# Metabolic Rate and Body Size Relationships in Adult and Growing Homeotherms

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In adult homeotherms the basal metabolic rate (*BMR*) changes proportionally with approximately 0.75 power of the body weight so it is possible to accept the kg$^{0.75}$ as metabolic unit of the body size. When the data on the *BMR* of adult homeotherms are expressed per this unit one can distinguish several metabolic levels characteristic for different groups of homeotherms. In growing homeotherms the relationship between the *BMR* and body weight even on a log. log. plot is not represented by a straight line. For this reason discussed relationship cannot be characterised by a single regression coefficient. It is concluded, therefore, that the analysis of intraspecific relation between *BMR* and body size with the help of equation $M = aW^b$ should be discarded as not giving clear and easily comparable results. In comparative studies the metabolic rate of growing homeotherms can be expressed per common metabolic unit of the body size *i.e.* kg$^{0.75}$ because this approach enables to compare the metabolic rates, both intra- and interspecifically.

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## I. INTRODUCTION

R u b n e r (1883) formulated the so called surface rule, which states that fasting homeotherm produces daily 1000 kcal of heat per square meter of body surface, on the basis of energy metabolism determinations in dogs of different size. Later on, however, scientists (*e.g.*, V o i t, 1901) were less concerned with intraspecific but primarily with interspecific comparisons of the metabolic rates in adult homeotherms of different size. Since the end of 19th century the relationship between body size and the metabolic rate of adult animals became more clear but the intraspecific relations between these variables still remains obscure. This paper has been written with the hope that it may contribute to clarification of this problem.

## II. INTERSPECIFIC RELATIONS BETWEEN BODY SIZE AND METABOLIC RATE

Since the rate of heat production in the same animal may vary within broad limits a rigorous standarization of conditions under which meas-

urements are carried out is needed, in order to enable valid comparisons of the metabolic rates in different animals. It is usual to compare the so called basal $(BMR)$ or standard $(SMR)$ metabolic rates which are measured when an animal is at complete rest, in the postapsorbtive state and in a thermoneutral environment.

As the reference standard of metabolic rate R u b n e r (1883) and many of his scientific successors used a square meter of the surface area. Because of difficulty in measuring animal surface area, different formulas for its estimation have been developed. Well known, and still used, is the formula proposes by M e e h (1879)

$$S = kW^{2/3} \tag{1}$$

where $S$=surface area in $dm^2$, $W$=body weight in kg and $k$=an empirically established constant for particular groups of animals. But owing to the difficulty in measuring animal surface area, established $k$ values usually are encumbered with considerable error, amounting to as much as 20 to 50 percent (K l e i b e r, 1947, 1961, 1965, P o c z o p k o, 1965, 1971). K r o g h (1916) suggested, therefore, the adoption of a value 10 as an approximation of the empirically derived $k$. However, the analysis of the relation between body size and $BMR$ based on a power equation proved to be more convenient. When the logarithms of body weight are plotted against logarithms of the $BMR$ then the relationship between these variables is represented by a straight line. This means that $BMR$ must be proportional to a given power of the body weight, since if

$$\log M = \log a + b \log W, \text{ then } M = aW^b, \tag{2}$$

where: $M = BMR$, $W$=weight of an animal in kg, whereas $a$ and $b$ are constants.

Table 1

The exponents $b$ in the equation $M = aW^b$, in interspecific relation between $BMR$ and body size.

| Animals | Range of body weights | $b$ | Authors |
|---|---|---|---|
| Mammals+3 sp. birds | 150 g — 679 kg | 0.739 | Kleiber, 1932 |
| Mammals | 21 g — 600 kg | 0.756 | Kleiber, 1947 |
| Mammals | 20 g — 1000 kg | 0.734 | Brody & Procter, 1932 |
| Birds | 10 g — 100 kg | 0.64* | Brody & Procter, 1932 |
| Birds | 0.1 — 10 kg | 0.744 | King & Farner, 1961 |
| Birds, passerine | 6.1 — 866 g | 0.724 | Lasiewski & Dawson, 1967 |
| Birds, nonpasserine | 3 g — 100 kg | 0.723 | Lasiewski & Dawson, 1967 |
| Marsupials | 14 g — 32.5 kg | 0.74 | Dawson & Hulbert, 1970 |
| Different poikilotherms | from microorganisms to 10 kg | 0.75 | Hemmingsen, 1960 |

All $b$ values except that marked  * are statistically indistinguishable from each other.

Table 1 shows that when interspecific comparisons of the metabolic rates are concerned the exponents $b$ are remarkably similar in spite of being calculated by different authors using data obtained on quite different groups of animals. Indeed, the exponents listed in the mentioned table in all but one case are statistically indistinguishable from each other, and now the exponent suggested by K l e i b e r (1947, 1961) i.e. $^3/_4$ or 0.75 is commonly accepted. Thus the weight of an animal in kg raised to 0.75 power makes a good reference standard, usually called the metabolic unit of the body size or simply metabolic body size. When the metabolic rate of different animals are to be compared one can simply divide their daily heat production by the metabolic unit of the body size. The quotient thus obtained is called by K l e i b e r (1961) the metabolic level.

K l e i b e r (1947, 1961) on the basis of results on $BMR$ in 36 groups of mammals (but only 12 species, sic!) obtained at different laboratories
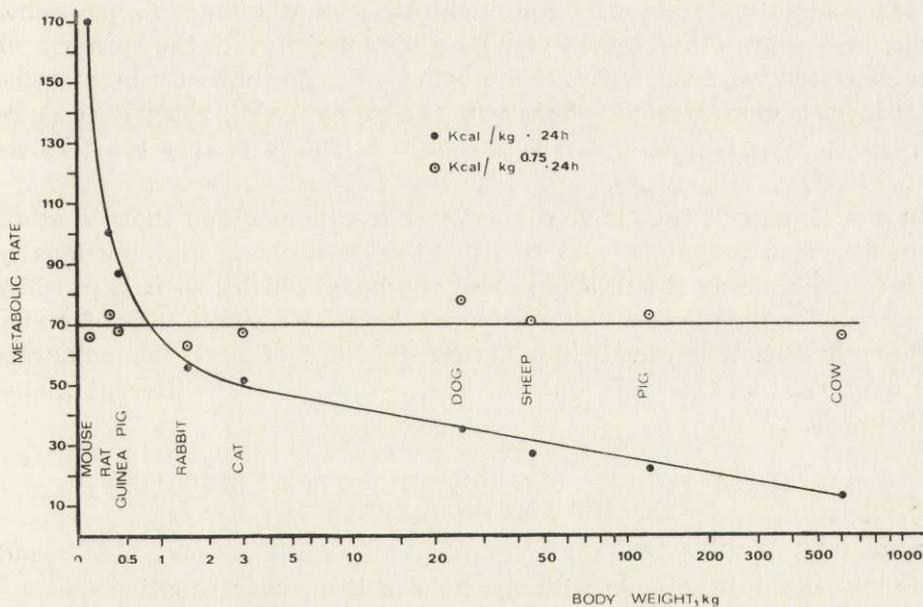


Fig. 1. Relationship between $BMR$ and body size in adult mammals expressed per kilogram of the body weight (curve) and per metabolic unit of the body size ($kg^{0.75}$). Data on $BMR$ from K l e i b e r, 1961.

concluded that the mean metabolic level for mammals is 70 $kcal/kg^{0.75}$ · 24 h. The data on which Kleiber based his conclusion are presented in Fig. 1 in which a curve represents the metabolic rate expressed per kg of the body weight, whereas a straight, horizontal line represents the same rates expressed per $kg^{0.75}$.

Kleiber's interspecific mean represents a convenient base line enabling one to decide whether the metabolic rate of a particular animal, or group of animals, is high or low.

Increasing amounts of data on *BMR* in adult homeotherms led some authors to conclude that some metabolic levels different than that suggested by Kleiber can be distinguished (L a s i e w s k i & D a w s o n. 1967; D a w s o n & H u l b e r t, 1970). P o c z o p k o (1971) after analysing a large body of published evidence concluded that at least four distinctly different metabolic levels exist in adult homeotherms, which expressed per $kg^{0.75}$ and per 24 hours are:

| | | |
|---|---|---|
| 1. | Australian marsupials | 48.6 kcal or 203.3 kJ |
| 2. | Eutherian mammals | 70.0 kcal or 293.0 kJ |
| 3. | Nonpasserine birds (excluding *Trochilidae*) | 80.1 kcal or 335.0 kJ |
| 4. | Passerine birds | 145.6 kcal or 619.2 kJ |

He suspected also that the metabolic level of bats conforms with that of Marsupials and that of hummingbirds with the level in passerine birds, and some other levels could be distinguished if the number of species tested were sufficient. Some evidence suggests that a high metabolic level is characteristic of shrews (G ę b c z y ń s k i, 1965; P o c z o p- k o, 1971; V o g e l, 1976), whereas that of *Edentata* is very low (D a w- s o n, 1973).

In a summary of the above discussion one can conclude that: in adult homeotherms (as well as poikilotherms) the *BMR* changes proportionally with approximately the 0.75 power of the body weight, so it is possible to accept, for the sake of uniformity, the $kg^{0.75}$ as a single unit of metabolic body size. When available data on the *BMR* of adult homeotherms are expressed as this unit, one can distinguish several different metabolic levels.

### III. INTRASPECIFIC RELATIONSHIP BETWEEN BODY SIZE AND METABOLIC RATE

A fruitful method of analysing the relationship between *BMR* and body size in adult animals with the help of the power equation encouraged many authors to analyse in a similar fashion the intraspecific relationship between these variables. However, the results obtained were definitely less satisfactory. Table 2 shows that the values of exponent *b* in equation (2) calculated by different authors vary considerably even for the same species. This is particularly evident in case of cattle and rat. So the exponent *b*, which in case of interspecific comparison can really by accepted as constant in the case of intraspecific analysis cannot be treated as such. Moreover, H a r t (1971) as well as B l a x- t e r (1972) stated that the *b* values compiled by them concerned adult

(but still growing, sic!) animals. Also the average weights of animals given in the table by T h o n n e y *et al.* (1976) suggest that the same concerns their data on *b* values. The question is, therefore, to what extent can we use the exponents compiled in Table 2 *i.e.* over what

Table 2

The exponent *b* in intraspecific power equation $M = aW^b$.

| Species | Range of body weights | No. of values | Range of values | Reference |
|---------|----------------------|---------------|-----------------|-----------|
| Mouse | 5— 40 g | 1 | 0.92 | 1 |
| Mouse | mature | 1 | 0.75 | 2 |
| *Clethrionomys glareolus* | 15— 30 | 5 | 0.64—0.75 | 1 |
| *Peromyscus m. nebrascensis* | 15— 23 | 1 | 0.43 | 1 |
| *P. m. austerus* | 14— 23 | 1 | 0.54 | 1 |
| *P. m. sonoriensis* | 17— 25 | 1 | 0.25 | 1 |
| *P. m. artemisiae* | 18— 30 | 1 | 0.94 | 1 |
| *P. m. areas* | 22— 37 | 1 | 0.76 | 1 |
| *P. sitkensis* | 22— 35 | 1 | 0.68 | 1 |
| *Microtus pennsylvanicus* | 15— 40 | 2 | 0.52, 0.64 | 1 |
| *Spermophilus tridecemlineatus* | 137—373 | 5 | 0.20—0.41 | 1 |
| Rat | mature | 1 | 0.82 | 2 |
| Rat | 180—430 | 4 | 0.63—1.02 | 3 |
| Rat | 95—400 | 5 | 0.62—0.94 | 1 |
| Guinea pig | mature | 1 | 0.80 | 2 |
| Rabbit | mature | 1 | 0.79 | 2 |
| Rabbit | 2.67—3.41 kg | 2 | 0.82, 0.85 | 3 |
| Chicken | 2.15—2.85 | 2 | 0.63, 1.02 | 3 |
| Cat | mature | 1 | 0.90 | 2 |
| Dog | 12— 15 | 4 | 0.52—0.80 | 3 |
| Sheep | mature | 1 | 0.88 | 2 |
| Sheep | 32— 46 | 3 | 0.61—0.71 | 3 |
| Goat | mature | 1 | 0.95 | 2 |
| Man | mature | 1 | 0.76 | 2 |
| Man | 53— 64 | 4 | 0.33—0.42 | 3 |
| Cattle | 279—575 | 10 | 0.33—4.96 | 3 |
| Horse | mature | 1 | 0.94 | 2 |

1 — H a r t,  1971; 2 — B l a x t e r,  1972; 3 — T h o n n e y  *et al.*, 1976.

range of changes in body weight and the metabolic rate do these exponents really show the degree of proportionality.

The search of literature for data revealed that only a few authors have studied the *BMR* alterations during the life span of animals, and most only during a particular period of development. The existing data, although scarce, show that the intraspecific relation between body size and *BMR* even on a log. log. plot is not represented by a straight line, as was pointed out by B r o d y (1945). This is well illustrated by Fig. 2 redrawn from the paper by P i e k a r z e w s k a (1977). This illustration shows that the relation between the changes in *BMR* of rabbits and the changes of their body weight from about 70 g to 2 kg is represented on a log. log. plot by a curve which the author divided into two

straight sections. The slope of the first section is represented by the exponent $b=1.532$ whereas of the second one by $b=0.712$, for addition, there are some data on metabolic rates in rabbits weighing from 2 to 5 kg, which are situated below the line of the second section. Analysing Fig. 2 one can easily imagine that if the author was studying the changes of *BMR* in rabbits accompanying the changes of body weight from approximately 100 to 300 g, then she would certainly feel justified to draw the line with a slope represented by $b \approx 1$. Similarly it would be possible to draw the line over the range of body weights
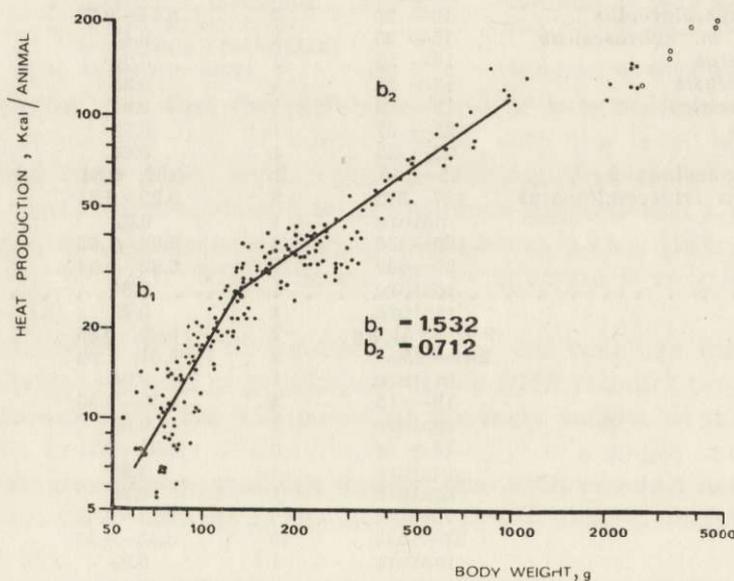


Fig. 2. Relationship between body size and the metabolic rate (expressed on a log. log. plot) in rabbits from birth to maturity. From P i e k a r z e w s k a, 1977.

from 500 g to 5 kg and to calculate the $b$ value which would be approximately 0.6. This explains why so many values of $b$ are reported even for the same animal species (see Table 2) and shows that these values in reality are useless.

A curvilinear relationship between the logarithms of body weight and logarithms of the metabolic rate in the chicken has been described by F r e e m a n (1964). The author studied changes in the metabolic rates of 4 breeds of chicken during the first 2 weeks of their post-embryonic life (from approximately 30 to 100 g. body weight). In each breed he distinguished 2 phases of metabolism. In the first phase the

regression coefficients (*i.e.* exponents *b*) were from 1.663 to 2.091 and
in the second phase 0.761 to 1.038. If Freeman had studied further chan-
ges in the metabolic rate in the chicken he would certainly have
found the third phases. Two phases of the metabolism were also repor-
ted by F r e e m a n (1967) for Japanese quail with regression coeffi-
cients 2.473 and 0.785. Three metabolic phases has been described in
developing Norwegian lemmings and golden hamsters (H i s s a, 1968).
It seems therefore, that multiphasic changes of the metabolic rate in
developing animals is a common phenomenon. The only exception found
so far is the guinea pig in which the metabolic rate changes throughout
postanatal development proportionally to 0.843 power of the body weight
(P i e k a r z e w s k a, 1977).

When the metabolic rate of developing homeotherms are expressed
per metabolic unit of the body weight *i.e.* $kg^{0.75}$ it appears that the level
of metabolism in new born specimens is approximately the same as in
adult ones then increases to reach at a certain stage of development
approximately double that level, and then gradually decreases. This is
shown in Table 3 consisting of the data on the metabolic rates in
6 species of mammals and 3 species of birds. Similar alterations of the
metabolic rates may be seen after recalculation of available data for
growing horses (B r o d y *et al.*, 1943), ducks (K o t r b á č e k, 1973),
and chicken (J a s t r z ę b s k i *et al.*, 1977).

The rate of increase of the metabolic level seems to depend on the
degree of maturity of an animal at its birth. This is illustrated by the
Fig. 3 in which the metabolic rates of rats and chicken are plotted
against their relative growth *i.e.* multiple of the average body weight
at birth or hatch. It is evident that the higest metabolic level in the
precocial chicken is at the time when its body weight is approximately
5 times that at hatch whereas in the »altricial« rat, only after a 15 fold
increase of its body weight at birth.

## IV. DISCUSSION AND CONCLUSIONS

The evidence in this paper shows that the relationship between the
changes of *BMR* and body weight in ontogeny of homeotherms even
on a log. log. plot is not represented by a straight line. For this reason
the calculations of power equations, usually based on data concerning
only a part of the animal's life span lead to quite different values of
the exponent *b*. Most of the published exponents are therefore ill-de-
fined and as such useless for prediction of the metabolic rates in animals
at particular stages of their development. One can conclude therefore,

that the analysis of intraspecific relations between *BMR* and body weight with the help of the known power equation (see eq. 2) should be discarded as not giving clear and easily comparable results.

Table 3

Alterations of the body weight and *BMR* during postnatal development of animals.

| Age | Av. body weight | $BMR/kg^{0.75} \times 24\ h$ | | Age | Av. body weight | $BMR/kg^{0.75} \times 24\ h$ | |
| --- | --- | --- | --- | --- | --- | --- | --- |
| | | kJ | kcal | | | kJ | kcal |
| | PIG | | | | COW | | |
| 1 d | 1.3 kg | 271.9 | 65 [1] | At birth | 25 kg | 485.3 | 116 |
| 4— 6 d | 1.6 | 514.6 | 123 [1] | not given | 50 | 527.2 | 126 |
| 14 d | 4.7 | 489.5 | 117 [2] | „ | 75 | 543.9 | 130 |
| 2 m | 8 | 343.1 | 82 [3] | „ | 125 | 497.9 | 119 |
| 4 | 23 | 343.1 | 82 | „ | 150 | 481.2 | 115 |
| 6 | 55 | 338.9 | 81 | „ | 175 | 468.6 | 112 |
| 8 | 94 | 293.0 | 70 | | 200 | 456.1 | 109 |
| 10 | 126 | 288.7 | 69 | | 250 | 435.1 | 104 |
| 12 | 152 | 267.7 | 64 | | 300 | 418.4 | 100 |
| 14 | 173 | 251.0 | 60 | | 350 | 410.0 | 98 |
| 18 | 213 | 234.3 | 56 | | 400 | 397.5 | 95 |
| | | | | | 600 | 263.6 | 63 |
| | SHEEP | | | | RABBIT | | |
| 1 w | 4.5 kg | 404.5 | 97 | <1 d | 71 g | 271.9 | 65 |
| 3 | 8.0 | 588.9 | 141 | 2 | 77 | 192.5 | 46 |
| 5 | 10.0 | 498.2 | 119 | 4—5 | 85 | 305.4 | 73 |
| 9 | 12.5 | 424.2 | 101 | 8 | 114 | 401.7 | 96 |
| 18 | 21.5 | 345.0 | 82 | 10 | 133 | 447.7 | 107 |
| 27 | 30.0 | 285.2 | 68 | 14 | 180 | 535.6 | 128 |
| 39 | 38.0 | 294.1 | 70 | 18 | 227 | 506.3 | 121 |
| 57 | 52.0 | 282.1 | 67 | 28 | 394 | 464.4 | 111 |
| 66 | 52.5 | 276.9 | 66 | 42 | 579 | 464.4 | 111 |
| 74 | 59.0 | 253.5 | 61 | 49—56 | 911 | 527.2 | 126 |
| 84 | 62.0 | 248.9 | 59 | 70 | 2450 | 276.1 | 66 |
| 93 | 68.5 | 228.9 | 55 | Adult | 3615 | 276.1 | 66 |
| 105 | 73.0 | 242.0 | 58 | | | | |
| | GUINEA PIG | | | | RAT | | |
| <1 d | 72 g | 305.4 | 73 | 0— 2 | 6.5 g | 355.6 | 85 |
| 1 | 75 | 326.3 | 78 | 12 | 14.0 | 414.2 | 99 |
| 2 | 73 | 338.9 | 81 | 14— 16 | 27.0 | 334.7 | 80 |
| 3 | 77 | 343.0 | 82 | 20 | 34 | 364.0 | 87 |
| 4— 5 | 82 | 359.8 | 86 | 21 | 45 | 368.2 | 88 |
| 6— 7 | 96 | 355.6 | 85 | 27— 29 | 52 | 451.9 | 108 |
| 9—10 | 116 | 364.0 | 87 | 30— 34 | 66 | 456.1 | 109 |
| 14 | 142 | 372.4 | 89 | 35— 36 | 76 | 464.4 | 111 |
| 17 | 162 | 384.9 | 92 | 37— 40 | 97 | 476.9 | 114 |
| 21 | 174 | 338.9 | 81 | 40— 44 | 105 | 485.3 | 116 |
| 56 | 464 | 343.0 | 82 | 50— 53 | 150 | 414.2 | 99 |
| 90 | 633 | 347.3 | 83 | 75— 79 | 179 | 401.7 | 96 |
| Adult | 690 | 334.7 | 80 | 81— 84 | 183 | 364.0 | 87 |
| | | | | 90— 94 | 208 | 355.6 | 85 |
| | | | | 100—116 | 230 | 330.5 | 79 |
| | | | | 140—159 | 243 | 322.2 | 77 |
| | | | | 202—227 | 273 | 313.8 | 75 |
| | | | | 267—280 | 281 | 305.4 | 73 |
| | | | | 282—289 | 289 | 305.4 | 73 |

CHICKEN

| | | | |
|---|---|---|---|
| <7 d | 43 | 389.1 | 93 |
| 7— 14 | 54 | 485.3 | 116 |
| 14— 21 | 91 | 514.6 | 123 |
| 21— 28 | 152 | 577.4 | 138 |
| 28— 35 | 216 | 577.4 | 138 |
| 35— 42 | 299 | 472.8 | 113 |
| 42— 49 | 355 | 405.8 | 97 |
| 49— 60 | 392 | 393.3 | 94 |
| 60— 90 | 631 | 351.4 | 84 |
| 90— 120 | 1048 | 334.7 | 80 |
| 120— 150 | 1479 | 351.4 | 84 |
| 150— 180 | 1319 | 372.4 | 89 |
| 180— 210 | 1679 | 355.6 | 85 |
| 210— 240 | 1820 | 284.5 | 68 |
| 240— 270 | 1864 | 292.9 | 70 |
| 270— 300 | 1944 | 334.7 | 80 |
| 300— 330 | 1818 | 263.6 | 63 |
| 330— 360 | 1835 | 376.6 | 90 |
| 1360—1390 | 2084 | 271.9 | 65 |

GOOSE

| | | | |
|---|---|---|---|
| 2— 4 d | 120 g | 242.7 | 58 |
| 6— 10 | 480 | 376.6 | 90 |
| 11— 15 | 670 | 589.9 | 141 |
| 27— 29 | 2140 | 548.1 | 131 |
| 41— 43 | 4000 | 506.3 | 121 |
| 75— 89 | 4600 | 376.6 | 90 |
| 92—100 | 5200 | 364.0 | 87 |

JAPANESE QUAIL

| | | | |
|---|---|---|---|
| 1 d | 6.5 g | 326.3 | 78 |
| 7 | 20 | 686.2 | 164 |
| 14 | 48 | 782.4 | 187 |
| 21 | 76 | 790.8 | 189 |
| 28 | 104 | 744.7 | 178 |
| 35 | 130 | 711.3 | 170 |
| 42 | 160 | 707.1 | 169 |

Explanations: Age of animals, d — days, w — weeks, m — months. Sources of data: pig [1]Mount & Stephens, 1970; [2]Mount & Rowell, 1960; [3]Brody 1945; Cow — Brody, 1945; Sheep — Graham et al., 1974; Guinea pig and rabbit — Piekarzewska, 1977; Rat — Kleiber et al., 1956; Chicken — Brody, 1945; — Goose — Poczopko, 1969; Japanese quail — Freeman, 1967.
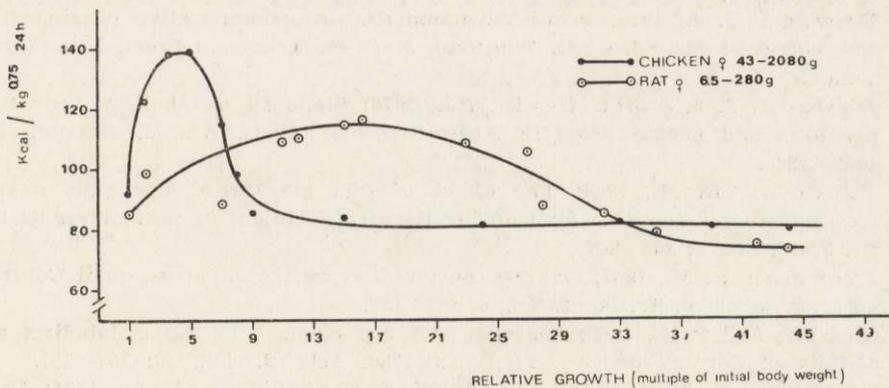


Fig. 3. Relationship between *BMR* (expressed per $kg^{0.75}$) and relative growth (multiple of mean initial body wieght) in growing rats and chicken. Data on *BMR* in rats from Kleiber et al., 1956 and that in chicken from Brody, 1945.

For comparative studies and for practical purposes the metabolic rates of growing animals can be expressed per common metabolic unit of body size *i.e.* $kg^{0.75}$, just as has been done in Table 3 and Fig. 3. Such a presentation of the data demonstrate that at certain stage of development of animals their metabolic rate is twice as high as in the adult and new born specimens. Similarly we can tell that the metabolic rate of the new born pig is low whereas that of new born calf is high.

Clinical and animal husbandry men prefered long ago to use tables

of energy metabolism of growing man and animals, in order to assess thyroid activity or nutrient requirements, rather than base these assessments on predicted values. It appears that this approach should be used also in comparative physiology.

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## ZALEŻNOŚĆ MIĘDZY TEMPEM METABOLIZMU A ROZMIARAMI CIAŁA DOROSŁYCH I ROSNĄCYCH ZWIERZĄT STAŁOCIEPLNYCH

### Streszczenie

Zależność między tempem przemiany podstawowej ($BMR$) a rozmiarami ciała dorosłych zwierząt stałocieplnych na układzie współrzędnych o skali podwójnie logarytmicznej ilustruje linia prosta. Zależność tę można zatem opisać równaniem $M=aW^b$, gdzie $M=BMR$, $W=$ciężar ciała w kg, a $a$ i $b$ są stałymi. Wykładnik potęgowy $b$ obliczony przez wielu autorów dla licznych grup dorosłych zwierząt nie różnił się istotnie od wartości 0.75, zatem ciężar ciała w kilogramach podniesiony do tej potęgi ($kg^{0.75}$) można przyjąć za ogólną metaboliczną jednostkę rozmiarów ciała dorosłych zwierząt. Gdy dostępne w literaturze dane o $BMR$ przeliczy się na tę jednostkę da się wyróżnić szereg poziomów metabolizmu charakterystycznych dla różnych grup zwierząt. U rosnących zwierząt stałocieplnych zależność między $BMR$ a ciężarem ciała nawet na układzie współrzędnych o skali podwójnie logarytmicznej nie jest reprezentowana przez linię prostą. Zatem zależności tej nie można charakteryzować jednym tylko współczynnikiem regresji. Wnioskuje się więc, aby w analizie wewnątrzgatunkowej zależności między $BMR$ i ciężarem ciała zaniechać posługiwania się równaniem $M=aW^b$, ponieważ nie prowadzi ono do łatwo porównywalnych wyników. W badaniach porównawczych można wyrażać tempo metabolizmu rosnących zwierząt w przeliczeniu na ogólną metaboliczną jednostkę rozmiarów ciała, tj. $kg^{0.75}$. Takie podejście umożliwia bowiem porównywanie tempa metabolizmu zarówno zwierząt należących do różnych gatunków, jak i różniących się ciężarem ciała osobników tego samego gatunku.