

## Time, Energy, and Body Size

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Different mammals and birds appear to be remarkably similar in their function but differ in their overall geometry as they increase in size. As Brody (1945) stated so well, "The organism changes geometrically so as to remain the same physiologically." In this context I want to examine these changes in terms of the allocation of time and energy as animals increase in size. Such considerations suggest that during the life span of mammals the total resting energy expenditure per unit body mass is similar, a concept that can be traced back to Max Rubner at the turn of the century. It also suggests, for example, that the number of heart beats and breaths during a life span are similar from mouse to elephant.

The evidence for such provocative statements is not new and is based on interpretations of allometric relationships which examine organ size, metabolic rates, physiological rates, and cycles as they vary with body size, and have most recently been discussed by Boddington (1978), Calder (1984), Lindstedt (1985), Lindstedt and Calder (1976, 1981), and Schmidt-Nielsen (1984).

As animals become larger, their physiological functions, or biological machinery, are remarkably similar, preserving throughout evolution a more or less constant cell size, capillary diameter, capillary distance from cells, blood pressure, electrolyte composition, and Starling's balance between hydrodynamic and osmotic forces. Similar are muscle filaments as well as their maximal force per cross-sectional area, body temperature, alveolar gas tensions, and blood pH, along with efficiencies of energy utilization.

While these dimensions and compositions are preserved, blood volume, heart volume, lung volume, and muscle volume must increase with size and do so in direct proportion to body mass.

However, energy production and the volume flows which provide for O<sub>2</sub> delivery and CO<sub>2</sub> elimination, the alveolar ventilation, and cardiac output increase as the  $\frac{3}{4}$  power of body mass. That is, for every 10-fold increase in body mass, these functions increase only 5.6-fold.

Lastly, we must look at what I call delivery systems. These decline as

animals get larger, namely, heart rate, breathing rate, cardiac output per kilogram, alveolar ventilation per kilogram, specific metabolic rate (kilocalories per kilogram), and some renal functions. As the recent review of Lindstedt and Calder (1981) reveals, these functions all appear to decline at similar rates; namely, they are proportional to  $\text{ca.} -0.25$  power of body mass. Some of these functions are more conveniently expressed in terms of cycles or time, such as cardiac cycle, respiratory cycle, life span, circulation time, and gestation time. These are all proportional to  $\text{ca.} +0.25$  power of body mass. The mass exponents for some of these functions are shown in Table 16.1.

Most of these specific generalizations were unknown to Max Rubner, professor of physiology at Berlin and director of the Kaiser Wilhelm Institute for Work Physiology and Nutrition around the turn of this century (Fig. 16.1). Rubner, a powerful scientist of this era, had finally established the fact that the heat production of animals measured by direct calorimetry could be explained by the combustion of food and also measured indirectly by the uptake of  $\text{O}_2$ . Today this is an accepted fact. In 1908 and 1909 toward the end of his career he published two books on the relationship between life span, growth, and nutrition. In them he presented a table which showed the body mass and estimated life span of five domestic animals. The last column showed the total calories per kilogram expended during the life span (basal metabolic rate per kilogram  $\times$  life span), and pointed out that these were essentially similar (Table 16.2). He was quick to note that humans did not fit into this scheme. He estimated the life span of the human to be 80 years, and his estimated total caloric expenditures per kilo was four times greater than that for all the other animals. (I shall return to this point later.) In any event, at that time to suggest that the lifetime caloric expenditure per unit body mass was similar in animals small and large was a very bold statement, and there it rested. During the following decades most biologists were skeptical since the data base was rather poor. Furthermore, estimates of life span are a rather elusive figure. Nevertheless, the concept was attractive, and over the following decades the data base increased.

TABLE 16.1. Specific rates or cycle times and their exponents when regressed upon body mass.

Rates		Time	
Specific metabolism	- 0.25	Life span	0.24
Heart contraction	- 0.23	Cardiac cycle	0.23
Breathing frequency	- 0.26	Respiratory cycle	0.26
Cardic output ( $\text{kg}^{-1}$ )	- 0.20	Gestation period	0.25
Alveolar ventilation ( $\text{kg}^{-1}$ )	- 0.26	Circulation time	0.21

Selected from the tables of Lindstedt and Calder (1981).

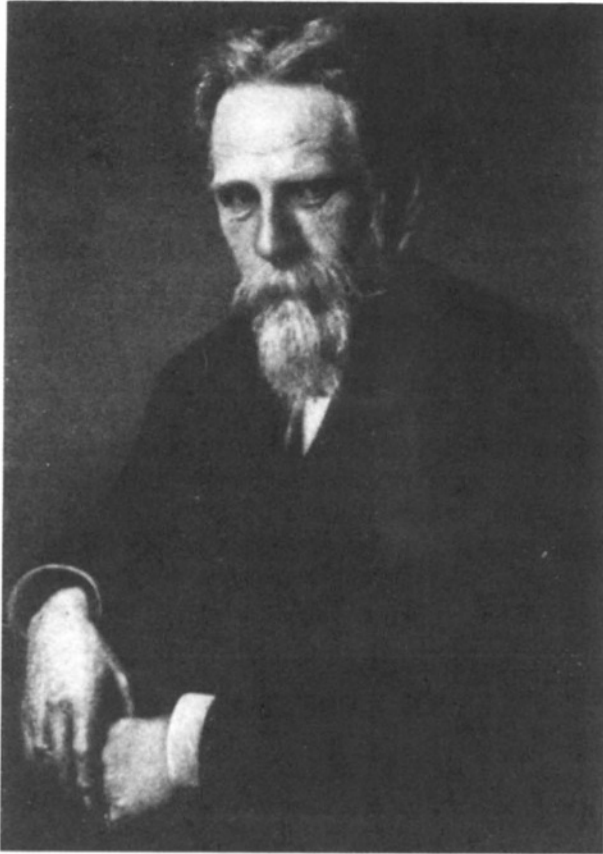


FIGURE 16.1. Max Rubner, appointed professor of physiology at Berlin, 1908, and founder of the Kaiser-Wilhelm Institute for Work Physiology. (Photo from *Geschichte der Physiologie*, K.E. Rothsuh, Springer, 1953.)

TABLE 16.2. Relationship between body mass, life span, and metabolic output presented by Rubner in 1908.

	Body weight	Length of life	kcal
	(kg)	(years)	kg·life span
Horse	450	30	170,000
Cow	450	26	141,000
Dog	22	9	164,000
Cat	3	8	224,000
Guinea pig	0.6	6	266,000

**Metabolic Rate.** One of the most reliable and accepted allometric relationships for mammals is that the basal metabolic rate is proportional to the body mass raised to the 0.75 power (Kleiber 1961). Dividing the metabolic rate by body mass we obtain the specific metabolic rate which now declines with an increase in body mass raised to the  $-0.25$  power, which tells us, for example, that a 3-g shrew burns its fuel about 20 times faster than a 4000-kg elephant.

**Life Span.** Our exact knowledge of life spans for various mammals is not easily established, and I have combined the allometric equations for life span as a function of body mass from the reports of Boddington (1978), Gunther and Guerra (1955), and Sacher (1959), which show that life span is proportional to the  $+0.25$  power of body mass, in contrast to the  $-0.25$  power which describes specific metabolic rate. In Fig. 16.2 these two functions are shown on a semilog plot where the specific metabolic rate is expressed per year and life span is expressed in years. These two reciprocal curves tell us that for any given body mass the product of specific metabolic rate and life span yields a constant, namely, 240,000  $\text{kcal}\cdot\text{kg}^{-1}$  ( $240 \text{ kcal}\cdot\text{g}^{-1}$ ), a value not too different from that predicted by Max Rubner 80 years earlier (Table 16.2). A recent study by Boddington (1978) yields a similar prediction and refers to this constant as the *absolute metabolic scope* of mammals.

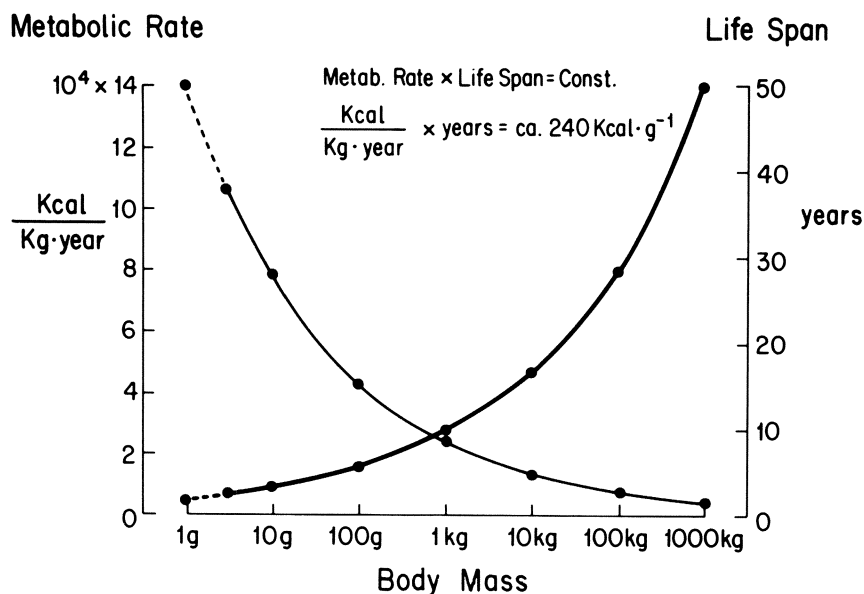


FIGURE 16.2. Relationship of specific metabolic rate and life span to body mass in mammals.

It is of interest to note that the metabolic rate of a 70-kg man fits well on the metabolic rate curve. However, the life span curve predicts a life span of ca. 25 years, which was the life expectancy of man prior to the seventeenth century (Brody 1945). The fact that humans have been able to rid themselves over the last millennium of many factors which limit the life span of other animals, such as predation, disease, and deleterious nutritional and environmental conditions, might explain man's extended period.

*Heart and Respiratory Rate.* The heart rate of mammals has been well established and is also proportional to the  $-0.25$  power of body mass. In Fig. 16.3, heart rate and life span are plotted against body mass, which tells us that during the life span of most mammals the heart beats about 1.2 billion times. A similar relationship can be established for the respiratory frequency, which yields an average predicted number of 300,000 per life span. Thus, on the average, from mouse to elephant, there are four heart beats for each respiration.

## The Typical 1-g Tissue

The typical 1-g tissue illustrated in Fig. 16.4. I call it the 1-g mammalian tissue "on the hoof." It represents all mammals, mouse to elephant. During its life span it burns the equivalent of 60 g of carbohydrates to

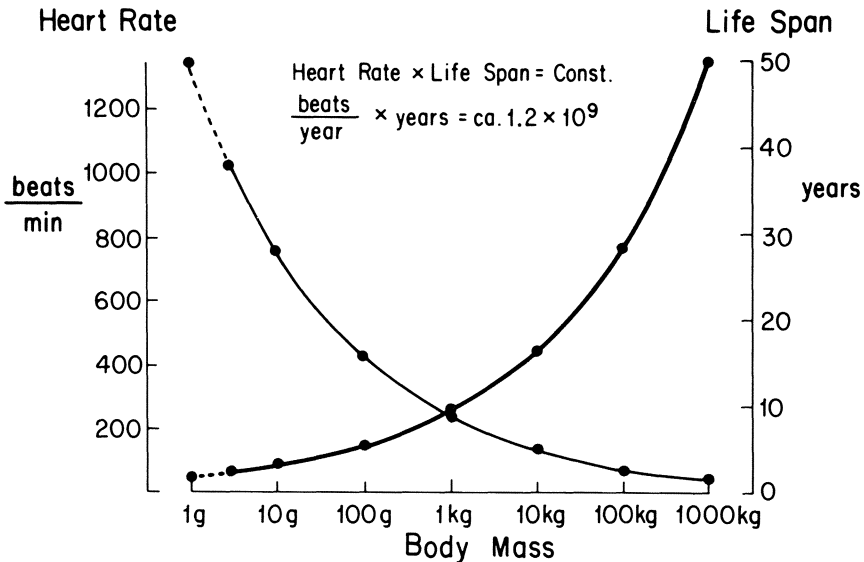


FIGURE 16.3. Relationship of heart rate and life span to body mass in mammals.

release 240 kcal. This requires 50 l of  $O_2$ , and with an RQ of 0.8 will release 40 l of  $CO_2$ .

We can describe additional functions. For example, what is the perfusion that this 1 g of tissue receives during its life span? Cardiac output per kilogram of body mass has a similar negative slope (Table 16.1). So during a life span mammals receive about 800 l of blood per gram of tissue. Since this tissue also consumes 50 l of  $O_2$ , it is easy to calculate the arterial-venous  $O_2$  difference, namely, 6 vol %. We also recall that it took about 1 billion heart contractions to pump this blood.

Before I launch into a critique of this recapitulation, let me bring you, for your possible amusement, another example of life span with which you may feel more at home. I began to wonder whether our modern engineer had succeeded in developing an organism which was more efficient than our typical mammalian tissue. I am referring to the American car. I assumed it weighed 2000 kg, had an average life span of 40,000 miles, and obtained 20 miles per gallon of gasoline. In Fig. 16.4 you

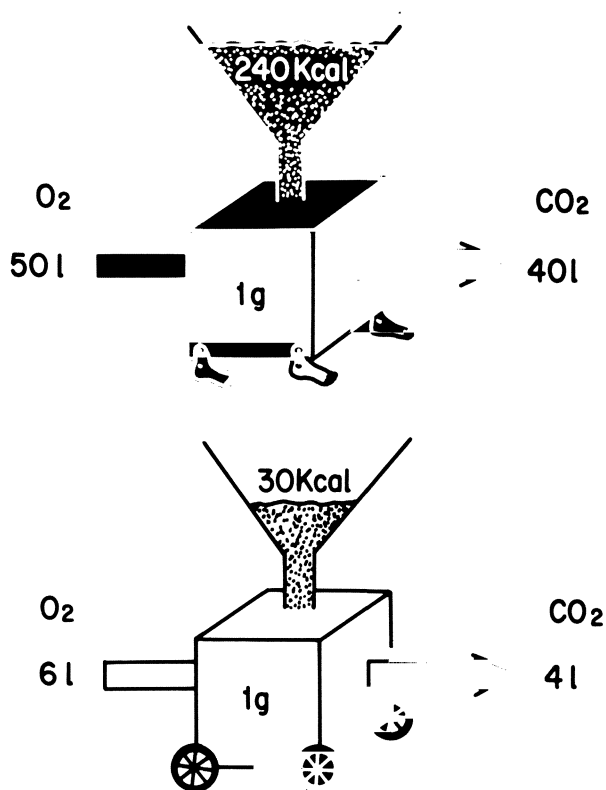


FIGURE 16.4. *Top:* An idealized 1-g mammalian tissue over its life span metabolizing 240 kcal of food by taking up 50 l of  $O_2$  and producing 40 l of  $CO_2$ . *Bottom:* Metabolic performance of an idealized 1 g of American automobile over its life span of 40,000 miles.

see 1 g of American car “on wheels.” Note that it consumed only one-eighth the amount of fuel before it landed in the junkyard. In other words, without the continuous repair that our tissues undergo, the engineer cannot compete, as yet, with the efficiency of protoplasm.

## Critique

There are, of course, many questions which arise from this oversimplified presentation of “Rubner’s law.” Nevertheless, it does indicate a general trend even though there are many species that do not fit on the idealized curves that were presented. For example, (1) Scholander et al. (1950) showed that certain species had metabolic rates that deviated significantly from the common 0.75 power function of body mass. Would these deviations be associated with a different life span? (2) Rubner’s law is based on basal metabolic rates, while these, of course, are normally exceeded during the daily activity of animals. Should, therefore, this overall metabolism be included in such calculations? And (3), finally, there is the question concerning the reliability of life-span estimates. These questions cannot be easily answered; instead I would like to provide other evidence in support of Rubner’s law.

## Metabolic Rates and Life Span in Birds

Metabolic rates and life span in birds were reviewed by Lindstedt (1985) and Lindstedt and Calder (1976). From these, one can calculate that the total energy per gram of tissue during the life span of passerine birds is also a constant, but considerably higher than in the mammal, namely, ca.  $1000 \text{ kcal} \cdot \text{g}^{-1}$  instead of  $240 \text{ kcal} \cdot \text{g}^{-1}$ . The explanation for this difference is not obvious, but the metabolic rate as well as the life span is higher than for a mammal of the same body mass. Nevertheless, it provides additional support for Rubner’s law, and in this case the life span data were determined from extensive bird-banding records, which are more reliable than those established for mammals.

## Embryonic Life Span

Can the overall life span be conveniently divided into three periods, namely, embryonic, juvenile, and adult, where each period functions energetically as described above for the adult mammal? This was originally proposed by Rubner (1909) and tested more recently by Rahn (1982) and Rahn and Ar (1980). The advantage that developing bird eggs provide in this context is that it is relatively easy to measure their oxygen consumption throughout the incubation period and that the incubation times are well established.

One can now ask the question: Is the total energy expenditure per gram of egg during incubation the same in all bird eggs, even though there are large differences in egg mass and incubation time? Do bird embryos have an *absolute metabolic scope* in the sense of Boddington (1978)? The total incubation energy expenditure has recently been measured in a large number of species (see Bucher and Bartholomew 1984 for major source). These values are regressed against egg mass in Fig. 16.5 and have a slope of 0.95, not significantly different from 1.0. The average energy loss was 2.3 kJ/g egg (0.55 kcal/g egg), where egg mass ranged from 1 g to the 1450-g ostrich egg (not shown in the figure), and incubation times ranged from 11 days to 65 days in two species of albatross. Since the hatchling mass is 67% of the initial egg mass, we can convert the total energy requirements of the embryo to hatchling mass. Thus, 0.82 kcal/g hatchling is the best estimate of the *absolute metabolic scope* during the embryonic life span. Furthermore, the gas tensions which exist in the air cell just

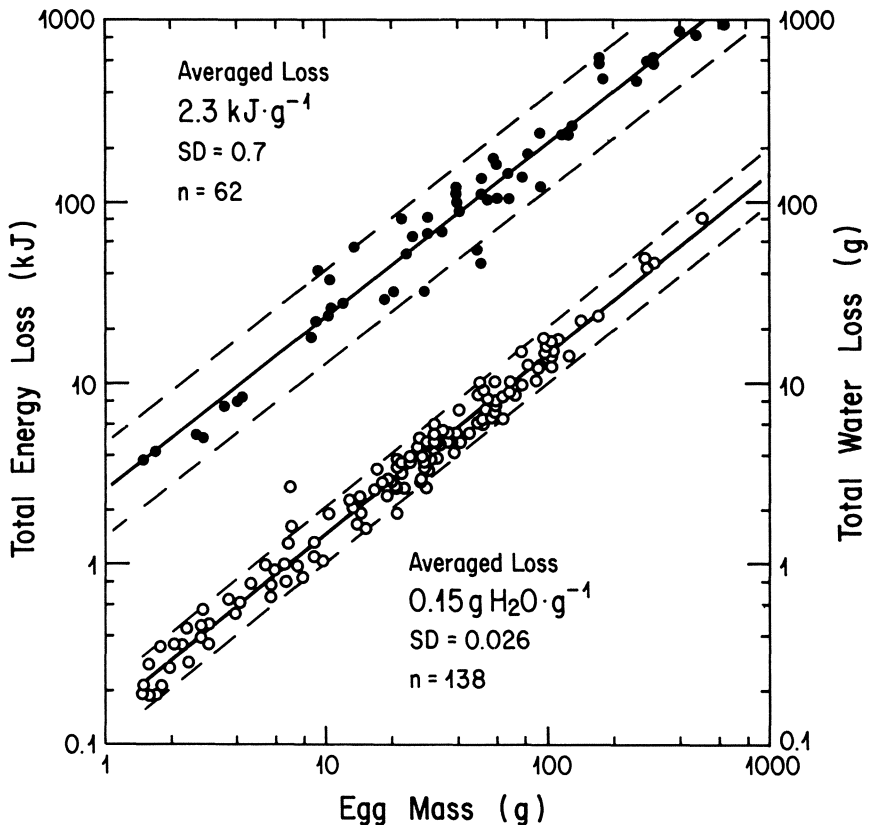


FIGURE 16.5. *Left ordinate*: Total energy loss during the development of an avian embryo as a function of the initial egg mass. *Right ordinate*: Total diffusive water loss during the development of avian eggs as a function of initial egg mass.



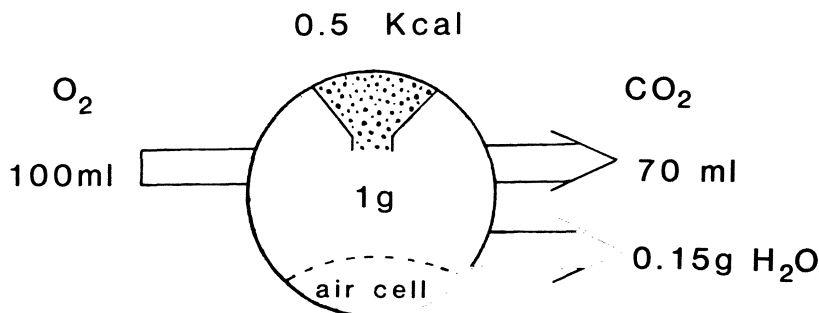


FIGURE 16.6. Idealized 1-g bird egg over its embryonic life span, metabolizing 0.55 kcal of stored energy by taking up 100 ml O<sub>2</sub>, producing 72 ml CO<sub>2</sub>, and releasing 0.15 g of water vapor.

before the first pipping stage are similar, namely,  $P_{O_2} = 100$  Torr and  $P_{CO_2} = 42$  Torr (Paganelli and Rahn 1984). These have now been directly measured in some 22 species ranging in size from 10 to 1500 g (ostrich) and with incubation periods varying from 15 to 65 days.

Also shown in Fig. 5 is the total diffusive water loss of eggs (daily water loss times total incubation days) during their natural incubation (Ar and Rahn 1980). The slope of this line is 0.99 and not significantly different from 1.0. Thus the average loss is  $0.15 \text{ g H}_2\text{O g}^{-1} \text{ egg}$ . This water is lost by diffusion through the pores of the eggshell and does not include the additional amount that is lost by convection after pipping of the eggshell occurs.

Fig. 16.6 depicts the idealized 1-g avian egg during its embryonic life span. It delivers a hatchling with similar caloric loss, water loss, and gas tensions, which are independent of incubation time or mass.

## Summary

In 1908 Rubner suggested that during the life span of mammals their total basal energy expenditure per kilo body mass is similar, namely, ca.200,000 kcal, a concept which is here reexamined. Today's evidence still fits this model and can be extended to adult passerine birds, while energy expenditure per unit mass of developing avian eggs also fits Rubner's law. The latter suggests that total life span can conveniently be divided into embryonic, juvenile, and adult life spans where during each period the total specific energy expenditure is similar.

As J.B.S. Haldane (1985) wrote, "For every kind of animal there is a most convenient size," to which we can add "and an optimal metabolic rate." Each gram of tissue, from mouse to elephant, is provided with the same potential for energy release, which can be spent quickly or slowly depending on the animal's size. The larger the animal, the smaller its maintenance cost and the longer the life span.

It may not be surprising that today Rubner's "law" has become the focus for one of our theories of aging, the *free radical* theory. It has been estimated that during tissue metabolism as much as 6 percent of the oxygen is converted to various reactive O<sub>2</sub> species, which in turn are countered by large numbers of antioxidants. Thus one might argue that after a life span delivery of 50 l of O<sub>2</sub> per gram of average tissue, the balance between reactive O<sub>2</sub> species and antioxidants is upset leading to the stage of "burn-out."

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