TOPIC 2. MEASUREMENTS OF ENERGY METABOLISM

Measurements of the metabolic rates of several species of wild ruminants have been made with a variety of methods at different times of the year. The results show variations in relation to several parameters of ecological importance. The time of the year is an important consideration for evaluating seasonal rhythms, and the day, week, or at least the month of the year in which the tests were conducted should always be given in the results. If the time of year cannot be determined, the results are relatively worthless.

Weights of the animals should also be given, of course. Metabolic expenditures can then be determined per unit weight, or per unit metabolic weight. Sex, age, and reproductive characteristics are also important characteristics for interpreting the results of metabolism tests.

The topics and units that follow give the results of metabolism tests and calculations for a variety of wild ruminants. Short-term chamber measurements are included, though it is difficult to derive equations for ecological metabolism over the entire annual cycle from such studies. Calculations by summation, estimations from vital signs and in relation to base-line metabolism provide estimates throughout the year.

UNIT 2.1: CHAMBER MEASUREMENTS

Direct measurements of metabolism involve the measurement of the heat production of the animal after the manner of Lavoisier in the latter part of the eighteenth century. His early methods have been replaced by very refined calorimetry chambers, however. Professor Armsby built one early in the 20th century at the Pennsylvania State University; it is still in existence but not currently being used. The basic principle is the same as the crude ice-box calorimeter, but circulating water removes heat from the chamber and calculations are based on the flow rate, temperature changes, and other thermal parameters of the water. Direct calorimetry chambers are not used extensively now because of the high cost of construction and the availability of simpler and less expensive oxygen consumption methods.

The calculation of heat production from oxygen consumption is based on the relationship between the volumes of oxygen consumed and heat production. The relationship is illustrated by equation (1) from Brody (1945).

This equation shows that the oxidation of one mol of hexose ($C_6H_{12}O_6$) requires 6 mols of O_2, with the resulting production of six mols of CO_2, 6 mols of H_2O, and 678 calories of heat energy.

$$C_6H_{12}O_6 + 6\ O_2 = 6\ CO_2 + 6\ H_2O + 678\ \text{Cal} \qquad (1)$$

(180 g.) (134.4 lit.) (134.4 lit.)

The heat production (678 calories) divided by the consumption of 134.4 liters of oxygen or the production of 134.4 liters CO_2 yields 5.047 calories (5.047 = 678/134.4). Thus 5.047 calories of heat are produced for each liter of O_2 consumed and each liter of CO_2 produced in carbohydrate oxidation. The oxidation of mixed fat results in the release of 4.69 calories per liter oxygen consumed, and 6.6 calories per liter carbon dioxide produced. For the oxidation of mixed protein, 4.82 calories are released per liter O_2 consumed, and 5.88 calories per liter CO_2 produced. The figures above indicate that the numbers of calories produced by oxidation varies with the carbohydrate, fat, and protein content of the food, so the proportion of carbohydrate, fat, and protein in the food should be known before calculating the heat production from either oxygen consumption or carbon dioxide production.

The amount of protein oxidized is determined from the urinary nitrogen excreted. This assumes that there is a constant quantity of nitrogen in the protein. If 16% of the protein is nitrogen, the protein catabolized is estimated by multiplying the urinary N by the ratio of total protein to nitrogen in the protein (100/16 = 6.25) (Equation 2)

$$\text{Urinary N} \times 6.25 = \text{protein catabolized} \qquad (2)$$

The example above is true for several animal proteins. Cereal proteins contain 17-18% N, so the conversion factor is 5.8 to 5.9. In practice, the assumption that protein contains 16% nitrogen is sufficient. The relative amounts of fat and carbohydrate oxidized are determined from the non-protein respiratory coefficient (R.Q.). The R.Q. is the ratio of mols or volumes of CO_2 produced to mols or volumes of O_2 consumed. Thus in equation (1), the R.Q. is equal to 1.0 because $6\ CO_2/6\ O_2 = 1.00$; only carbohydrates had been consumed.

The R.Q. for mixed fats is 0.71, and for mixed protein, 0.81. These are averages only, as fatty acids vary in their R.Q. (short-chain fatty acids have an R.Q. nearer 0.8) and each protein and amino acid has its distinctive R.Q. The relative amount of heat produced by the oxidation of carbohydrates and fats can be computed from the R.Q., and these are presented in tabular form in Brody (1945:308-310), the source of information for the material discussed in the previous paragraphs.

The respiratory quotient does not always have the simplicity of interpretation implied in the foregoing discussions. In ruminants, large quantities of CO_2 are produced by the rumen bacteria, and this cannot be distinguished from the CO_2 resulting from internal respiration. The measurement of oxygen consumption and its multiplication by the caloric equivalent of oxygen is a satisfactory method for estimating heat production by the ruminant. Note in Table 1 that the calories per liter of oxygen cosumed ranged from 4.686 to 5.047. The mean value is about 4.86, and this occurs at an R.Q. of 0.85. The R.Q. of protein is about 0.82, so if one is satisfied with an approximation of mean values, the rate of heat production can be calculated by multiplying the liters of oxygen consumed by 4.82 to 4.85 without correcting for protein metabolism. This method is often used by comparative physiologists (Hoar 1966).

BASAL METABOLISM

The tabular format shown below includes columns for the information necessary for interpreting published results of basal metabolism tests. The first three items identify the conditions for a basal test. Completion of the blanks results in KCAL and KJOU being expressed on an absolute basis, and MBLM provides for comparisons of the results on a relative basis.

FORMAT FOR COMPARING BASAL METABOLISM TESTS

				Time of	Weight in		24-hour basal metabolism		
Reference	Species	Sex	Age	Year	Kg	IFMW	KCAL	KJOU	MBLM
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-

Basal metabolism tests on white-tailed deer showed seasonal variations, with the lowest metabolism occurring when the deer were in winter coat and the highest when they were in summer coat (Silver 1968). Seasonal variations in basal metabolism may be expressed with a sine wave in the same manner that seasonal variations in weight were, showing seasonal metabolic rhythms as an animal goes from a winter low to a summer high in a gradual way. There is no general formula available yet for the expression of seasonal rhythms in metabolism. Results of curve fitting the data for white-tailed deer are given in the WORKSHEETS.

FASTING METABOLISM

Fasting metabolism measurements are expected to show seasonal variations, just as basal metabolism tests did. The differences between the two tests is that basal tests are for animals at rest, and fasting tests are uncorrected for activity. Both tests are conducted on post-absorptive animals in thermoneutral conditions.

A tabular format for comparing the results of fasting metabolism tests is shown on the next page.

FORMAT FOR COMPARING RESULTS OF FASTING METABOLISM TESTS

Reference	Species	Sex	Age	Time of Year	Weight in Kg	IFMW	24-hour fasting metabolism KCAL	KJOU	MBLM
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-
-	-	-	-	-	-	-	-	-	-

LITERATURE CITED

Brody, S. 1945. Bioenergetics and growth. Reinhold Publ. Co., New York. 1023 pp.

Hoar, W. S. 1966. General and comparative physiology. Prentice-Hall, Inc., Englewood Cliffs, New Jersey. 815 pp.

REFERENCES, UNIT 2.1

CHAMBER MEASUREMENTS

SERIALS

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS------------------	AUTHORS----------	YEAR
CJZOA	53--6	679	685	odvi	ambien temp effect, physio	holter,jb; urban/	1975
JPHYA	194-1	22	24	odvi	energy metabolism, red dee	brockway,jm; mal/	1968
JWMAA	23--4	434	438	odvi	basal metab, a pilot study	silver,h; colovo/	1959
JWMAA	33--1	204	208	odvi	cage, metab, radioiso stud	cowan,rl hartso/	1969
JWMAA	33--3	490	498	odvi	fasting metabolism	silver,h; colovo/	1969
JWMAA	35--1	37	46	odvi	effect falli temp, heat pr	silver,h; holter/	1971

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS------------------	AUTHORS----------	YEAR
				odhe			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
JPHYA	194-1	22	24	ceel	energy metabolism, red dee	brockway,jm; malo	1968

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				alal			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
CJZOA	39--7	845	856	rata	clima, metab, therm, infan	hart,js; heroux,/	1961
CJZOA	48--2	391	392	rata	energy metab, barren groun	mcewan.eh	1970

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
JWMAA	34--4	908	912	anam	energ flux, water kinetics	welsey,de; knox,/	1970
JWMAA	37--4	563	573	anam	energy metabolism, prongho	wesley,de; knox,/	1973

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				bibi			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				ovca			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				ovda			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				obmo			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
AJPHA	178-3	515	516	oram	metabolism of mountai goat	krog,h; monson,m	1954

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
AJAEA	13--1	144	164	dosh	energy meta, new-born lamb	alexander,g	1962
AJAEA	18--1	127	136	dosh	fastng metab rate reln wt,	graham,nm	1967
BJNUA	16--4	615	626	dosh	fast metab, adul wether sh	blaxter,kl	1962

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
ATRLA	22--1	3	24	caca	energy metabolism, roe dee	weiner,j	1977

OTHER PUBLICATIONS

Davydov, A. F. On the processes of muscular activity in reindeer during procurement of feeds from under the snow. Russian original from Sbornik "opyt izucheniya regulyatsii fiziologicheskikh funkstii v estestvennykh uslovyakh sushchestvovania organizmov," Vol. 6:35-40. 1963. Translation available from U.S. Dept. Commerce, Clearinghouse for Federal Scientific and Technical Information, Springfield, Va.

CHAPTER 7, WORKSHEET 2.1a

Basal metabolism of white-tailed deer

Measured basal metabolic rates of white-tailed deer show differences between winter and summer coat. These are summarized in Moen (1973:117) based on data in Silver (1968). The average multiple of base-line metabolism for the winter coat is 75.6 and for the summer coat, 84.4.

How can these limited data be used to represent a seasonal rhythm in basal metabolism of deer? Suppose the summer peak was reached on August 15, which is JDAY 227, and the winter low six months later, which is JDAY 45. The sine wave is again employed to determine a smooth transition from maximum to minimum, and a phase correction is needed to make JDAY 227 equivalent to 90° when sin 90 = +1.

The primary phase correction is 90 - (227)(0.9863) = -134 = PRPC. Therefore:

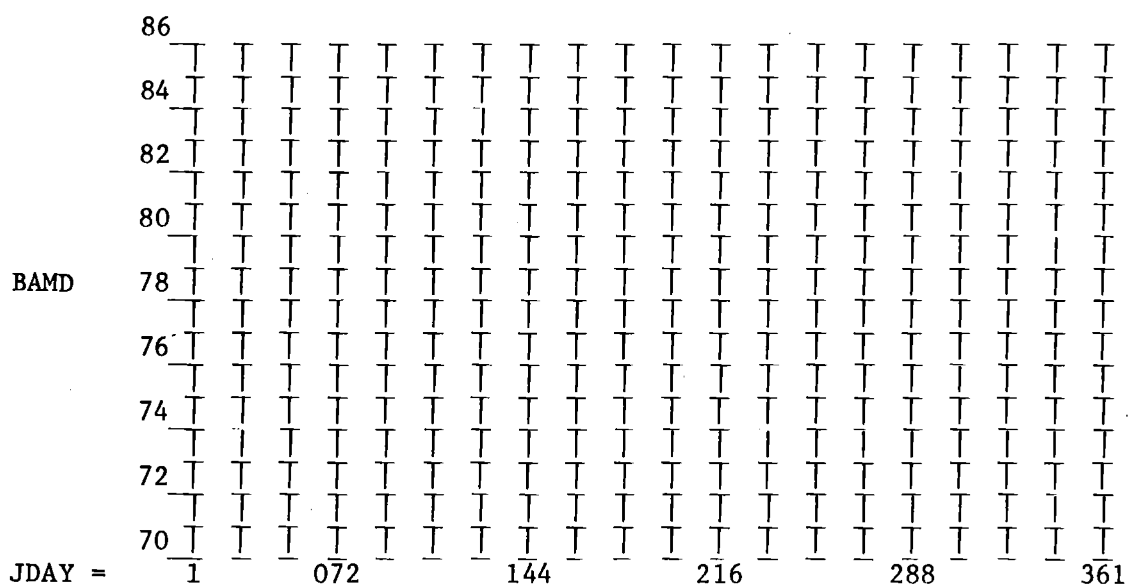
$$\sin[(227)(0.9863)]-134 = +1.0, \text{ and } \sin[(45)(0.9863)]-134 = -1.0$$

The equation for predicting the seasonal rhythm in basal metabolism per day (BAMD) is:

$$BAMD = [(84.4 + 75.6)/2] + \{\sin[(JDAY)(0.9863)]-134\}\ \{[84.4 - 75.6]/2\}$$

This simplified deviation of BAMD illustrates another use for the sine wave equation for smoothly correcting observed biological values over an annual cycle. The deviation is illustrative, and not meant to prove that basal metabolism values through the year are exactly these values.

Complete the calculations and plot the results below.



LITERATURE CITED

Moen, A. N. 1973. Wildlife ecology. W. H. Freeman & Co., San Francisco. 458 pp.

Silver, H. 1968. Deer nutrition studies. In The white-tailed deer of New Hampshire, ed. H. R. Siegler. Survey Report No. 10, Concord: New Hampshire Fish and Game Department, pp. 182-196.

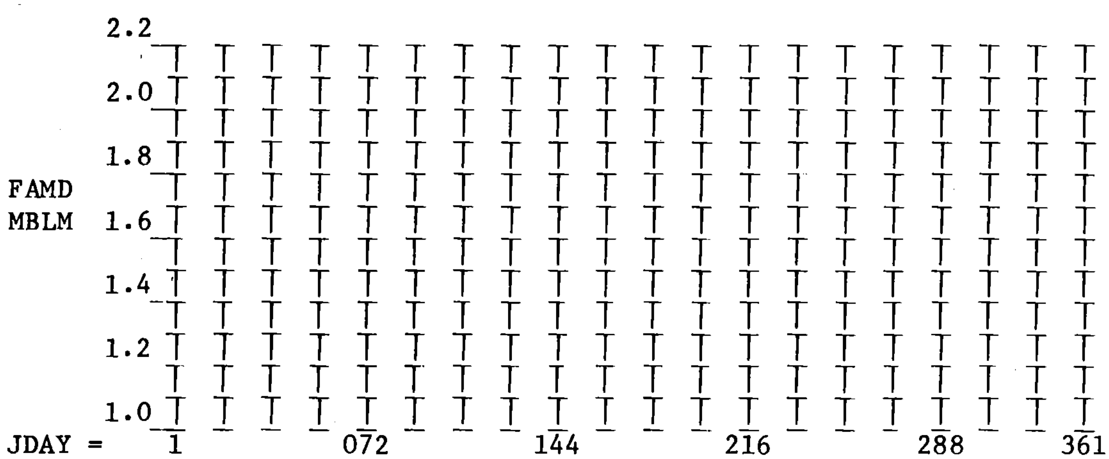
CHAPTER 7, WORKSHEET 2.1b

Fasting metabolism of white-tailed deer

The fasting metabolism of white-tailed deer has been measured by Silver et al. (1969) and the data recalculated and compiled in Moen (1973:118). Average heat production values in kcal per $W_{kg}^{0.75}$ are as follows:

Age	Sex	Coat	Heat production	MBLM
Adult	male	winter	95.6	1.37
Adult	male	summer	141.4	2.02
Adult	female	winter	97.5	1.39
Adult	female	summer	146.3	2.09
	yearlings	summer	130.6	1.87
	fawns	winter	90.1	1.29

The differences in MBLM between sexes are very slight. The values 1.38 = MBLM in winter coat and 2.06 = MBLM in summer coat could be used for both sexes. Using the procedures described in WORKSHEET 2.1a, derive a sine wave equation for fasting metabolism expressed as a multiple of base-line metabolism and plot the results below.



LITERATURE CITED

Moen, A. N. 1973. Wildlife ecology. W. H. Freeman & Co., San Francisco. 458 pp.

Silver, H. 1968. Deer nutrition studies. In The white-tailed deer of New Hampshire, ed. H. R. Siegler. Survey Report No. 10, Concord: New Hampshire Fish and Game Department, pp. 182-196.

CHAPTER 7, WORKSHEET 2.1c

Metabolism of a mountain goat

The metabolism of a 1 1/2 year-old male mountain goat was measured in February and March in a temperature-controlled chamber by Krog and Monson (1954).

The measured values are:

Weight	Ambient Temperature	Total Heat Production (kcal per 24 hour)	Kcal per $LWKG^{0.75}$	MBLM
32 kg	20 to -20	1027	____	____
	-30	1304	____	____
	-50	2362	____	____

Complete the "kcal per $W_{kg}^{0.75}$" column by dividing total heat production by $32^{0.75}$, and the MBLM column by dividing the previous answer by $(70)(32^{0.75})$. Note the MBLM values for later comparisons with seasonal rhythms in different species discussed in TOPIC 6 of this CHAPTER.

LITERATURE CITED

Krog, H. and M. Monson. 1954. Notes on the metabolism of a mountain goat. Am. J. of Physiol. 178:515-516.

UNIT 2.2: OUTDOOR MEASUREMENTS

It is difficult to get good direct measurements of the heat production of wild ruminants in chambers because of the extensive training required and the potentials for psychological effects, and it is impossible to measure heat production directly when they are ranging freely of course. How may the "cost of living" of free-ranging animals be quantified? Since it is impossible to measure ecological metabolism directly over 24-hour periods throughout the annual cycle, it must be calculated based on biological evidence for general patterns and magnitudes of metabolic rates of specific activity and productive functions.

Outdoor measurements may be made in several ways, including the use of respiratory masks, tracheal cannulae, calculations of the cost of movement of mass over distance, and by converting vital signs to estimates of metabolic rates. Closed circuit spirographic-masks, consisting of an oxygen spirometer which measures the rate of oxygen consumption, are one of the least expensive methods for measuring enerby expenditures, although not all animals are willing to wear the masks. Closed-circuit systems involve rebreathing of the same air, except that CO_2 is absorbed by porous soda lime after passing through one-way valves. Open-circuit mask methods for larger animals involve the measurements of CO_2 increases and O_2 decreases of directly inspired air. Gas analyzers are used to determine the amounts of oxygen consumed, and these measurements are converted to estimates of heat production.

The basic equations for determining metabolism using heart rates and activity patterns and heart rate to metabolism conversions have been described, and can be assembled into a sequence of calculations throughout the year to predict ecological metabolism throughout the year. While these calculations can be repeated for every day, 365 times for a year, that is unnecessary as 15-day intervals are sufficiently close to result in a smooth curve over the annual cycle.

REFERENCES, UNIT 2.2

OUTDOOR MEASUREMENTS

SERIALS

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
JWMAA	20--3	221	232	odvi	nutrient req, growth, antl	french,ce; mcewa/	1956
JWMAA	27--2	185	195	odvi	rumen ferment, ener relati	short,hl;	1963
JWMAA	33--3	482	490	odvi	diges ener, win, mich does	ullrey,de; youat/	1969
JWMAA	34--4	863	869	odvi	diges metab ener mich does	ullrey,de; youat/	1970
JWMAA	37--3	301	311	odvi	nutrition requiremen, fawn	thompson,cb; hol/	1973
JWMAA	42--4	715	738	odvi	seas rhyth, heart rat, met	moen,an	1978
JWMAA	43--4	880	888	odvi	predict energ, nitro reten	holter,jb; urban/	1979

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
CJZOA	48--2	275	282	odhe	feed intake, heat prod, yo	nordan,hc; cowan/	1970
JWMAA	43--1	162	169	odhe	energ requirem fawn, winte	baker,dl; johnso/	1979

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
CBPAB	59A-1	95	100	ceel	effic of utili diet energy	sipson,am; webst/	1978
CBPAB	61A--	43	48	ceel	oxyg use, calves, locomotn	cohen,y; robbins/	1978
JWMAA	43--2	445	453	ceel	energy expenditure, calves	robbins,ct; cohe/	1979

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				alal			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
BPURD	1----	335	339	rata	meth meas ener exp, unrstr	young,ba; mcewan,	1975
CJZOA	56--2	215	223	rata	energ expnd, walk, rd,tund	white,rg; yousef,	1978

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				anam			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				bibi			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				ovca			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				ovda			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				obmo			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
				oram			

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
PAANA	7----	335	341	dosh	co2, index ener expen, lmb	white,rg; leng,ra	1968

CODEN	VO-NU	BEPA	ENPA	ANIM	KEY WORDS-----------------	AUTHORS----------	YEAR
PNUSA	37--1	13	19		altern meth, larg anim cal	brockway,jm	1978

CHAPTER 7, WORKSHEET 2.2a

Caloric value of oxygen at different respiratory quotients

Calculations of heat production based on oxygen consumed are made by multiplying the liters of oxygen consumed by the caloric value of O_2 at the respiratory quotient (R. Q. = REQO) characteristic of the diet of the animals at the time of measurement.

The abbreviated table below, based on data in Brody (1945:310) illustrates differences in the kcal per liter of oxygen at REQOs ranging from 0.70 to 1.00.

REQO	Kcal per liter O_2
0.70	4.686
0.75	4.729
0.80	4.801
0.85	4.863
0.90	4.924
0.95	4.985
1.00	5.047

The table in Brody gives the kcal per liter O_2 for R. Q. from 0.70 to 1.00 at 0.01 intervals. While the table covers more than half a page vertically, curve-fitting with linear regression reduces the tabular information to a simple equation. Thus, the kcal per liter of O_2 (KCLO) at different respiratory quotients (REQO) can be calculated:

$$KCLO = 3.818 + 1.229\ REQO;\ R^2 = 1.00$$

LITERATURE CITED

Brody, S. 1964. Bioenergetics and growth. Hafner Publishing Co., Inc. New York. 1023 pp.