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## Metabolic Levels in Adult Homeotherms

[With 5 Tables &amp; 1 Fig.]

Metabolic level has been defined as daily heat production, at standard conditions, divided by metabolic unit of body size *i.e.* by weight of an animal in kg raised to  $3/4$  power. In literature prevails the opinion that average metabolic level of adult mammals amounts to 70 kcal/kg $^{3/4}$  × 24 hr, and that metabolic level of birds is much similar to that. Re-evaluation of recently published data permit to conclude that there are at least four different metabolic levels in homeotherms, namely: (1)  $48.6 \pm 1.00$  kcal/kg $^{3/4}$  × 24 hr in marsupials (8 sp., 14.1 g to 32.490 kg, n = 8); (2)  $69.0 \pm 1.20$  kcal/kg $^{3/4}$  × 24 hr in mammals (12 sp., 21 g to 679 kg, n = 36); (3)  $80.14 \pm 3.04$  kcal/kg $^{3/4}$  × 24 hr in nonpasserine birds (57 sp. from 12 families, 40 g to 100 kg, n = 63); (4)  $145.60 \pm 3.99$  kcal/kg $^{3/4}$  × 24 hr in passerine birds (35 sp., 6.1 g to 866 g, n = 48). The differences among all these metabolic levels are highly significant ( $P < 0.0001$ ). Somewhat less reliable data suggest that metabolic level of bats (*Chiroptera*) is low; similar to that of marsupials. On the other hand metabolic level of small (but not large) *Insectivora* is very high; even higher than that of passerine birds.

## I. INTRODUCTION

Energy which is usually defined as capacity to do work is required for variety of processes taking place in an organism. All these processes are performed on account of the food consumed. Since, however, the efficiency at which chemical energy of the food is transformed into useful energy is limited a part of this energy is inevitably liberated as heat. The amount of heat liberated can be measured by direct or indirect calorimetry described in many manuals *e.g.* Brody (1945), Dukes (1947), Kleiber (1950, 1961), Cherednichenko (1955).

Heat production of a homeothermic animal may vary, depending on conditions, from a certain minimal value to hundred times of this value (Bladergroen, 1955; Brody, 1945, 1948; Dill, 1936; Graham, 1964; Hall & Brody, 1933; Hart, 1952; Hayward, 1966; Janský, 1965; Poczopko, 1969). A rigorous standardization of conditions, at which the measurements of heat production are carried out,

is therefore needed for valid comparisons of this production in different animals. It is logical to accept as such conditions those at which all activities of an investigated animals are reduced to a possible minimum. This is attained when an animal is in complete physical and psychological rest, in postabsorptive state and in thermoneutral surrounding. The metabolic rate determined at such conditions is called by many authors »basal« (*BMR*) or, following Krogh's suggestion (1916) »standard«. It is believed that *BMR* represents the heat expenditure associated only with those processes which are indispensable to sustain the life.

The purpose of this paper is to compare the available data on *BMR* of variety of adult homeotherms in order to find possible differences and similarities.

## II. THE CHOICE OF METHOD FOR COMPARISON OF *BMR* IN DIFFERENT ANIMALS

Any comparison requires a common basis. We must decide, therefore, what to accept as such a basis for intended comparisons of *BMR* of different homeotherms.

*BMR* of an animal during a definite unit of time (hour, day) is the greater the larger is an animal. When, however, *BMR* is expressed per unit of body weight (gram, kilogram) it declines with an increase of body size. These relationships between metabolic rate and body size have been known long ago, and the attempts have been made to find such an unit of body size for which recalculated heat production would be equal in large and small animals. From these attempts the so called »surface rule« or »surface law« had been emerged, (Benedict, 1938; Brody, 1945; Kleiber, 1947, 1961; Zeuthen, 1953). The »surface rule« states that heat production rate is proportional to the surface area. According to Rubner (1883) large as well as small animals produce  $1000 \text{ kcal/m}^2 \times 24 \text{ hr}$ . According to this author (*l.c.*) proportionality of heat production to the surface area developed in evolution as adjustment to homeothermy. Body temperature of all homeotherm is approximately  $37^\circ\text{C}$  and because the heat is dissipated from the external surface the same amount of calories per unit of surface area must be produced in large and small animals in order to keep the body temperature constant. This explanation, called often »heat transfer theory« (Kleiber, 1961), at first sight seems to be very convincing, but is not so satisfactory when considerable differences in thermal insulation of animals, afforded by hair or feather covers are taken into consideration. Moreover, metabolic rate of poikilothermic animals also follows the »surface rule« (Zeuthen, 1947, 1953; Bertalanffy, 1957; Hem-

mingsen, 1960) and one should agree with Bertalanffy (1957) that homeothermy cannot be used as explanation of the surface dependant metabolic rate in these animals, because it does not exist. It seems, also, that the metabolic rates of poikilothermic ancestors of the to-day's homeotherms were roughly proportional to the surface area. It would mean that proportionality of the metabolic rate to the surface area is phylogenetically older than homeothermy.

There were some other theories developed in order to explain the »surface rule«. They are listed and discussed by Kleiber (1947, 1961) and Bertalanffy (1957). Applicability of interpretations of the »surface rule« by these theories is usually limited to a certain group of animals. If so, there is serious doubt concerning their validity. The fact, however, remains that the metabolic rate of animals is roughly proportional to the surface area, and therefore, square meter or decimeter may be accepted as metabolic unit of body size. Yet this unit is not accurate enough to be good reference standard in comparative studies Kleiber (1965) has pointed out that results of measurements of the surface area, even of the same species and performed by the same investigator, may differ by 20 to 50 percent. The surface area is not often measured but it is usually estimated from body weight, using known M e e h formula (1879),

$$S = kW^{2/3} \quad (1)$$

where  $S$  is surface area in  $\text{dm}^2$ ,  $W$  is body weight in kilograms and  $k$  is a constant for animals of similar body shape. When body weight is determined and surface area measured then  $k$  value can be calculated. Since, however, measurements of the surface areas are inaccurate the  $k$  constants, empirically derived by different authors for particular species, are widely differentiated. This fact has been stressed many times (e.g. Kleiber, 1947, 1961, 1965; P o c z o p k o, 1965, 1967) and additional evidences given in table 1 illustrate this point. The number of  $k$  values given for particular species, varies from 3 to 11. When the surface areas are estimated using the extreme values of these constants the differences between estimates vary from approximately 20 to 50 percent odd (Table 1). Thus it is clear that so vaguely estimated surface areas cannot make a reliable basis for comparison metabolic rates of different animals. Definitely more reliable comparison can be made when the  $2/3$  power of the body weight as approximate measure of the surface area is adapted, as suggested by K r o g h (1916). The »surface rule« would then be expressed by the statement: »The basal metabolic rate of homeotherms is proportional to the  $2/3$  power of their body weight« (Kleiber, 1965). The results obtained in numerous laboratories have shown,

however, that *BMR* of animals expressed per  $2/3$  power of body weight increased systematically with body size (Kleiber, 1932). This finding stimulated Kleiber to look for a function of body weight describing more accurately the relationship between body size and metabolic rate. Plotting the logarithms of *BMR* against logarithms of body weight one obtains linear relation between the two variables. It means that *BMR* must be proportional to a given power of body weight since if

$$\log M = \log a + b \log W, \text{ then } M = a W^b \quad (2)$$

where *M* is the basal metabolic rate, *W* is body weight and *a* and *b* are constants. Kleiber's calculations (1932), based on data concerning 10 groups of mammals, revealed that the best fitting exponent in this

Table 1

A comparison of the surface areas of some mammals, calculated from Meeh's formula using extreme values of *k* constants given in Spector's handbook (1956 p. 175).

Species	Number of <i>k</i> values	<i>k</i> <sub>min.</sub>	<i>k</i> <sub>max.</sub>	Body weight	<i>S</i> at <i>k</i> <sub>min.</sub>	<i>S</i> at <i>k</i> <sub>max.</sub>	Minimal surface as percent of maximal
Mouse	9	6.9	15.9	20 g	51.4 cm <sup>2</sup>	118.3 cm <sup>2</sup>	43.45
Rat	11	7.15	11.6	200 g	248.9 "	403.8 "	61.64
Guinea pig	6	7.1	10.4	250 g	287.0 "	420.4 "	68.27
Cat	3	8.7	10.7	1500 g	1166.0 "	1437.0 "	81.14
Rabbit	4	5.7	10.0	2500 g	1053.0 "	1848.0 "	59.98
Dog	6	9.9	12.3	18 kg	68.6 dm <sup>2</sup>	85.3 dm <sup>2</sup>	80.42
Sheep	5	8.3	11.0	60 kg	129.4 "	170.9 "	75.71
Pig	4	8.8	15.3	80 kg	165.8 "	288.3 "	57.51
Cow	6	7.6	9.9	500 kg	488.8 "	636.7 "	76.77
Horse	3	8.2	10.5	700 kg	660.7 "	845.6 "	78.13

power function is 0.739. In 1947 Kleiber recalculated another set of data, concerning 26 groups of mammals, and found the exponent to be 0.756. In both instances, therefore, these exponents were nearer to the value  $3/4$  than to  $2/3$ . Similar calculations were performed by Brody & Procter (1932). These authors concluded that *BMR* of mammals and birds is proportional to 0.734 power of the body weight. In 1935, at the Conference on Energy Metabolism, held at State College, Pennsylvania, the 0.73rd power of body weight (suggested by Brody) was accepted as the metabolic body size. Practically, however, this acceptance has been quite limited. Many workers calculated anew the relationship between body size and metabolic rates. As early as in 1938 Benedict found that metabolic rate was proportional to 0.75 power of body weight *i.e.* to the fractional power previously suggested by Kleiber. Other workers

found different metabolic body sizes. In most instances they were statistically undistinguishable from each other but still different enough to make comparative studies on metabolism somewhat tedious. Disadvantages resulting from the existence of different metabolic units of body size were discussed in 1964 at 3rd Symposium on Energy Metabolism at Troon, Scotland (see discussion to the paper by Kleiber, 1965) and the proposal has been finally made that weight in kg raised to  $3/4$  power should be used as the reference base in comparing the metabolism of different species of animals. All participants of the Symposium voted in favour of this proposal. In 1966 this unit of metabolic body size was accepted in U.S.A. by National Research Council (see Harris, 1966).

Although this review is concerned with homeotherms it is worth mentioning that the metabolic rate of poikilotherms, at standard conditions, varies more closely with  $3/4$  than with  $2/3$  power of body weight. This has been found by Hemming sen (1960) who evaluated numerous data concerning poikilothermic animals, from unicellular organisms through invertebrates to vertebrates.

In the present paper all the data used were converted, if necessary, to kcal/kg $^{3/4}$  × 24 hr. If BMR's had been originally expressed in terms of oxygen consumption the data were recalculated to heat production using conversion factor of 4.8 kcal per 1 litre of oxygen.

When this paper had been ready for publication the 5th Symposium on Energy Metabolism took place (Vitznau, Switzerland, 13—19 September, 1970). At this Symposium the proposal has been made (Blaxter, 1970) for change from the calories to the Joule, which would be in line with general trend to adopt the International System of Units (SI). The problem of converting calories to Joules is, however, not as simple as it looks at the first sight, because the calorie which is used in bioenergetics has never been rigorously defined. Theoretical equivalent of calorie, defined as the amount of heat necessary to rise the temperature of a gram of water from 14.5 to 15.5° is 4.1868 J. However, all measurements of heat of combustion of foodstuffs, biological materials and pure chemicals have been made in calorimeters calibrated with benzoic acid of known combustion value as given in the certificates of the National Physical Laboratory in the U.K., National Bureau of Standards in the U.S.A., Free University of Amsterdam and some other laboratories. The measurements of the combustion value of benzoic acid in these laboratories are made in electrical units and computed in terms of J/g mole. The conversion to the kcal/mole is made using the factor 4.184 J = 1 cal, which is Joule equivalent of the thermochemical calorie as defined by Rossini. It is thus logical to accept the factor 4.184 when converting

back calories used in bioenergetics to Jules. Accepting the proposal to change from calories to the Joules it was decided to express the metabolic levels both in kcal and in kJ.

### III. METABOLIC LEVELS

Metabolic level has been defined by Kleiber (1961) as daily heat production of an animal divided by the metabolic body size.

In 1932 Kleiber compiled the results concerning the *BMR* of 13 groups of animals, among which 10 groups were mammals, from 200 g rat to 679 kg steer. Average metabolic level of these animals proved to be  $71 \pm 1.8 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$ . In 1947 he compiled again the data concerning 26 groups of mammals, from 21 g mouse to 600 kg cow, and found that the metabolic level averaged  $69 \pm 1.5 \text{ kcal/kg}^{3/4} \times \text{hr}$ . The average metabolic level of all 36 groups of mammals amounted to  $69 \pm 1.2 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$ . Kleiber (1947, 1961) then concluded: »For all practical purposes, one may assume that the mean standard metabolic rate of mammals is seventy times the three-fourth power of their body weight (in kg) per day, or about three times the three-fourth power of their weight (in kg) per hour«. Concerning the birds Kleiber (1947, 1961) writes »This review is limited to mammals, but the conclusions are also applicable to birds, whose metabolic rate was found to be in line with that of mammals«.

It appears at present that Kleiber's opinion, expressed above, represents a too far going generalization of the inductive rule, as at least four different metabolic levels in homeotherms can be distinguished.

#### 1. Data on Metabolic Levels in Some Mammals

Marsupials, even in recent handbooks, are considered as animals representing a level of physiological development intermediate between »lower« monotremes and »higher« eutherians, especially in regard to thermoregulation and to the metabolic rate. This belief is based on questionable results obtained by Martin (1903), who claimed that these animals are poor thermoregulators and their metabolic rate (measured as  $\text{CO}_2$  production) is one third that of eutherians. Recent studies have shown that numerous marsupials can regulate their body temperature as efficiently as eutherians (Robinson, 1954; Bartholomew, 1956; Robinson & Morrison, 1957) although their normal body temperature is, indeed, somewhat lower. Martin's statement concerning the low metabolic rate of marsupials could be, therefore, doubted. Recently Dawson & Hulbert (1969, 1970) have measured

the *BMR* in eight species of marsupials, of average body weight ranging from 14 g (fat tailed marsupial mouse) to 32.5 kg (red kangaroo), in well standardized conditions and using good modern techniques. They found that *BMR* of marsupials varies with 0.74 power of the body weight. This power exponent is practically identical with that accepted in the metabolic body size. The metabolic level of marsupials is, however, about 30 percent lower from Kleiber's interspecific mean (Table 2).

Bats (*Chiroptera*) represent another group of mammals which has been claimed to have low metabolic level (Morrison, 1948). There may be some doubt, however, whether the metabolic rates found in bats can be directly compared with *BMR*'s of other homeotherms, as many of the bats are poor thermoregulators. The studies on the metabolism of the

Table 2

Metabolic rate of some Australian marsupials at standard conditions (means for 6 specimens  $\pm$  S.D., after Dawson & Hulbert, 1970).

Species	Avg. body wt., g	Body temperature, °C	Metabolic rate		
			kcal/hr	Per kg <sup>3/4</sup> × 24 hr	
				kcal	kJ
<i>Sminthopsis crassicaudata</i>	14.1	33.8	0.090 $\pm$ 0.018	52.7 $\pm$ 3.9	220.50
<i>Antechinus stuartii</i>	36.5	34.4	0.174 $\pm$ 0.051	50.1 $\pm$ 5.7	209.62
<i>Petaurus breviceps</i>	128.1	36.4	0.424 $\pm$ 0.053	47.7 $\pm$ 4.8	199.58
<i>Perameles nasuta</i>	686.0	36.1	1.54 $\pm$ 0.31	48.9 $\pm$ 3.2	204.60
<i>Issodon macrourus</i>	880	34.7	1.85 $\pm$ 0.40	49.9 $\pm$ 5.4	208.78
<i>Trichosurus vulpecula</i>	1982	36.2	2.99 $\pm$ 0.29	43.0 $\pm$ 4.2	179.91
<i>Macropus eugenii</i>	4796	36.4	6.64 $\pm$ 0.60	49.1 $\pm$ 2.4	205.43
<i>Megalcia rufa</i>	32490	35.9	26.78 $\pm$ 9.39	47.1 $\pm$ 4.0	197.07
Mean $\pm$ S.D. $\pm$ S.E.				48.6 $\pm$ 2.815 S. E. $\pm$ 1.00	203.34

bats, carried out during last decade (Bartholomew *et al.*, 1964; Leitner, 1966; Leitner & Nelson, 1967; Licht & Leitner, 1967), have shown, that metabolic responses of these animals to ambient temperature are basically the same as of good thermoregulators, but the zones of thermal neutrality for these animals, in general, are narrow. Nevertheless these zones can be distinguished, and when the metabolic rate of the bats is determined at the ambient temperature lying within them the results can be, at least roughly, compared with *BMR* of other mammals. Some data obtained on *Microchiroptera*, under required conditions, are presented in Table 3. The data by Morrison (1948) placed in this table were obtained at the body temperatures approximately 26°C *i.e.* in the state of hypothermia. They were corrected, therefore, to the expected value at body temperature 36°C, on the assumption that  $Q_{10} = 2.4$ . This  $Q_{10}$  value has been found by Kayser (1939). Average

metabolic level of 9 species of *Microchiroptera*, presented in table 3, amounts to  $53.40 \pm 4.69 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$ , so it is indeed relatively low; approximately equal to that in marsupials.

*Megachiroptera* are, probably, better thermoregulators than *Microchiroptera*, and at least some of them can maintain constant body temperature at ambient temperatures ranging from 0 to 35°C (Bartholomew *et al.*, 1964). This condition enables better standardization of measurements of the heat production than in the case of *Microchiroptera*, but reliable data are scarce so far. In table 3 the data concerning

Table 3  
Metabolic rate (comparable to basal) of some bats.

Species	Avg. body wt., g	Body temp., °C	Temp. range of thermo-regulation capacity, °C	kcal/24 hr	Per $\text{kg}^{3/4} \times 24 \text{ hr}$	
					kcal	kJ
<b>MICROCHIROPTERA</b>						
<i>Myotis lucifugus</i> <sup>1</sup>	5	36*	?	0.36	57.60	241.00
<i>Myotis yumanensis</i> <sup>2</sup>	6	35.5	30—40	1.44	80.00	334.72
<i>Eptesicus fuscus</i> <sup>1</sup>	12	36*	?	0.547	37.51	156.94
<i>Tadarida brasiliensis</i> <sup>2</sup>	11	35.5	32—38	1.980	60.00	251.04
<i>Vesperugo noctula</i> <sup>1</sup>	21	36*	?	1.008	43.99	184.05
<i>Antrozous pallidus</i> <sup>2</sup>	22	35.5	32.5—38	2.534	44.45	165.98
<i>Plecotus auritus</i> <sup>1</sup>	24	36*	?	3.041	49.85	208.57
<i>Eumops perotis</i> <sup>3</sup>	56	31.0	0—30	4.580	39.82	166.61
<i>Macroderma gigas</i> <sup>4</sup>	150	35—39	0—35	16.234	67.39	281.96
Mean					53.40	223.43
S.D. ±					14.06	
S.E. ±					4.69	
<b>MEGACHIROPTERA</b>						
<i>Pteropus poliocephalus</i> <sup>5</sup>	598	no data	no data	36.394	55.52	232.30
<i>Pteropus scapulatus</i> <sup>5</sup>	362	no data	no data	27.941	59.45	248.74
<i>Syconycteris australis</i> <sup>5</sup>	17	no data	no data	3.780	82.17	343.80

\* Determinations were made at body temperature 26°C and metabolic rate was corrected to the value expected at 36°C, assuming that  $Q_{10} = 2.4$ . For further explanation see text. References: <sup>1</sup> Morrison, 1948; <sup>2</sup> Licht & Leitner, 1967; <sup>3</sup> Leitner, 1966; <sup>4</sup> Leitner & Nelson, 1967; <sup>5</sup> Bartholomew, Leitner & Nelson, 1964.

BMR in three species of flying foxes are presented. In two of them the metabolic level is not much different from that in *Microchiroptera* but in one of the species amounts to  $82.17 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$ .

*Insectivora* according to Morrison (1948) have very high metabolic level. Data by Morrison, after recalculation, are presented in table 4 together with some items, namely those which were obtained at thermoneutral surroundings, selected from the paper by Gębczyński (1965). The smallest species of *Insectivora* showed really high meta-



bolic level; approximately two to four times that of Kleber's interspecific mean. Larger species (60 g *Scalopus aquaticus*, and 684 g *Erinaceus europeus*) have, however, the metabolic level not much different from the value regarded as interspecific mean. Because of observed in

Table 4  
Metabolic rate of *Insectivora* and *Rodentia* at close to basal conditions.

Species	Avg. body weight, g	kcal	Per kg <sup>3/4</sup> × 24 hr	
			kcal	kJ
<b>INSECTIVORA</b>				
<i>Sorex cinereus</i> <sup>1</sup>	3.5	2.940	294.00	1230.10
<i>Cryptotis parva</i> <sup>2</sup>	5.7	8.208	482.82	2020.12
<i>Crocidura cassiteridum</i> <sup>2</sup>	7.6	5.016	200.64	839.48
<i>Sorex araneus</i> <sup>2</sup>	8.1	4.293	159.00	665.26
<i>Neomys fodiens bicolor</i> <sup>2</sup>	13.1	5.895	159.32	666.59
<i>Blarina brevicauda</i> <sup>1</sup>	21.0	6.401	116.38	486.93
<i>Scolopus aquaticus</i> <sup>1</sup>	60.0	9.072	74.36	311.12
<i>Erinaceus europeus</i> <sup>1</sup>	684.0	59.097	78.58	328.78
<b>RODENTIA</b>				
<i>Peromyscus maniculatus</i> <sup>1</sup>	16	2.880	65.45	273.84
<i>Mus musculus</i> <sup>1</sup>	16	2.995	68.04	284.68
<i>Mus musculus</i> <sup>1</sup>	19	3.420	68.40	286.19
<i>Peromyscus leucopus</i> <sup>1</sup>	22	3.802	66.07	279.07
<i>Clethrionomys sp.</i> <sup>1</sup>	26	4.554	71.15	297.69
<i>Glaucomys volans</i> <sup>1</sup>	70	8.736	65.71	274.93
<i>Cricetus auritus</i> <sup>1</sup>	100	11.760	66.07	276.44
<i>Myoxus glis</i> <sup>1</sup>	195	19.656	66.86	279.74
<i>Citellus citellus</i> <sup>1</sup>	250	24.000	68.00	284.51
White rat <sup>1</sup>	351	30.326	66.50	278.24
White rat <sup>1</sup>	400	33.600	66.67	278.95
Guinea pig <sup>1</sup>	410	35.424	69.05	288.90
Guinea pig <sup>1</sup>	590	38.232	56.82	237.73
Mean			66.58	278.57
S.D. ±			3.33	
S.E. ±			0.92	
<i>Micromys minutus</i> <sup>3</sup>	8	6.156	228.00	953.95
<i>Pitymus subterraneus</i> <sup>3</sup>	13	5.631	152.2	636.80
<i>Apodemus agrarius</i> <sup>3</sup>	21	4.086	74.3	310.87
<i>Apodemus sylvaticus</i> <sup>3</sup>	22	6.589	115.9	484.93
<i>Clethrionomys glareolus</i> <sup>3</sup>	22	8.921	156.5	654.80
<i>Microtus arvalis</i> <sup>3</sup>	23	10.492	177.8	743.91
<i>Microtus agrestis</i> <sup>3</sup>	24	8.488	139.1	581.99
<i>Apodemus flavicollis</i> <sup>3</sup>	30	7.880	109.6	458.57

<sup>1</sup> From Morrison (1948); <sup>2</sup> from Gębczyński (1965); <sup>3</sup> from Grodziński & Górecki (1967).

*Insectivora* the decline of the metabolic level with increasing body size a mean for the group has not been calculated.

Some rodents, commonly used as laboratory animals, are well known in regard to *BMR*, but it can be doubted whether these few species represent well the whole group of rodents, consisting of approximately

one third species of all mammals (A b r i k o s o v *et al.*, 1952). In table 4 two sets of data concerning rodents are presented. The set 1 contains the results obtained and compiled by M o r r i s o n (1948), which agree pretty well with Kleiber's interspecific mean. There is, however, another set of data, compiled by G r o d z i ń s k i & G ó r e c k i (1967), which in original sources are referred to as basal, but considerably higher than results given by M o r r i s o n. The possible reason of this discrepancy will be discussed later in this paper.

## 2. Metabolic Levels in Birds

B r o d y & P r o c t o r (1932) derived following equation relating *BMR* of birds with their body weight:

$$\log M = \log 89 + 0.64 \log W$$

This equation has been widely accepted, although many data used by the mentioned authors were not too reliable. K i n g & F a r n e r (1961) compiled the data concerning *BMR* of 60 species of birds, rigorously rejecting all questionable, and re-evaluated the relationship between body size and metabolic rate. The equation by K i n g & F a r n e r is as follow:

$$\log M = \log 74.3 + 0.744 \log W,$$

thus the average metabolic level, according to this equation, is almost identical with mean K l e i b e r's metabolic level for mammals. K i n g & F a r n e r (*l.c.*) stated, however, that their equation does not adequately describe the metabolic level of birds weighing less than 0.1 kg, which appeared to be higher than that predicted from the above equation. Although the data on small birds were scarce, they suspected the possibility that relation is curvilinear in the lower range of body weights. L a s i e w s k i & D a w s o n (1967) checked this possibility, supplementing the data compiled by K i n g & F a r n e r (*l.c.*), by more recent ones; mostly from their own measurements. On the basis of the gathered results concerning *BMR* of 35 species of passerine birds (from 6.1 g *Estrilda troglodytes* to 886 g *Corvus corax*) and 57 species of nonpasserines (from 3 g *Stellula caliope* to 100 kg *Strutio camelus*), L a s i e w s k i & D a w s o n (*l.c.*) concluded that the slope of the regression lines relating metabolic rate with body size is practically identical in both groups of these birds, but passerine birds operate on higher metabolic level. The regression equations by L a s i e w s k i & D a w s o n (1967) are as follow:

$$\text{Passerines:} \quad \log M = \log 129 + 0.724 \log W \pm 0.113,$$

$$\text{Nonpasserines:} \quad \log M = \log 78.3 + 0.723 \log W \pm 0.068.$$

Data by Lasiewski & Dawson, converted to common metabolic body size are presented in table 5. The readers who would be interested in the original source of these data may find them in the paper by mentioned authors. Average metabolic levels in birds are approximately  $145 \text{ kcal}^{3/4} \times 24 \text{ hr}$  in passerines and *Apodiformes* and about  $80 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$  in nonpasserines.

Lasiewski & Dawson (1967) have included *Apodiformes* to other nonpasserines. In this paper separation of this group has been preferred because its metabolic level appeared to be considerably higher than that of remaining nonpasserines; in fact identical with that of passerines.

Table 5  
Metabolic rate of some birds at standard conditions  
(from Lasiewski & Dawson, 1967).

Species	Avg. body weight	kcal/24 hr	Per $\text{kg}^{3/4} \times 24 \text{ hr}$	
			kcal	kJ
1	2	3	4	5
PASSERINES				
<i>Estrilda troglodytes</i>	6.1 g	2.8	155.56	650.86
<i>Ureaginus bengalis</i>	8.1	2.8	103.70	433.88
<i>Troglodytes aedon</i>	9.0	5.3	182.76	764.67
<i>Vidua paradisaea</i>	10.5	4.0	125.00	523.00
<i>Carduelis flammea</i>	11.2	5.8	175.75	735.34
<i>Taeniopygia castanotis</i>	11.7	5.0	147.06	615.30
<i>Taeniopygia castanotis</i>	11.7	4.5	132.35	553.75
<i>Pipra mentalis</i>	12.0	6.5	185.71	777.01
<i>Carduelis spinus</i>	13.0	5.8	156.75	655.84
<i>Carduelis cannabina</i>	15.5	7.3	169.76	710.28
<i>Spizella arborea</i>	16.6	6.8	151.11	632.24
<i>Junco hyemalis</i>	18.0	6.1	127.08	531.70
<i>Parus major</i>	18.5	8.4	171.43	717.26
<i>Melospiza melodia</i>	18.6	7.8	159.18	666.01
<i>Emberiza hortulana</i>	22.0	8.7	152.63	638.60
<i>Passer montanus</i>	22.0	8.5	149.12	623.92
<i>Zonotrichia albicollis</i>	22.5	7.1	122.41	512.16
<i>Zonotrichia albicollis</i>	23.6	9.5	158.33	662.45
<i>Passer domesticus</i> (Winter)	22.4	9.5	166.67	697.35
<i>Passer domesticus</i> (Spring)	23.5	11.0	183.33	767.05
<i>Passer domesticus</i>	23.7	10.1	168.33	704.30
<i>Passer domesticus</i>	25.0	6.9	111.29	465.64
<i>Passer domesticus</i>	25.5	6.9	109.52	458.23
<i>Passer domesticus</i>	26.0	9.4	146.87	614.50
<i>Passer domesticus</i>	26.0	7.0	109.37	457.60
<i>Passer domesticus</i>	27.3	8.5	128.79	538.86
<i>Chloris chloris</i>	24.5	11.1	182.00	761.49
<i>Chloris chloris</i>	31.1	11.2	151.36	633.29
<i>Fringilla montifrigilla</i>	24.8	9.5	153.22	641.07
<i>Emberiza citrinella</i>	26.4	9.4	146.87	614.50
<i>Zonotrichia leucophrys</i>	28.6	8.0	115.94	485.03
<i>Loxia curvirostra</i>	29.4	10.5	150.00	627.60
<i>Loxia leucoptera</i>	29.8	9.6	135.21	565.72
<i>Passerella iliaca</i>	31.7	11.3	150.66	630.36

	1	2	3	4	5
<i>Molothrus ater</i>		33.7	11.0	139.24	582.58
<i>Richmondia cardinalis</i>		40.0	12.2	135.55	567.14
<i>Plectrophenax nivalis</i>		41.8	11.4	122.58	512.87
<i>Pipilo fuscus</i>		43.7	13.7	142.70	597.06
<i>Pipilo eberti</i>		46.8	15.0	150.00	627.60
<i>Hesperiphona vespertina</i>		58.0	16.7	141.52	592.12
<i>Perisoreus canadensis</i>		64.5	20.0	156.25	653.75
<i>Perisoreus canadensis</i>		71.2	14.3	103.62	433.55
<i>Cyanocitta cristata</i>		80.0	17.6	115.79	484.46
<i>Corvus caurinus</i> (Summer)		282	73.2	189.64	793.45
<i>Corvus caurinus</i> (Winter)		306	96.7	235.28	984.41
<i>Corvus cryptoleucus</i>		640	79.0	110.49	462.29
<i>Corvus corax</i>		850	92.0	104.00	435.14
<i>Corvus corax</i>		866	94.9	105.67	442.12
Mean:				145.6	609.19
S.D. $\pm$				27.63	
S.E. $\pm$				3.99	

## NONPASSERINES

Apodiformes					
<i>Stellula calliope</i>		3.0	1.4	175.00	732.20
<i>Calypte costae</i>		3.2	1.1	137.50	575.30
<i>Archilochus colubris</i>		3.2	1.6	200.00	836.80
<i>Archilochus alexandri</i>		3.3	1.3	144.44	604.34
<i>Selasphorus sasin</i>		3.7	1.6	145.45	608.56
<i>Selasphorus rufus</i>		3.8	1.5	125.00	523.00
<i>Calypte anna</i>		4.8	2.2	157.15	657.52
<i>Eugenes fulgens</i>		6.6	2.4	126.31	528.48
<i>Lampornis clemenciae</i>		7.9	2.6	100.00	418.40
Mean:				145.4	608.35
S.D. $\pm$				29.40	
S.E. $\pm$				9.8	
Caprimulgiformes					
<i>Phalacroptilus nuttalli</i>		0.040 kg	3.7	41.11	172.00
<i>Nyctidromus albicollis</i>		0.0430	7.7	81.05	339.19
<i>Chordeiles minor</i>		0.075	9.5	65.97	276.02
Strigiformes					
<i>Micrathene whitneyi</i>		0.0377	6.7	77.90	325.93
<i>Aegolius acadicus</i>		0.1059	16.2	87.56	366.35
<i>Aegolius acadicus</i>		0.0855	14.5	91.77	383.97
<i>Asio otus</i>		0.252	19.7	55.18	230.87
<i>Asio flammeus</i>		0.406	26.6	52.36	219.07
<i>Strix aluco</i>		0.520	43.	70.27	294.01
<i>Bubo virginianus</i>		1.450	108.	74.48	311.62
Columbiformes					
<i>Scardafella inca</i>		0.0405	5.2	57.78	241.75
<i>Zenaidura macroura</i>		0.0914	13.4	80.72	337.73
<i>Zenaidura macroura</i>		0.123	15.2	73.08	305.77
<i>Columba palumbus</i>		0.150	17.0	70.54	295.14
<i>Streptopelia decaocto</i>		0.152	21.8	89.71	375.35
<i>Streptopelia decaocto</i>		0.155	18.3	73.79	308.74
Domestic pigeon		0.266	37.7	90.83	380.03
Domestic pigeon		0.300	30.	73.89	309.16
Domestic pigeon		0.311	32.9	78.90	330.12
Domestic pigeon		0.372	35.5	74.77	312.84

	1	2	3	4	5
<i>Galliformes</i>					
<i>Excalfactoria chinensis</i>		0.0427	6.0	63.16	264.26
<i>Coturnix coturnix</i>		0.097	23	132.18	553.04
<i>Lophortyx californicus</i>		0.1371	16.0	71.11	297.52
<i>Colinus virginianus</i>		0.194	23.0	78.50	328.44
Domestic fowl		2.0	97.5	58.00	242.67
Domestic fowl ♀		2.0	137	81.45	340.79
Domestic fowl ♀		2.0	115	68.37	286.06
Domestic fowl		2.006	130.7	77.70	325.10
Domestic fowl ♀		2.430	164.2	84.20	352.29
Domestic fowl ♀		2.71	124	58.78	245.93
<i>Penelope purpurescens</i>		2.04	112	66.27	277.27
<i>Grax alberti</i>		2.80	136	62.96	263.42
Domestic turkey		3.7	184	68.91	288.32
<i>Gruiformes</i>					
<i>Grus canadensis</i>		3.89	186	60.87	254.68
<i>Anthropoides paradisea</i>		4.03	220	77.74	325.26
<i>Charadriiformes</i>					
<i>Catharacta skua</i>		0.97	98	100.30	419.65
<i>Gabianus pacificus</i>		1.21	127	110.14	460.83
<i>Larus hyperboreus</i>		1.60	304	213.78	894.45
<i>Falconiformes</i>					
<i>Falco tinnunculus</i>		0.108	17.0	90.00	376.56
<i>Geranoaëtus melanoleucus</i>		2.86	106	48.62	203.43
<i>Aquila chrysaëtos</i>		3.0	102	44.73	187.15
<i>Gypaëtus barbatus</i>		5.07	228	67.65	283.05
<i>Vultur gryphus</i>		10.32	351	62.12	259.91
<i>Anseriformes</i>					
<i>Aix sponsa</i>		0.485	65.	111.87	468.06
<i>Branta bernicla</i> (Summer)		1.130	108.5	99.00	414.22
<i>Branta bernicla</i> (Winter)		1.168	93.4	83.09	347.65
Domestic duck		1.87	157	98.12	410.53
<i>Chauna chavaria</i>		2.62	142	68.93	288.40
Domestic goose		3.3	219	89.38	373.95
Domestic goose		5.0	280	83.58	349.70
Domestic goose		5.89	271	71.88	300.75
<i>Cygnus buccinator</i>		8.88	418	81.00	338.90
<i>Ciconiiformes</i>					
<i>Botaurus lentiginosus</i>		0.60	56	82.11	343.55
<i>Guara alba</i>		0.94	85	89.10	372.79
<i>Ardea herodias</i>		1.87	128	80.00	334.72
<i>Mycteria americana</i>		2.5	201	101.00	422.58
<i>Phoenicopterus antiquorum</i>		3.04	215	93.88	392.79
<i>Jabiru mycteria</i>		5.47	272	76.19	318.78
<i>Leptoptilos javanicus</i>		5.71	307	83.20	348.20
<i>Pelecaniformes</i>					
<i>Pelecanus occidentalis</i>		3.51	264	103.12	431.45
<i>Pelecanus conspicillatus</i>		5.09	374	110.32	461.58
<i>Casuariformes</i>					
<i>Casuarius bennetti</i>		17.6	516	60.28	252.21
<i>Struthioniformes</i>					
<i>Struthio camelus</i>		100	2350	74.37	311.16
Mean:				80.14	335.31
S.D. ±				24.15	
S.E. ±				3.04	

## IV. DISCUSSION

The main purpose of this article was to present the facts. All remarks concerning these facts should be treated as working hypotheses rather than as suggested interpretations.

In all recently calculated equations relating *BMR* of adult animals with their body size the fractional power of the body weight, to which metabolism is proportional, is close to  $3/4$  (e.g. King & Farner, 1961; Lasiewski & Dawson, 1967; Dawson & Hulbert, 1969, 1970). It is possible therefore, to accept, for the sake of uniformity, the  $\text{kg}^{3/4}$  as a single metabolic unit of body size. When available data on *BMR* of homeotherms are expressed per this unit it becomes clear that at least four different metabolic levels exist in these animals. These levels, stated as means with standard errors, are as follow:

1. Marsupials:  $48.6 \pm 1.00 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$ ,
2. Mammals (mouse to steer, according to Kleiber, 1947)  
 $69.0 \pm 1.20 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$ ,
3. Nonpasserines (excluding *Apodiformes*)  
 $80.14 \pm 3.04 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$ ,
4. Passerines:  $145.60 \pm 3.99 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$ .

The differences between the consecutive metabolic levels are highly significant ( $P < 0.0001$ ).

The above, rather unquestionable, data can be supplemented with some of less certain value. Because of poor thermoregulation in bats their metabolic rate may be only roughly compared with *BMR* of good thermoregulators. It seems, however, that the metabolic level of bats conforms with that of marsupials.

Morrison's claim (1948) that *Insectivora*, as a group, have high metabolic level cannot be proved as yet. It is true that the results obtained on *Insectivora*, ranging in body weight from 3.5 to 21 g are very high, but in two larger species tested, they were in line with that of mammals considered by Kleiber (1932, 1947, 1961). In order to answer the question whether the metabolic level of the whole group of *Insectivora* is relatively high, definitely more results on large and intermediate members of this group should be obtained.

Standard deviation of the mean metabolic level of nonpasserines is quite large in spite of as many as 47 degrees of freedom. This may result from not quite well standardized conditions, at which some results have been obtained. There is also another possibility, namely that if the number of species tested could be sufficient, some metabolic levels would be distinguished, or groups of birds »transferred« from the present

position to another. This possibility cannot be excluded because some groups of birds show high metabolic levels. Only three species of *Charadriiformes* were investigated but the metabolic level in all of them amounted to over  $100 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$ . The same concerns two species of *Pelecaniformes*. It is interesting to note that body weights of birds from these groups are quite large; ranging from 0.97 to 5.09 kg.

The existence of the several metabolic levels in mammals and birds seems to be an evidence against explanation of the »surface rule« by the heat transfer theory. It is true that the body temperature of marsupials is a little lower than that of eutherians which in turn is lower than that in birds. It seems, however, that these differences in body temperature are too small to account for such considerable differences in the metabolic levels. Moreover, the average metabolic level of nonpasserines equals only 55 percent of that of passerines, although probably no significant difference in average body temperatures of these two groups of birds can be found.

From the above reasoning one may conclude that the metabolic level, in general, cannot be treated as adjustment to thermoregulation, although in some cases it may be so. It is probable that high metabolic level of very small homeotherms developed in evolution as a result of difficulty in maintaining constant body temperature. Small mammals and birds cannot have, for obvious reason, too thick insulating cover of pelage or feathers. Besides insulating value of clothing depends on the shape of the clothed body. This value, per unit of thickness, is less when fixed on cylinder or sphere than on a plane surface (van Dilla *et al.*, 1949). The radius of the body of shrews or hummingbirds is definitely within the limits where curvature is considerably diminishing insulating value of the body coverings. This requires from the small homeothermic animals to have high metabolic level.

Pearson (1948) found that the line illustrating the relationship between body size and metabolic rate of small mammals is curved at the point of body weight from 8 to 10 g, so that in animals weighing less than 10 grams the metabolic rate is higher than could be expected. Similar curvilinear relationship has been noticed by King & Farnner (1961) in small birds. Lasiewski & Dawson (1967) presented convincing evidences that this was due to the high metabolic level of the whole group of passerine birds to which belong even quite large birds; weighing almost 1 kg. On the other hand these authors supplied unwittingly the data which are in favour of the hypothesis that small homeotherms should have relatively high metabolic level, namely the data concerning *Apodiformes* ranging in body weight from 3 to 7.9 g (Table 5).

Heat production mechanisms (including voluntary muscular activity) of small homeotherms with high metabolic level should be, of course, constantly in action, and this may explain their great agility. Morrison & Pearson (1946) complained that owing to this agility they could not measure the *BMR* of shrew. But when as *BMR* the heat production associated with physiological processes indispensably necessary to sustain life is understood (and I would like to add »without disturbance of homeostasis«) then one may consider that for sustaining the life and homeostasis of very small homeotherms certain amount of muscular activity is absolutely necessary and it would be unnatural to eliminate this activity during measurements of *BMR*.

Certain amount of muscular activity may be also indispensable for sustaining homeostasis even in animals weighing somewhat more than 10 g. This would partly explain the high metabolic levels of rodents

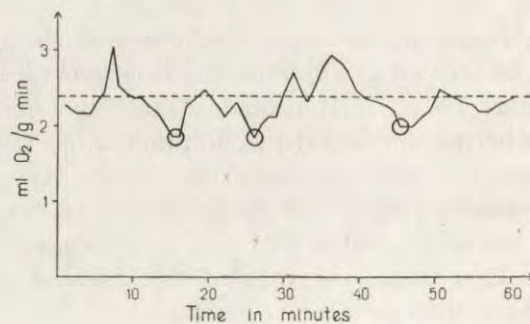


Fig. 1. Diagram of a record of the oxygen consumption by a rodent. Dashed line and circles show the values accepted by different authors as *BMR*.

given in part 2 of the Table 4. The results used for calculating of these levels were obtained in experiments lasting from half an hour to a few hours. The ambient temperatures during measurements were kept within the range of thermal neutrality but the possibility of some movements of the experimental animals was, not fully eliminated. As *BMR* average oxygen consumption for the whole measurement time has been accepted, as illustrated by dashed line in Fig. 1. The values of the metabolic levels presented in part 1 of the Table 4 were calculated from data by the authors who accepted as *BMR* mean from a few pieces of the record of oxygen consumption, namely those at which this consumption was minimal. These low metabolic levels agree well with Kleiber's interspecific mean for mammals, but one can agree with Slonim (1961) that it is only thanks to the employed trick. Some authors prefer, therefore,



to accept as *BMR* the average oxygen consumption from longer measurement than the average from minimal values, and to agree that the metabolic levels of mice and voles are relatively high.

There is about one million of species in animal kingdom. Approximately 700000 of them are vertebrates, and only about 12500 species are homeotherms; 8500 of birds and 4000 of mammals (A b r i k o s o v *et al.*, 1949). There is no need to argue that animals, even within each of the mentioned group, are morfologically widely differentiated. On the basis of these differences they are divided by taxonomists into numerous groups. In fact taxonomists are more eager to find differences than similarities. It seems that physiologists, quite contrary, are eager to find general rules applicable to large groups of animals if not to all animal kingdom. This tendency may remind, to some extent, futile search for philosophers' stone, because it is difficult to understand what could be the reason of existence of general rules, obeyed by animals of different organization and living in different conditions. Such reasons have been looked for, and some »have been found«. One of the »found« reason is the heat loss from the surface. This reason has been supposed to explain proportionality of heat production rate to the surface area of homeothermic animals. But the nature has played a trick with scientists and made the metabolic rate of poikilothermic animals proportional to the same fractional power of the body weight as in homeotherms; although heat transfer theory has no explanatory value in this case. On the other hand one could expect the metabolic level of poikilothermic and homeothermic animals to be different, but could not expect that those levels are differentiated within each of these groups. Average metabolic level of poikilothermic animals (at body temperature 20°C) has been reported to be  $7 \text{ kcal/kg}^{3/4} \times 24 \text{ hr}$  (H e m m i n g s e n, 1961). One may suspect, however, that in almost one million species of poikilotherms many metabolic levels can exist, and indeed K a y s e r & H a u s n e r (1964) have found three different levels in three groups of insects. There is a great jump between the metabolic levels of poikilotherms and homeotherms, but much higher level in homeotherms is not uniform but splitted into several groups. These facts show that animal kingdom is quite differentiated not only morfologically but also in regard to metabolism. The results concerning the metabolic rate of 36 groups of mammals, and actually only 12 species (K l e i b e r, 1932, 1947, 1961) could not reveal this fact as the sample was too small to represent adequately 4000 species of mammals, the more so all 12500 species of homeotherms. Even the data presented in this review, although quite numerous, do not permit to conclude whether four or more metabolic levels exist in homeotherms. The facts presented in this paper show, that any generalization

concerning the diverse nature should be made, and then treated with utmost caution.

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#### REFERENCES

1. Abrikosov G., Becker E., Bobrinski N., Ježikov I., Levinson L., Matveyev B. & Paramonov A., 1952: Zoologia. 2 volumes: 1—680 and 1—671. PWRiL, Warszawa (Polish translation from Russian).
2. Bartholomew G. A., 1956: Temperature regulation in the macropod marsupial, *Setonix brachyurus*. *Physiol Zool.*, 29: 26—40.
3. Bartholomew G. A., Leitner P. & Nelson J. E., 1964: Body temperature, oxygen consumption and heart rate in three species of Australian flying foxes. *Physiol Zool.*, 37: 179—198.
4. Benedict F. G., 1938: Vital energetics: a study in comparative basal metabolism. Carnegie Inst. Wash. Publ. No. 503: 133—164.
5. Bertalanffy L., (von), 1957: Quantitative laws in metabolism and growth. *Quart. Rev. Biol.*, 32: 217—231.
6. Bladergroen W., 1955: Einführung in die Energetik und Kinetik biologischer Vorgänge. Wept & Co.: 1—368, Basle.
7. Blaxter K. L., 1970: Energy units. Proposal for change from the calorie to the Joule. Proc. 5th Symposium on Energy Metabolism. EAAP Publ. No. 13: 14—15 p. Juris Verlag, Zürich.
8. Brody S., 1945: Bioenergetics and growth. Reinhold: 1—1023, New York.
9. Brody S., 1948: Environmental physiology with special references to domestic animals. I. Physiological backgrounds. *Res. Bull. Mo. agric. Exp. Stn.*, 423: 1—43.
10. Brody S. & Procter R. C., 1932: Growth and development with special references to domestic animals. XXIII. Relation between basal metabolism and mature body weight in different species of mammals and birds. *Res. Bull. Mo. agric. Exp. Stn.*, 166: 89—101.
11. Cherednichenko L. K., 1965: Fiziologičeskaja kalorimetrija. Nauka: 1—136, Moskva—Leningrad.
12. Dawson T. J. & Hulbert A. J., 1969: Standard energy metabolism in marsupials. *Nature, Lond.*, 221: 383 only.
13. Dawson T. J. & Hulbert A. J., 1970: Standard metabolism, body temperature, and surface areas in Australian marsupials. *Am. J. Physiol.*, 218: 1233—1238.
14. Dill D. B., 1936: The economy of muscle exercise. *Physiol. Rev.*, 16: 236—291.
15. Dilla M. (van), Day R. & Siple P. A., 1949: Physiology of heat regulation and the science of clothing. Ed. L. H. Newburg. p. 378, Saunders, Philadelphia—London. (Quoted by Hutchinson, 1954).
16. Dukes H. H., 1947: The physiology of domestic animals. Comstock Publ. Co.: 1—817. Ithaca—New York.
17. Gębczyński M., 1965: Seasonal and age changes in the metabolism and activity of *Sorex araneus* Linnaeus 1758. *Acta theriol.*, 10: 303—331.

18. Graham N. McC., 1964: Energy cost of feeding activities and energy expenditure in grazing sheep. *Aust. J. agric. Res.*, 15: 969—973.
19. Grodziński W. & Górecki A., 1967: Daily energy budgets of small rodents. [In: »Secondary productivity of terrestrial eco-systems«. Ed. K. Petruszewicz], Państw. Wyd. Nauk.: 295—314. Warszawa—Kraków.
20. Hall W. C. & Brody S., 1933: The energy increment of standing over lying and the cost of getting up and lying down in growing ruminants (cattle and sheep); comparison of pulse rate, respiration rate, tidal air, and minute volume of pulmonary ventilation during lying and standing. *Res. Bull. Mo. agric. Exp. Stn.*, 180: 1—26.
21. Harris L. E., 1966: Biological energy interrelationships and glossary of the energy terms. National Res. Council. Publ. No. 1411: 1—35, Washington.
22. Hart J. S., 1952: Effect of temperature and work on metabolism, body temperature and insulation: results with mice. *Can. J. Zool.*, 30: 90—98.
23. Hayward J. S., 1965: Metabolic rate and its temperature-adaptative significance in six geographical races of *Peromyscus*. *Can. J. Zool.*, 43: 309—323.
24. Hemmingsen A., 1960: Energy metabolism as related to body size and respiratory surface and its evolution. *Rep. Steno. Hosp. Nord. Insulin lab.*, 9: 1—110.
25. Hutchinson J. C. D., 1954: Heat regulation in birds. [In: »Progress in the physiology of farm animals«, J. Hammond], 1: 299—359. Butterworths Sci. Publ., London.
26. Janský L., 1965: Adaptability of heat production mechanisms in homeotherms. *Acta Univ. Car., Biol.*, 1: 1—91.
27. Kayser C., 1939: Echanges respiratoires des hibernants reveilles. *Ann. Physiol.*, 15: 1087 (Quoted by Morrison, 1948).
28. Kayser C. & Hausner A., 1964: Etude comparative du métabolisme énergétique dans la série animale. *J. Physiol., Paris*, 56: 489—524.
29. King J. R. & Farner D. S., 1961: Energy metabolism, thermoregulation and body temperature. [In: »Biology and comparative physiology of birds«, Ed. A. J. Marshall], 2: 215—288. Academic Press, New York—London.
30. Kleiber M., 1932: Body size and metabolism. *Hilgardia*, 6: 315—353.
31. Kleiber M., 1947: Body size and metabolic rate. *Physiol. Rev.*, 27: 511—541.
32. Kleiber M., 1950: Calorimetric measurements. [In: »Biophysical research methods«, Ed. F. F. Uber], Interscience: 175—209, New York.
33. Kleiber M., 1961: The fire of life. J. Wiley & Sons: 1—454, New York—London.
34. Kleiber M., 1965: Metabolic body size. [In: »Energy metabolism«, Ed. K. Blaxter]: 427—435. Academic Press, London—New York.
35. Krogh A., 1916: The respiratory exchange of animals and man. Longmans Green, London.
36. Lasiewski R. C. & Dawson W. R., 1967: A re-examination of the relation between standard metabolic rate and body weight in birds. *Condor*, 69: 13—23.
37. Leitner P., 1966: Body temperature, oxygen consumption, heart rate and shivering in the California mastiff bat, *Eumops perotis*. *Comp. Biochem. Physiol.*, 19: 431—443.
38. Leitner P. & Nelson J. E., 1967: Body temperature, oxygen consumption and heart rate in the Australian false vampire bat, *Macroderma gigas*. *Comp. Biochem. Physiol.*, 21: 65—74.

39. Licht P. & Leitner P., 1967: Physiological responses to high environmental temperature in three species of microchiropteran bats. *Comp. Biochem. Physiol.*, 22: 371—387.
40. Martin C. J., 1903: Thermal adjustment and respiratory exchange in monotremes and marsupials. A study in the development of homeothermism. *Phil. Trans. Soc. London, B*, 195: 1—37.
41. Meeh K., 1879: Oberflächenmessungen des menschlichen Körpers. *Z. Biol.*, 15: 425—458.
42. Morrison P. R., 1948: Oxygen consumption in several mammals under basal conditions. *J. cell. comp. Physiol.*, 31: 281—291.
43. Morrison P. R. & Pearson O. P., 1946: The metabolism of a very small mammal. *Science*, 104: 287—292.
44. Pearson O. P., 1948: Metabolism of small mammals, with remarks on lower limit of mammalian size. *Science*, 108: 44 only.
45. Poczopko P., 1965: Contribution to the studies on changes of energy metabolism during postnatal development. II. Changes of surface to weight ratio in developing rats. *Acta physiol. pol.*, 16: 752—756.
46. Poczopko P., 1969a: Effect of fasting time on respiratory quotient and metabolic rate in geese of different age. [In: »Energy metabolism of farm animals«. Eds K. Blaxter, J. Kielanowski & G. Thorbek]: 361—367. Oriel Press Ltd., Newcastle upon Tyne.
47. Poczopko P., 1969b: The development of resistance to cooling in baby rabbits. *Acta theriol.*, 14: 449—462.
48. Robinson K. W., 1954: Heat tolerance of Australian monotremes and marsupials. *Aust. J. biol. Sci.*, 7: 348—360.
49. Robinson K. W. & Morrison P. R., 1957: The reaction to hot atmospheres of various species of Australian marsupials and placental animals. *J. cell. comp. Physiol.*, 49: 455—478.
50. Rubner M., 1883: Über den Einfluss der Körpergrösse auf Stoff- und Kraftwechsel. *Z. Biol.*, 19: 535—562.
51. Slonim A. D., 1961: Osnovy obščej ékologičeskoj fiziologii. A. N. SSSR: 1—430. Moskva—Leningrad.
52. Spector W. S., 1956: Handbook of biological data. Saunders Co., Philadelphia—London.
53. Zeuthen E., 1947: Body size and metabolic rate in the animal kingdom with special regard to marine micro-fauna. *C. r. Lab. Carlsberg. Sr. chim.*, 26: 17—161.
53. Zeuthen E., 1953: Oxygen consumption as related to body size in organisms. *Q. Rev. Biol.*, 28: 1—12.

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## POZIOMY METABOLIZMU DOROSŁYCH ZWIERZĄT STAŁOCIEPLNYCH

## Streszczenie

Poziomem metabolizmu określa się dobową produkcję ciepła przez zwierzę znajdujące się w standardowych warunkach (w pełnym spokoju, na czczo, przy neutralnej temperaturze otoczenia) podzieloną przez metaboliczną jednostkę rozmiarów ciała, to znaczy przez ciężar ciała w kilogramach podniesiony do potęgi  $3/4$ . Liczni autorzy podzielają pogląd Kleibera (1947, 1961), że poziom metabolizmu ssaków wynosi średnio  $70 \text{ kcal/kg}^{3/4} \times 24 \text{ h}$ , a średni poziom metabolizmu ptaków jest bardzo bliski tej wartości. Przeliczenie ostatnio publikowanych danych pozwala jednak stwierdzić, że u zwierząt stałocieplnych można wyróżnić co najmniej 4 różne poziomy metabolizmu, mianowicie:  $48,6 \pm 1,00 \text{ kcal/kg}^{3/4} \times 24 \text{ h}$  u *Marsupialia* (8 gatunków, 14,1 g do 32,490 kg,  $n = 8$ );  $69,0 \pm 1,20 \text{ kcal/kg}^{3/4} \times 24 \text{ h}$  u ssaków analizowanych przez Kleibera (12 gatunków, 21 g do 679 kg,  $n = 36$ );  $80,14 \pm 3,04 \text{ kcal/kg}^{3/4} \times 24 \text{ h}$  u ptaków z wykluczeniem *Passeriformes* i *Apodiformes* (57 gatunków z 12 rodzin, 40 g do 100 kg,  $n = 63$ );  $145 \pm 3,99 \text{ kcal/kg}^{3/4} \times 24 \text{ h}$  u *Passeriformes* (35 gatunków, 6,1 g do 866 g,  $n = 48$ ). Różnice między wymienionymi poziomami metabolizmu są wysoce istotne ( $P < 0,0001$ ). Nieco mniej porównywalne dane pozwalają przypuszczać, że poziom metabolizmu nietoperzy jest względnie niski i niewiele różni się od poziomu metabolizmu torbaczy. Z drugiej zaś strony poziom metabolizmu drobnych zwierząt owadożernych jest wysoki, przewyższający nawet poziom metabolizmu u *Passeriformes*. Liczba gatunków zwierząt, których przemiana podstawowa została dokładnie określona jest jeszcze mała w porównaniu z ogólną liczbą zwierząt stałocieplnych. Możliwe więc, że gdy ilość wiarygodnych danych wzrośnie, będzie można wyróżnić jeszcze inne poziomy metabolizmu.