon the conclusion that bird temperatures are determined in the same manner as those of mammals.

Lasiewski & Dawson (1967) suggest on the basis of energetics that birds can best be broken into two groups, passerines and non-passerines, the curve of metabolism on weight for each having an exponent similar to that of mammals and differing each from the other and from mammals only by a coefficient. Without doubt marked

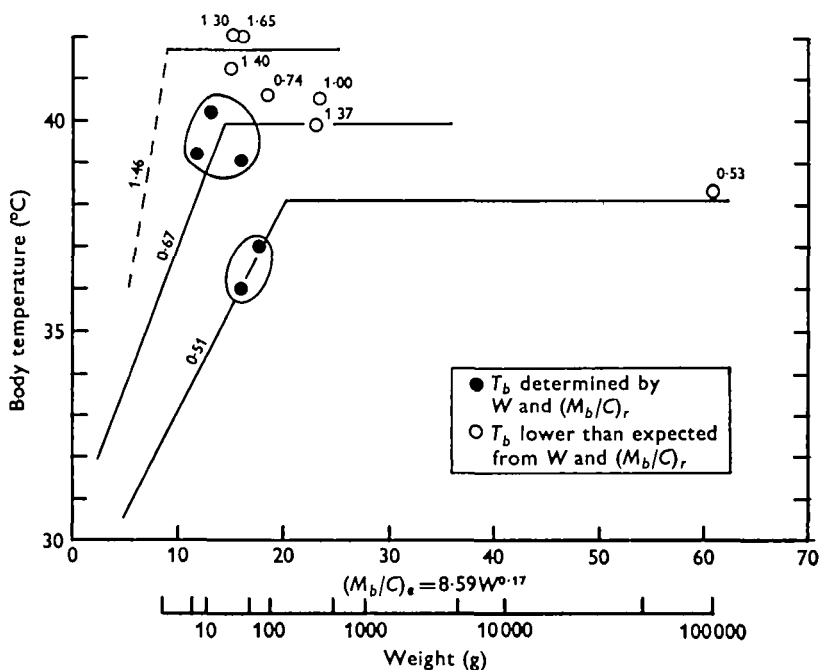


Fig. 9. Body temperature in birds as a function of the ratios $(M_b/C)_r$ and $(M_b/C)_s$. Data from Table 3.

differences exist among birds, but one could as well divide birds into familial or generic groups (e.g. Zar, 1968). How animals are divided into categories depends upon the questions being asked, not simply upon whether one can find statistically significant differences. Thus, one may be interested in the differences existing between homoiotherms and poikilotherms, as was Hemmingsen (1960), who combined mammals and birds into one equation. Or, one may be interested in the differences existing between mammals and birds (King & Farner, 1961; McNab, 1966*a*). Each of these viewpoints is legitimate.

Herreid & Kessel (1967) measured cooling constants for dead birds from which they calculated thermal conductances; they also summarized the data available in the literature on the conductances of live mammals. They concluded that there is no difference between the conductances of mammals and birds. However, conductances measured on live animals and those calculated from the cooling curves of dead individuals often do not give identical results (e.g. McNab & Morrison, 1963), which may have obscured any inequality in conductance occurring between birds and mammals. This suggestion is borne out by Lasiewski, Weathers & Bernstein (1967), who described an equation for the conductances of live birds as a function of weight that is identical in the exponent to that of Herreid and Kessel for mammals, differing only in the coefficient, which is 17% less than that for mammals. Thus, birds do in fact have lower conductances than mammals of the same weight.

The question remains whether these differences are sufficient to account for the higher temperatures of birds, especially given the effect of weight in mammals. That is, if a mammal of a given weight had the rate of metabolism and conductance of a bird of the same weight, would the mammal have the same temperature as the bird? Or do mammals operate at lower temperatures than birds for reasons other than those of M_b and C ? Unfortunately, there are very few complete sets of data on birds.

The expected ratio $(M_b/C)_e$ for birds is equal to $(7.3W^{-0.34})/(0.85W^{-0.51}) = 8.59W^{0.17}$ (McNab, 1966a; Lasiewski *et al.* 1967). Therefore, if the analysis described for mammals works for birds as well, T_b should be given by

$$T_b = 8.59(M_b/C)_r W^{0.17} + K. \quad (9)$$

Since $8.59W^{0.17} = (2.58W^{-0.09})(3.33W^{0.26})$, the ratio $(M_b/C)_r$ in birds is equal to $2.58W^{-0.09}$ times that of mammals, which will insure that the temperatures of small birds will be appreciably higher than those of mammals of the same weight.

The body temperatures of birds are plotted in Fig. 9 as a function of $8.59W^{0.17}$ (data from the literature, see Table 3): there is an acceptable agreement between the temperatures measured in birds and the parameters of $(M_b/C)_r$ and $W^{0.26}$. Furthermore, the interactions that exist between T_b , $(M_b/C)_r$, and $W^{0.26}$ in these birds are similar to those found in mammals (Fig. 7), the major difference between these groups being that birds have higher values for the ratio $(M_b/C)_r$. But an important point must be made here: in spite of the many comparative studies on the metabolism of birds, *most of these data have little or no value in studies of the energetics of temperature regulation because body temperatures corresponding to the rates of metabolism were not reported*. This deficiency is very important, since conductance cannot be evaluated without T_b , especially when a bird's response to a change in T_a involves both M and C . To interpret rates of metabolism in terms of temperature regulation, one must have at least the following data: (1) W , (2) T_a , (3) T_b , and (4) the animal's activity.

Obviously, more complete data on the energetics of birds are required over a large weight range. Nevertheless, one can tentatively conclude that temperature regulation in birds is determined as it is in mammals; the differences in body temperature between these groups are primarily due to differences in M_b and C . The variation of M_b and C among birds depends upon their body weight and the conditions existing in their normal environments (Fig. 1).

Table 3. *The energetics of birds*

Species	Weight (g)	Basal metabolism		Conductance		$(M_b/C)_s$ §	T_b (°C)	References
		(c.c. O ₂ /g-h)	%†	(c.c. O ₂ /g-h °C)	%‡			
<i>Struthio camelus</i>	100 000	60.8	185	0.0083	346	0.53	38.3	Crawford & Schmidt-Nielsen (1967)
<i>Ardeola ibis</i>	350	23.3	—	—	—	1.00	40.5	Sigfried (1968)
<i>Lagopus leucurus</i>	326	22.9	127	0.041	93	1.37	39.9	Johnson (1968)
<i>Lophortyx californicus</i>	139	18.4	74	0.069	100	0.74	40.6	Brush (1965)
<i>Scardafella inca</i>	40.5	16.1	56	0.11	85	0.66	39.0	MacMillen & Trost (1967)
<i>Phalaenoptilus nuttalli</i>	40	16.1	38	0.11	85	0.45	36.0	Bartholomew <i>et al.</i> (1962); Brauner (1952)
<i>Chordeiles minor</i>	70	17.7	110	0.11	110	0.58	37.0	Lasiewski & Dawson (1964)
<i>Passer domesticus</i>	25.8	14.9	148	0.17	106	1.40	41.2	Hudson & Kimzey (1966)
<i>Richmondia cardinalis</i>	40	16.1	127	0.10	77	1.65	42.0	Dawson (1958)
<i>Estrilda troglodytes</i>	6.2	11.7	92	0.50	152	0.61	39.2	Lasiewski <i>et al.</i> (1964)
<i>Taeniopygia castanotis</i>	11.7	13.1	104	0.34	142	0.73	40.2	Calder (1964)
<i>Zonotrichia leucophrys</i>	28.6	15.2	104	0.12	80	1.30	42.0	King (1964)

Note. Italicized numbers represent questionable values or values that are poorly substantiated.

• $(M_b/C)_s = 8.59 W^{0.17}$.

† $M_b(\%) = 100 \text{ mean}/7.3 W^{-0.24}$.

‡ $C(\%) = 100 \text{ mean}/0.85 W^{-0.61}$.

§ $(M_b/C)_s = M_b(\%)/C(\%)$.

SUMMARY

1. The interactions of basal rate of metabolism, thermal conductance, body temperature, lower limit of thermoneutrality, and body weight in mammals are compatible with Newton's law of cooling.

2. A small body weight will normally reduce the level and preciseness of body temperature, but a high basal rate of metabolism or a low thermal conductance may compensate for a small size and permit a high, precise temperature to be maintained.

3. The parameters of energetics that fix the level and preciseness of body temperature in mammals are ultimately correlated in turn with the environmental parameters of climate and food habits.

4. Birds generally have higher temperatures than mammals because the basal rates of metabolism are higher and the conductances lower in birds than in mammals of the same weight.

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Table of Symbols

Symbol	Factor	Units
A	Surface area	cm ²
C	Thermal conductance (coefficient of heat transfer)	c.c. O ₂ /g-h °C, or cal/h °C
c_1, c_2	Thermal coefficients	c.c. O ₂ /g-h °C, or cal/h °C
h	Convective coefficient	cal/cm ² -h °K
K	Temperature constant	°C
k	Conductive coefficient	cal/cm ² -h °K
L	Heat of vaporization	(c. 540) cal/g H ₂ O
M	Rate of metabolism	c.c. O ₂ /g-h, or cal/h
M_b	Basal rate of metabolism	c.c. O ₂ /g-h, or cal/h
Q	Heat	cal
s	Specific heat	cal/g °C
T_a	Ambient temperature	°C, or °K
T_b	Body (core) temperature	°C, or °K
T_l	Lower limit of thermoneutrality	°C
T_0	Temperature constant	°C
t	Time	h
W	Body weight	g
w	Rate of water loss	g H ₂ O/h
x	Temperature constant	°C
ϵ	Emissivity	None
ϕ	Cooling constant	1/h
σ	Stefan-Boltzmann constant	(4.88 × 10 ⁻⁸) cal/cm ² h °K ⁴