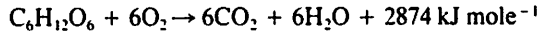


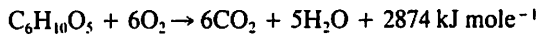
Supplement 4-1

Stoichiometry for Carbohydrate, Lipid, and Protein Metabolism

The complete oxidation of one mole of glucose consumes six moles of oxygen, releases six moles of carbon dioxide, and liberates 2874 kJ energy.

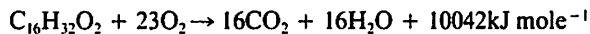


The energy equivalence of glucose is 2874 kJ mole⁻¹ or 15.9 kJ g⁻¹. Other useful ratios calculated from this stoichiometry of glucose metabolism are 21.4 kJ liter O₂⁻¹, 21.4 kJ liter CO₂⁻¹, and RQ = 1. The metabolism of C₆-subunits of glycogen yields slightly different values for kJ O₂⁻¹ and kJ CO₂⁻¹, because there is one less H₂O per C₆-subunit.



	Glucose	Glucosyl Unit	Lipid	Protein
kJ g ⁻¹	15.9	17.7	39.2	20.1
kJ mole ⁻¹	2870	2870	10042	64400
L O ₂ g ⁻¹	0.75	0.83	2.01	1.07
L CO ₂ g ⁻¹	0.75	0.83	1.40	0.91
kJ L O ₂ ⁻¹	21.4	21.4	19.5	18.8
kJ L CO ₂ ⁻¹	21.4	21.4	27.9	24.0
RQ	1.0	1.00	0.70	0.84
g H ₂ O kJ ⁻¹	0.038	0.031	0.029	0.021
M urea mole ⁻¹	0	0	0	19.5
kJ g N ⁻¹	0	0	0	126

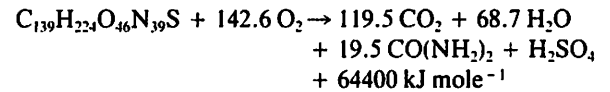
The stoichiometry for lipid metabolism is quite different, and the indirect calorimetric ratios (kJ g⁻¹, kJ O₂⁻¹, kJ CO₂⁻¹, RQ) differ substantially from those for glucose and glycogen metabolism. For example, combustion of palmitate, a long-chain fatty acid, is as follows.



The energy equivalents for palmitate are 39.2 kJ g⁻¹, 19.5 kJ liter O₂⁻¹, 27.9 kJ liter CO₂⁻¹, and RQ = 0.70. Not all lipids have the same stoichiometry, however. For ex-

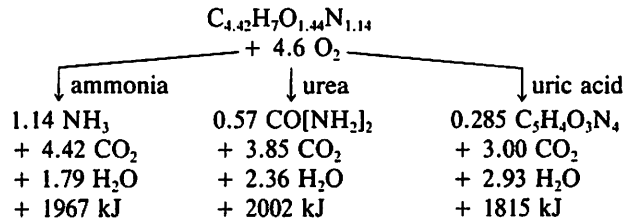
ample, metabolism of a short-chain triglyceride, C₃H₅(CH₂CH₂COO)₃, has an RQ of 0.81.

The stoichiometry of protein metabolism is complex because it contains N and S as well as C, H, and O. There is about 52g C, 7g H, 23g O, 17g N, and 1g S in 100 g of "meat protein". The final form of the N and S complicates the stoichiometry. An approximate stoichiometry for metabolism of 1 mole (3205) g of meat protein is



if the N is converted to urea and the S to SO₄²⁻. The metabolic energy yield is 20.1 kJ g⁻¹, but the energy yield is higher when measured by bomb calorimetry (about 23.8 kJ g⁻¹) because the nitrogenous product is not urea. The RQ for metabolism of "meat protein" is 0.84. The RQ for a typical amino acid, alanine, is 0.81.

The stoichiometry for protein metabolism depends on whether ammonia (NH₃), urea (CO(NH₂)₂), or uric acid (C₅H₄O₃N₄) is the nitrogenous waste product. Consider the metabolism of 100 g protein (2364 kJ energy).



None of these pathways yield 2364 kJ of energy. The energy yield is less because of the energy content of the nitrogenous waste: ammonia, 347.9 kJ/1.14 mole; urea, 362 kJ/0.57 mole; uric acid, 549 kJ/0.285 mole. The joule equivalent for protein is fairly similar for each pathway; 19.1 (ammonia), 17.6 (urea), and 19.4 (uric acid) kJ liter O₂⁻¹. The RQ values are quite different, being 0.96, 0.84, and 0.72, respectively.

Supplement 4-2

Energetics of Nitrogenous Waste Products

The three main nitrogenous wastes from protein metabolism, ammonia, urea, and uric acid differ considerably in their energy contents, but the comparison is complicated by the variety of ways to express energy content.

The energy content of ammonia, urea, and uric acid, measured by bomb calorimetry, is different from that calculated from their biosynthetic pathways from ammonia.

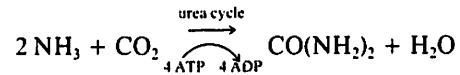
		Ammonia NH ₃	Urea CO(NH ₂) ₂	Uric Acid C ₅ H ₄ O ₃ N ₄
	Mol Wt	17	60	168
Energy Content	kJ g ⁻¹	20.5	10.6	11.5
	kJ mole ⁻¹	347.9	634.3	1926
	kJ g N ⁻¹	24.9	22.7	34.5
Energy of Biosynthesis ¹	kJ g ⁻¹	0	3.1	1.7
	kJ mole ⁻¹	0	122	244
from NH ₃	kJ g N ⁻¹	0	8.7	4.9

¹ Biosynthesis from ammonia, assuming 1 mole ATP is equivalent to 30.5 kJ and urea synthesis requires 4 ATP per urea and uric acid synthesis requires 8 ATP per molecule.

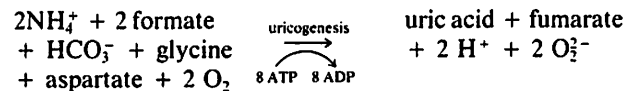
Ammonia has the highest energy content per gram but the lowest per mole (measured by bomb calorimetry). Ammonia has an intermediate energy content per gram of nitrogen between urea (lowest value) and uric acid (highest value). Uric acid would therefore appear to be the most energetically wasteful and urea the most energetically conserving waste product if the primary objective of N excretion is to minimize the energy loss. However, much of the chemical energy associated with nitrogen waste products is unavailable to animals because they cannot further oxidize ammonia despite its 20.5 kJ g⁻¹ energy content.

Another important consideration concerning the energetics of nitrogen waste products is the biological cost for

synthesis of the waste product. This is not taken into account by the bomb calorimetric energy content. Ammonia is the initial waste product of amino acid metabolism (except for arginine). Energy is therefore required for conversion of ammonia to urea or uric acid, regardless of their respective joule energy content. The overall conversion of ammonia to urea by the urea cycle (see Chapter 17) requires 4 moles of ATP per mole of urea, i.e., about 122 kJ mole⁻¹.



The overall conversion of ammonia to uric acid requires 8 moles of ATP per mole of uric acid, i.e., about 244 kJ mole⁻¹.



These estimated costs for biochemical conversion of ammonia to urea and uric acid are quite substantial compared to their joule contents, and they provide a clear energetic incentive for ammonia excretion rather than urea or uric acid excretion.

Energy content is, however, only one aspect concerning the relative advantages and disadvantages of the various nitrogenous waste products. Water conservation and osmoregulation are probably much more important than energetics in determining the most favorable nitrogenous waste product for particularly terrestrial animals (see Chapters 16 and 17; see Pilgrim 1954).

Supplement 4-3

Allometric Analysis of Metabolic Rate

Allometry is the study of the way that a dependent variable Y (e.g., metabolic rate) varies in relation to an independent variable X (e.g., body mass); it is the study of scale effects. For a simple linear relationship between X and Y ,

$$Y = a + bX$$

where b is the slope $(Y_2 - Y_1)/(X_2 - X_1)$ and a is the Y -intercept (the Y value when $X = 0$). Analysis of linear data is often accomplished by the method of least-squares linear regression analysis. The informative statistics summarizing the goodness of fit for a linear regression relationship include the slope of the relationship (b); the Y -intercept (a); the correlation coefficient (r), which varies from -1 (perfect inverse correlation) to 0 (no significant correlation) to $+1$ (perfect positive correlation); the square of the correlation coefficient (r^2), which is the fraction of the variation in Y values that is explained by

the variation in the X values; and the standard errors or 95% confidence limits for the slope (b) and intercept (a).

The relationship between metabolic rate and body mass is generally not linear, but is curvilinear. For example, the metabolic rate (kJ day⁻¹) of a variety of mammals and birds is definitely curvilinear, when graphed as a function of body mass (kg) using normal (nonlogarithmic) axes. Three different panels are required to graph the relationship over a mass range from 0.01 kg to 5000 kg. One solid line ($b = 1$) indicates the expected metabolic rate if it were directly proportional to body mass (calculated from the metabolic rate of a canary). The other line ($b = 0.67$) is the expected metabolic rate if it were proportional to mass^{0.67}.

These curvilinear data can be fitted by various types of curve (e.g., quadratic, polynomial, hyperbolic, exponential) but a power curve provides an excellent and convenient fit.

$$Y = aX^b$$

For the metabolic data,

$$\text{kJ day}^{-1} = 289 \text{ kg}^{0.734}$$

It is not possible to derive statistics for a curvilinear relationship as conveniently as for a linear regression analysis. However, curvilinear relationships can generally be made into a linear relationship by appropriately transforming the X and Y variables.

A power curve can be transformed into a straight line by a logarithmic transformation of both X and Y , to give the following.

$$\begin{aligned} (\log Y) &= (\log a) + b(\log X) \\ &= a' + b(\log X) \end{aligned}$$

Either \log_{10} or \log_e can be used; this changes the value of a but not b . For example, the curvilinear relationship between metabolic rate and body mass is linearized by

transforming and plotting \log_{10} (metabolic rate) as a function of \log_{10} (body mass). For the metabolic data,

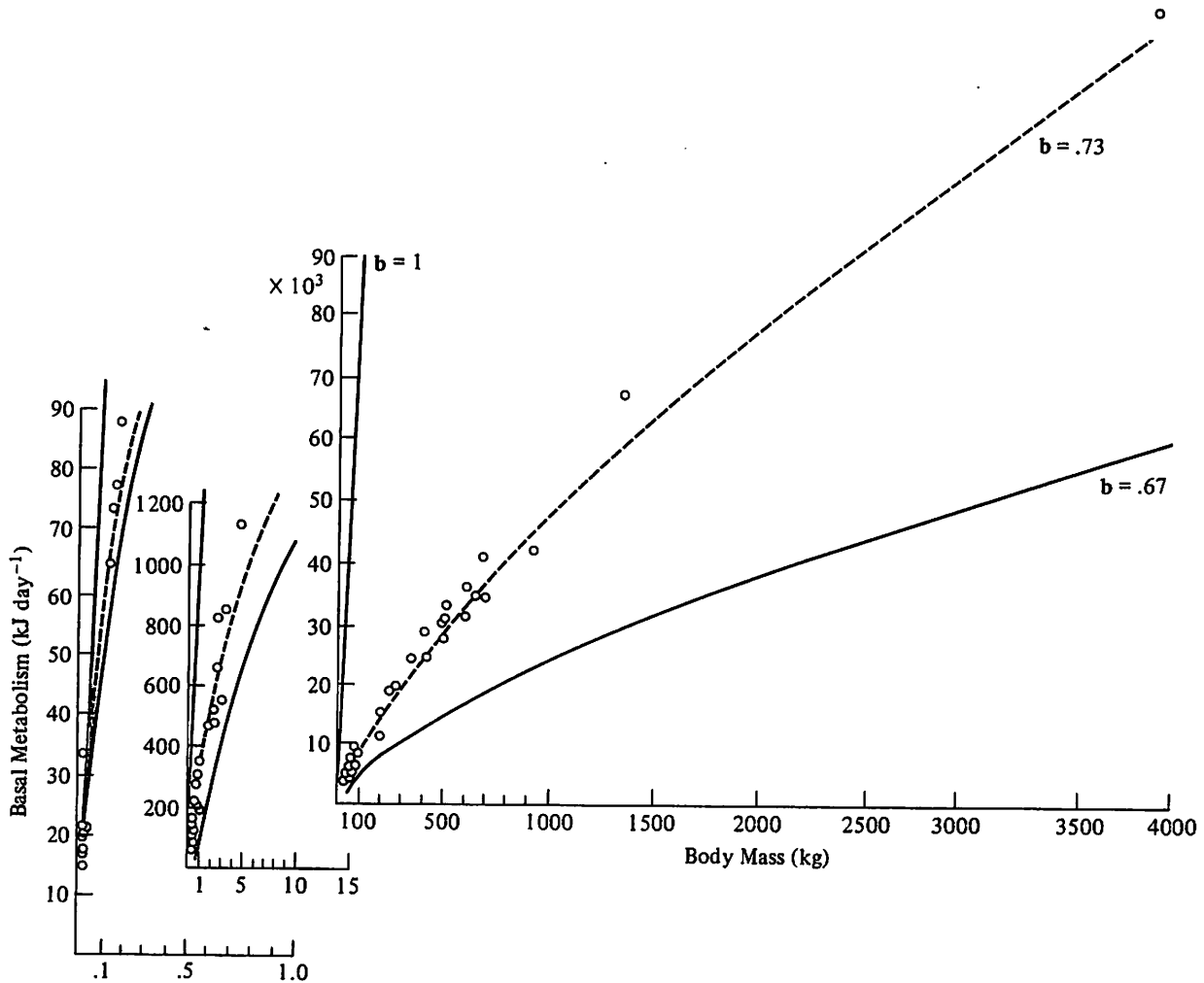
$$\log_{10} \text{ kJ day}^{-1} = 2.46 + 0.734 (\log_{10} \text{ kg})$$

A \log_{10} - \log_{10} transformation of data is commonly used to summarize and analyze many physiological relationships.

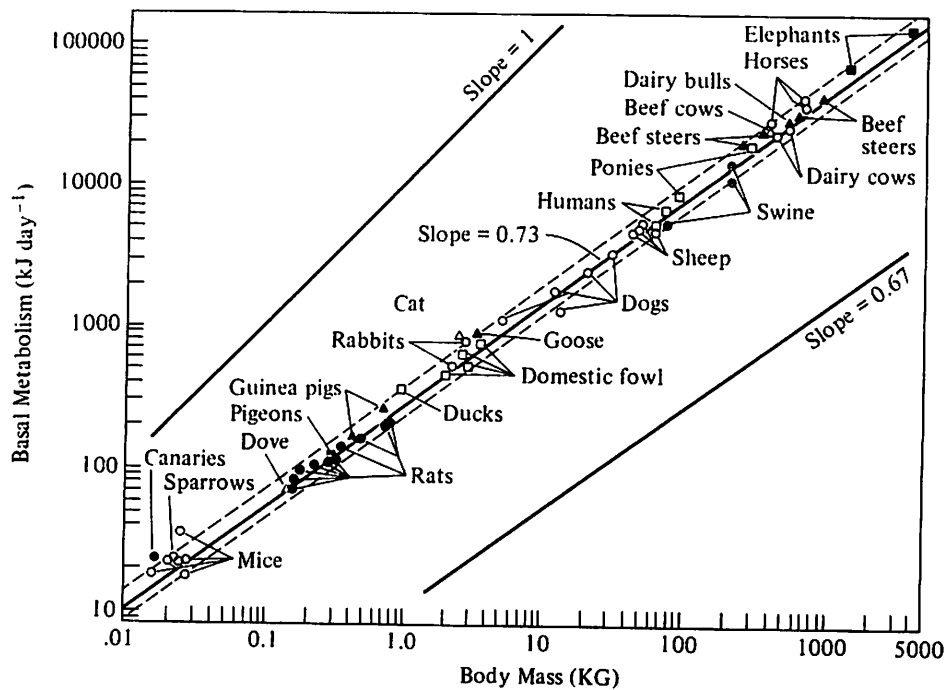
Transformation to a linear relationship allows the calculation of the linear regression coefficients, e.g., a' and b . The relationship can then be "detransformed" to the original data form

$$Y = aX^b$$

where $a = 10^{a'}$. The detransformed equation shows the curvilinear relationship between metabolic rate and body mass (e.g., with arithmetic axes) but the statistical analysis of the transformed data cannot be validly applied to the detransformed data.



Linear ($b = 1$) and power ($b = 0.67$ and $b = 0.75$) relationships between metabolic rate and body mass for birds and mammals.



Relationship between \log_{10} metabolic rate and \log_{10} body mass for birds and mammals. (Modified from Brody 1945.)

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