

developmental stage, body mass, food or oxygen availability, the nature of their diet, photoperiod, hormonal balance, salinity for aquatic animals, and taxonomy. Some of these important determinants of metabolic rate are discussed next.

Body Size

One of the most intriguing, and yet unresolved, problems in comparative animal physiology is the observed relationship between metabolic rate and body mass. Metabolic rate must be greater for animals of larger mass. An elephant is bigger than a mouse and has a proportionately higher metabolic rate. But the fundamental question concerns the rule of proportionality.

The relationship between metabolic rate (e.g., VO_2) and body mass is of the general form of a power curve,

$$Y = a \text{ Mass}^b \quad (4.5a)$$

where a is the intercept (the metabolic rate when mass = 1) and b is the mass exponent. This power

curve can be transformed to a linear relationship by taking the \log_{10} of both metabolic rate and body mass values (see Supplement 4-3, page 119). The slope of the linear relationship is equal to the mass exponent of Equation 4.5a.

$$(\log_{10} Y) = (\log_{10} a) + b(\log_{10} \text{Mass}) \quad (4.5b)$$

A classical analysis for mammals and birds (Kleiber 1932) showed that the relationship between metabolic rate and body mass was not linear. The metabolic rate of large mammals and birds was considerably lower than expected from a direct proportionality, and that of small mammals and birds was greater than expected. The difference between the metabolic rate predicted from a linear relationship and actual metabolic rate is immense over many orders of magnitude, e.g., a mouse compared to an elephant. The relationship was linear for \log_{10} metabolic rate as a function of \log_{10} mass (Figure 4-6). The equation describing this relationship is

$$\begin{aligned} VO_2 &= 3.9 \text{ g}^{0.738} \text{ (ml O}_2 \text{ hr}^{-1}) \\ &= 1.9 \text{ g}^{0.738} \text{ (kJ day}^{-1}) \end{aligned} \quad (4.6)$$

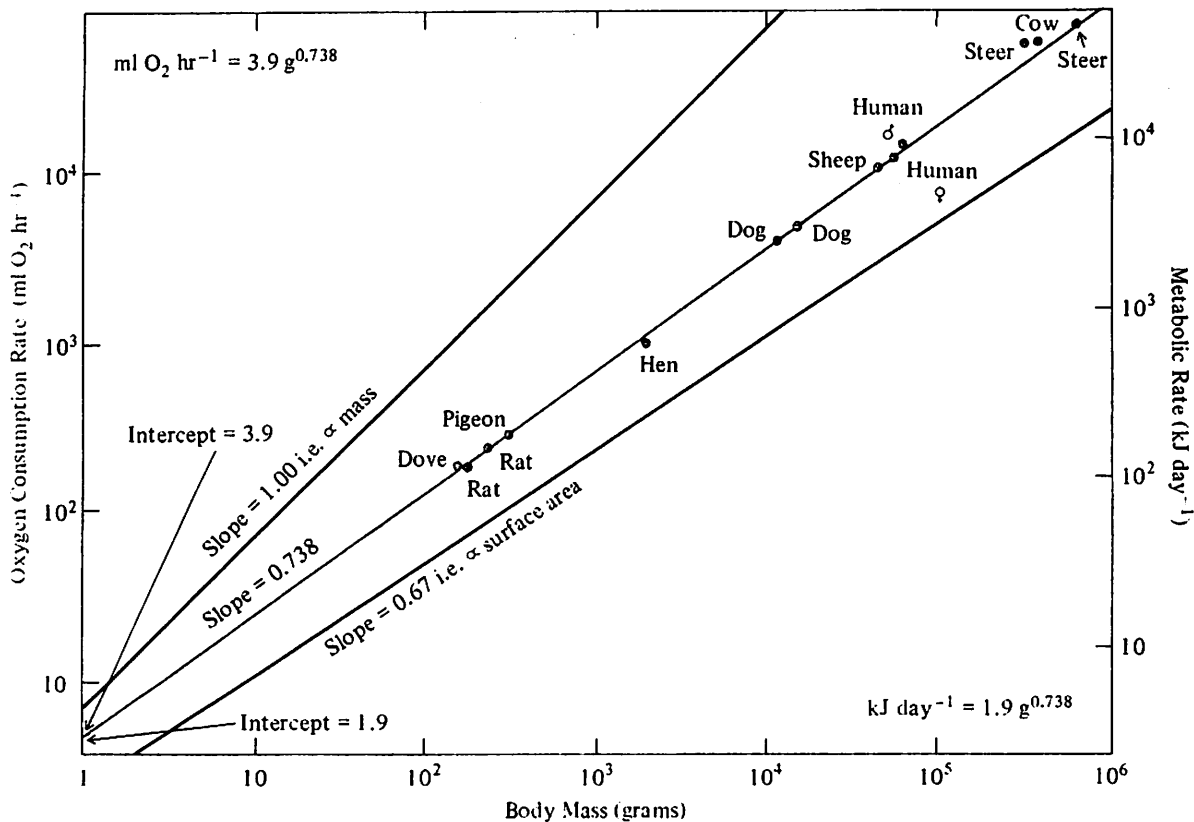


FIGURE 4-6 Relationship between \log_{10} metabolic rate and \log_{10} body mass for mammals and birds. (Modified from Kleiber 1932.)

where g is the body mass in grams. The mass exponent, or slope, is 0.738 and the intercept is 3.9 $\text{ml O}_2 \text{ hr}^{-1}$, or 1.9 kJ day^{-1} (i.e., this is the metabolic rate for a 1-gram mammal or bird). It has become common practice as a consequence of this study to summarize metabolic rate data not only in absolute units (e.g., $\text{ml O}_2 \text{ hr}^{-1}$) and mass-specific units (e.g., $\text{ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$), but also in mass-independent units (e.g., $\text{ml O}_2 \text{ g}^{-0.738} \text{ hr}^{-1}$ in the above example of mammals and birds). The mass-independent units give a metabolic rate that is independent of body mass and is therefore convenient for comparing the metabolic rates of animals of differing body mass. However, $\text{mass}^{-0.738}$ is not necessarily the most appropriate correction factor to standardize metabolic rate for all animals (see below).

The allometric relationship between metabolic rate and body mass is probably the best documented but least understood topic in comparative animal physiology. There are many studies of the allometry of metabolic rate for numerous taxa of animals, and for single species (Table 4-5).

This comprehensive summary of interspecific and intraspecific allometric relationships for various animals is presented because of the considerable interest of comparative physiologists in this topic. Compilation of such a table of data is fraught with difficulties, necessary extrapolations, and calculations from the original data because of the great diversity in experimental approaches, conditions, the nature of the animals studied, and the units used for metabolic rate. Body temperature is also an important variable in determining the standard metabolic rate of ectotherms (see below) and so the a values for ectotherms have been converted to a temperature of 20° C if necessary. The a values for endotherms are for their normal body temperatures (generally 35° to 41° C). Mass was standardized to grams, but it is important to appreciate that the extrapolation of allometric relationships from pg mass (e.g., unicells) or ktonne (e.g., large mammals) to an intercept value of 1 gram mass may result in an almost meaningless a value. Only a values for wet mass are included in Table 4-5. The a value depends on the unit for mass, e.g., wet mass, dry mass, ash-free dry mass, soft body mass, shell-free dry mass, or even in terms of nitrogen content; for example, a is about five times higher for dry mass than wet mass. Perusal of this large summary of allometric data reveals considerable taxonomic diversity in allometric relationships, with respect to both a and b values, even for taxonomically similar animals. For example, placental mammals have higher a values than marsupials, which in turn are higher than monotreme a values. Even within placental mammals, there are considerable differ-

ences in a values for various taxa. Birds exhibit similar taxonomic groupings based on metabolic rate, i.e., passerine birds (highest), nonpasserine carinate birds (intermediate), and ratite birds (lowest). Lower vertebrates and invertebrates also exhibit great diversity in a values.

A summary and analysis of these numerous data for allometric slopes (Figure 4-7) and intercepts

(Text continues on page 99)

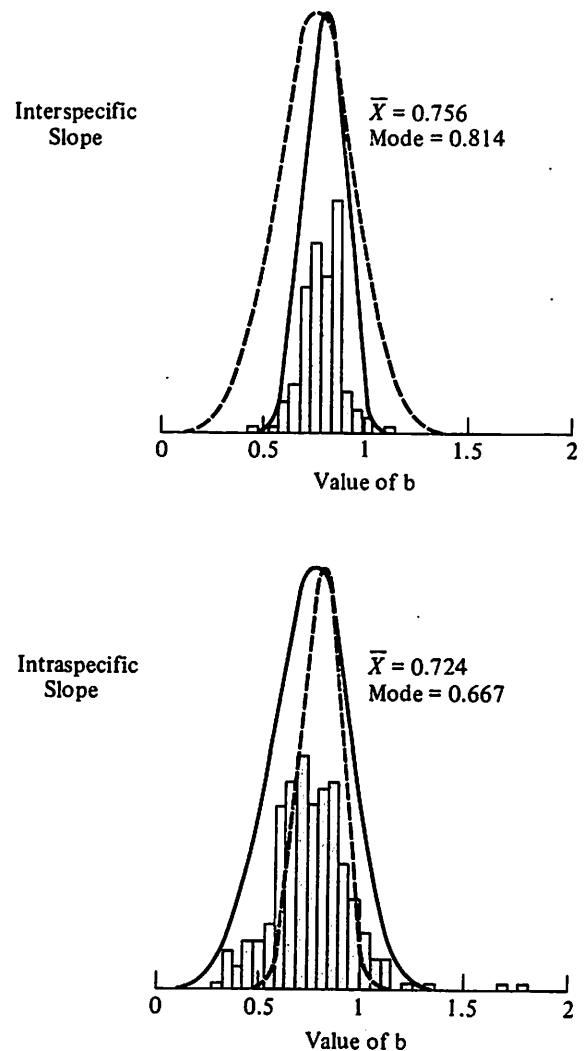


FIGURE 4-7 Summary of slope coefficients b for the allometric relationship between basal metabolic rate (BMR; J h^{-1}) and body mass (M ; grams). Allometric equations are of the form $\text{BMR} = aM^b$. The solid envelope is the normal distribution fitted to the data, and the broken envelope is the distribution for the other data set. Both distributions have similar means, but the mode for intraspecific analyses is 0.67 and the mode for interspecific analyses is 0.81. Sample size is 107 for interspecific allometric analyses and 220 for intraspecific analyses.

TABLE 4-5

Interspecific and intraspecific allometry of metabolic rate ($J\ hr^{-1}$) for various animals. Intercept values for ectotherms are corrected to a temperature of $20^{\circ}\ C$ if necessary; the Q_{10} was obtained from the original source or assumed to be 2.5. In some instances, intercept values were estimated or calculated from the original data or figure (or the slope was assumed to be 0.75). Body mass (M) is in grams.

INTERSPECIFIC			INTRASPECIFIC		
MAMMALS					
Placentals					
All	63.6	$M^{0.76}$	<i>Peromyscus</i>	12.8	$M^{0.72}$
Edentates	63.9	$M^{0.66}$	<i>Mus</i>	58	$M^{0.91}$
Ground squirrels	65.1	$M^{0.66}$	<i>Rattus</i>	146	$M^{0.64}$
Megachiroptera	67.4	$M^{0.73}$	<i>Ovis</i>	147	$M^{0.72}$
Chiroptera	73.1	$M^{0.71}$	<i>Canis</i>	207	$M^{0.65}$
Heteromyids	74.3	$M^{0.72}$	<i>Felis</i>	220	$M^{0.58}$
Small mustelids	74.3	$M^{0.72}$	<i>Homo</i>	382	$M^{0.60}$
All	89.6	$M^{0.70}$	<i>Bos</i>	456	$M^{0.56}$
Crocidurine shrews	136	$M^{0.75}$			
Soricine shrews	272	$M^{0.75}$			
Large mustelids	374	$M^{0.55}$			
Marsupials					
All	47.6	$M^{0.75}$			
Dasyurids	49.2	$M^{0.74}$			
All	50.1	$M^{0.75}$			
Monotremes					
			<i>Zaglossus</i>	17.4	$M^{0.75}$
			<i>Tachyglossus</i>	19.8	$M^{0.75}$
			<i>Ornithorhynchus</i>	44.7	$M^{0.75}$
BIRDS					
Passerines					
All	132	$M^{0.73}$			
All	151	$M^{0.72}$			
Nonpasserines					
All	80.5	$M^{0.73}$			
All	80.5	$M^{0.72}$			
Honey eaters	134	$M^{0.68}$			
Small species	138	$M^{0.72}$			
Procellariiformes	153	$M^{0.66}$			
Ratites					
All	50.4	$M^{0.73}$			
REPTILES					
Lizards					
All	1.5	$M^{0.80}$	<i>Ctenosaura</i>	1.4	$M^{0.86}$
Varanids	1.9	$M^{0.82}$	<i>Chalcides</i>	1.7	$M^{0.65}$
Xantusids	2.2	$M^{0.56}$	<i>Amblyrhynchus</i>	2.9	$M^{0.78}$
Lacertids	2.6	$M^{0.76}$	<i>Lygosoma</i>	6.2	$M^{0.63}$
Snakes					
All	2.4	$M^{0.77}$	<i>Lampropeltis</i>	3.9	$M^{0.65}$
Boids	0.8	$M^{0.81}$			
Colubrids	0.8	$M^{0.98}$			
Turtles					
All	1.3	$M^{0.86}$	<i>Geochelone</i>	1.9	$M^{0.82}$
			<i>Chelonia</i>	2.5	$M^{0.83}$
Crocodylians					
			<i>Caiman</i>	1.1	$M^{0.93}$
			<i>Crocodylus</i>	6.0	$M^{0.65}$

continues

TABLE 4-5

<i>continued</i>			
INTERSPECIFIC		INTRASPECIFIC	
AMPHIBIANS			
Apoda		<i>Typhlonectes</i>	1.5 M ^{0.78}
Salamanders			
Neotropical	0.7 M ^{0.86}		
Temperate	1.1 M ^{0.82}		
Lungless	1.2 M ^{0.78}		
Lunged	3.5 M ^{0.86}		
Lungless	3.8 M ^{0.72}		
Anura			
All	4.2 M ^{0.68}	<i>Rana</i>	1.7 M ^{1.06}
		<i>Xenopus</i>	1.8 M ^{1.08}
		<i>Bufo</i>	3.7 M ^{0.75}
FISH			
All	2.5 M ^{0.70}	<i>Cyprinus</i>	0.1 M ^{0.98}
All	4.8 M ^{0.88}	<i>Ictalurus</i>	0.1 M ^{1.00}
		<i>Catostomus</i>	0.1 M ^{0.99}
		<i>Notothenia</i>	0.4 M ^{0.96}
		<i>Carassius</i>	0.6 M ^{0.91}
		<i>Notothenia</i>	1.6 M ^{0.79}
		<i>Gobius</i>	1.6 M ^{0.89}
		<i>Kuhlia</i>	2.6 M ^{0.79}
		<i>Cirrhinus</i>	2.8 M ^{0.80}
		<i>Onchorhynchus</i>	9.2 M ^{0.78}
		<i>Scophthalmus</i>	13.4 M ^{0.71}
		<i>Gadus</i>	16.5 M ^{0.83}
ARTHROPODS			
Crustaceans	3.4 M ^{0.81}		
Horseshoe crab		<i>Limulus</i>	1.7 M ^{0.81}
Crabs	0.9 M ^{0.80}	<i>Uca</i>	0.3 M ^{0.62}
		<i>Hemigrapsis</i>	1.2 M ^{0.56}
		<i>Ocypoda</i>	2.2 M ^{0.56}
		<i>Hemigrapsis</i>	2.6 M ^{0.32}
		<i>Carcinus water</i>	2.8 M ^{0.52}
		<i>Carcinus air</i>	3.0 M ^{0.61}
		<i>Pachygrapsis</i>	3.0 M ^{0.61}
Amphipods			
Temperate	2.9 M ^{0.85}	<i>Vibilia</i>	0.6 M ^{0.58}
Seawater	3.0 M ^{0.7}	<i>Talitrus</i>	0.6 M ^{0.65}
All	3.8 M ^{0.57}	<i>Lygia</i>	1.4 M ^{0.73}
		<i>Ampelissa</i>	4.1 M ^{0.69}
		<i>Mesothidia</i>	1.8 M ^{0.85}
Fresh water	5.1 M ^{0.7}	<i>Gammarus</i>	7.0 M ^{0.70}
Cold water	5.3 M ^{0.86}		
Antarctic	6.4 M ^{0.81}		
Euphasiids	6.7 M ^{0.50}	<i>Artemia male</i>	1.0 M ^{0.62}
		<i>Artemia female</i>	2.1 M ^{0.72}
		<i>Palaemonetes</i>	3.4 M ^{0.76}
Spiders			
All	1.0 M ^{0.65}	<i>Sericopelma</i>	0.7 M ^{0.80}
Wolf spiders	1.7 M ^{0.67}		

INTRASPECIFIC

INTERSPECIFIC

Host	Species	Value	Sample		
Insects	Coleoptera	1.3	M ⁰¹		
	Beetles	3.5	M ⁰²		
	Scarabids	5.4	M ⁰³		
	Spilimids	6.4	M ⁰⁴		
	Diptera	7.4	M ⁰⁵		
	Coleoptera	10.7	M ⁰⁶		
	All	11.3	M ⁰⁷		
	All	13.7	M ⁰⁸		
	Mollusks	Operculates	0.3	M ⁰⁹	
		Merrenurta	1.2	M ¹⁰	
		Patella	1.7	M ¹¹	
		Orula	2.4	M ¹²	
		Patella	2.5	M ¹³	
		Lymnaea	2.6	M ¹⁴	
		Lymnaea	2.9	M ¹⁵	
Lymnaea		5.1	M ¹⁶		
Mollusks		Polychaetes	1.9	M ¹⁷	
		Clymenella	0.9	M ¹⁸	
		Polychaetes	2.6	M ¹⁹	
		Oligochaetes	1.9	M ²⁰	
		Hirudinea	2.1	M ²¹	
		Nematodes	Caenorhabditis	0.6	M ²²
			Cysticercus	0.4	M ²³
	Schistosomophidus		0.5	M ²⁴	
	Taenia		1.0	M ²⁵	
	Onchopeltus		0.05	M ²⁶	
	Pyura		0.60	M ²⁷	
	Ophiroids		Ophioreis	1.1	M ²⁸
			Ophioreis	1.3	M ²⁹
			Ophioreis	1.4	M ³⁰
			Scherodactylus	2.9	M ³¹
Cucumaria			4.6	M ³²	
Asteroidea			Strongylocentrotus	0.2	M ³³
			Strongylocentrotus	0.7	M ³⁴
			Strongylocentrotus	1.1	M ³⁵
			Ophiroids	Ophioreis	1.1
		Ophioreis		1.3	M ³⁷
		Ophioreis		1.4	M ³⁸
		Ophioreis		2.9	M ³⁹
		Scherodactylus		4.6	M ⁴⁰
		Cucumaria		2.2	M ⁴¹
		Strongylocentrotus		0.2	M ⁴²
	Strongylocentrotus	0.7		M ⁴³	
	Strongylocentrotus	1.1		M ⁴⁴	
	Mollusks	Merrenurta		1.2	M ⁴⁵
		Patella		1.7	M ⁴⁶
		Orula		2.4	M ⁴⁷
Patella		2.5		M ⁴⁸	
Lymnaea		2.6		M ⁴⁹	
Lymnaea		2.9		M ⁵⁰	
Lymnaea		5.1	M ⁵¹		
Mollusks		Merrenurta	1.2	M ⁵²	
		Patella	1.7	M ⁵³	
		Orula	2.4	M ⁵⁴	
		Patella	2.5	M ⁵⁵	
		Lymnaea	2.6	M ⁵⁶	
		Lymnaea	2.9	M ⁵⁷	
		Lymnaea	5.1	M ⁵⁸	
		Mollusks	Merrenurta	1.2	M ⁵⁹
	Patella		1.7	M ⁶⁰	
	Orula		2.4	M ⁶¹	
	Patella		2.5	M ⁶²	
	Lymnaea		2.6	M ⁶³	
	Lymnaea		2.9	M ⁶⁴	
	Lymnaea		5.1	M ⁶⁵	
	Mollusks		Merrenurta	1.2	M ⁶⁶
Patella			1.7	M ⁶⁷	
Orula			2.4	M ⁶⁸	
Patella			2.5	M ⁶⁹	
Lymnaea			2.6	M ⁷⁰	
Lymnaea			2.9	M ⁷¹	
Lymnaea			5.1	M ⁷²	
Mollusks			Merrenurta	1.2	M ⁷³
		Patella	1.7	M ⁷⁴	
		Orula	2.4	M ⁷⁵	
		Patella	2.5	M ⁷⁶	
		Lymnaea	2.6	M ⁷⁷	
		Lymnaea	2.9	M ⁷⁸	
		Lymnaea	5.1	M ⁷⁹	
		Mollusks	Merrenurta	1.2	M ⁸⁰
	Patella		1.7	M ⁸¹	
	Orula		2.4	M ⁸²	
	Patella		2.5	M ⁸³	
	Lymnaea		2.6	M ⁸⁴	
	Lymnaea		2.9	M ⁸⁵	
	Lymnaea		5.1	M ⁸⁶	
	Mollusks		Merrenurta	1.2	M ⁸⁷
Patella			1.7	M ⁸⁸	
Orula			2.4	M ⁸⁹	
Patella			2.5	M ⁹⁰	
Lymnaea			2.6	M ⁹¹	
Lymnaea			2.9	M ⁹²	
Lymnaea			5.1	M ⁹³	
Mollusks			Merrenurta	1.2	M ⁹⁴
		Patella	1.7	M ⁹⁵	
		Orula	2.4	M ⁹⁶	
		Patella	2.5	M ⁹⁷	
		Lymnaea	2.6	M ⁹⁸	
		Lymnaea	2.9	M ⁹⁹	
		Lymnaea	5.1	M ¹⁰⁰	

continues

TABLE 4-5

continued	
INTERSPECIFIC *	INTRASPECIFIC
<i>COELENTERATES</i>	
Anthozoa	0.69 $M^{0.86}$
<i>UNICELLS</i>	
All	0.001 $M^{0.42}$
All	0.025 $M^{0.55}$
All	0.03 $M^{0.66}$
All	0.35 $M^{0.75}$
All	0.56 $M^{0.68}$
All	1.58 $M^{0.83}$

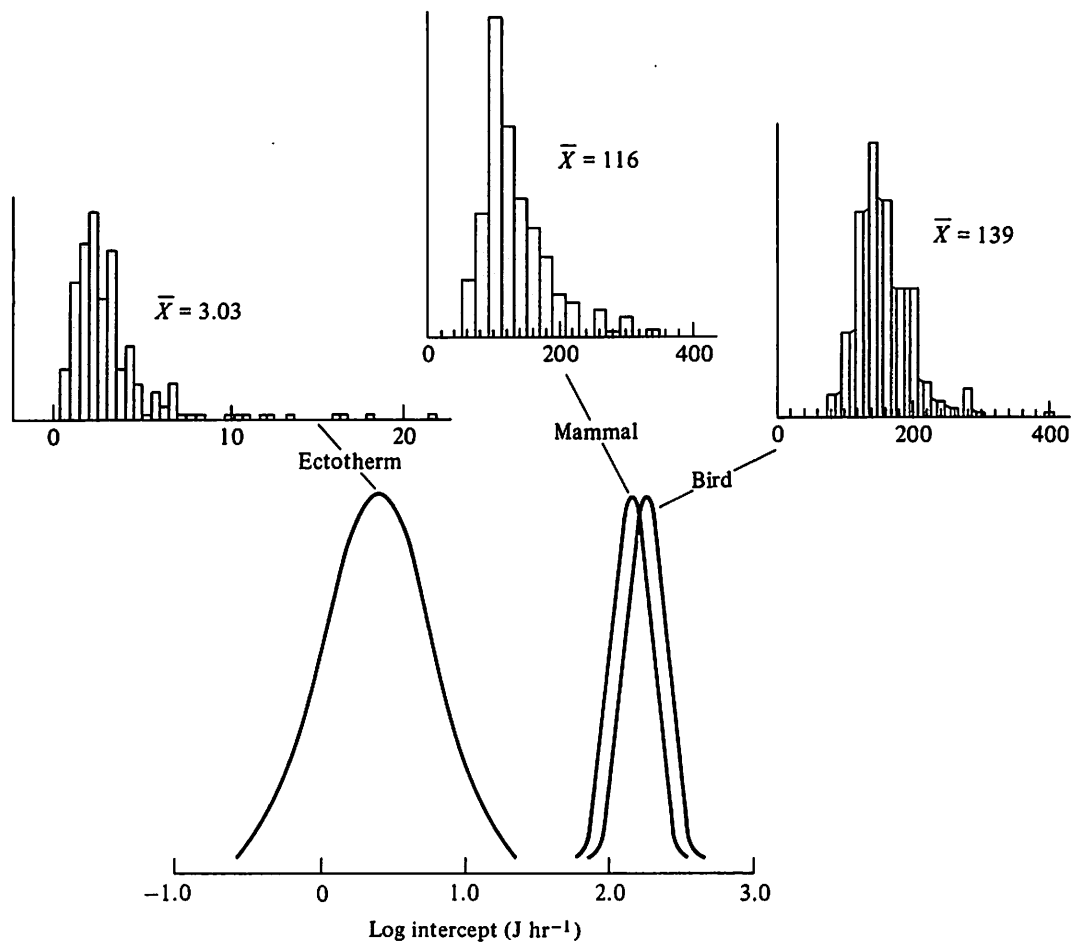


FIGURE 4-8 The frequency histograms for intercept value (a) for the relationship between \log_{10} metabolic rate as a function of \log_{10} body mass are positively skewed for ectotherms, birds, and mammals. The a values for ectotherms are considerably lower than the values for mammals and birds, as is evident from the graph of the normal curves fitted to the frequency histograms for \log_{10} a of ectotherms, mammals, and birds.

(Figure 4-8) reveal some consistent trends. The slope varies from <0.5 to >1.0 , but on average is about 0.76 for interspecific relationships (i.e., for various species of animals), and about 0.72 for intraspecific relationships (i.e., a single species). Why the slope is about 0.75 is one of the most perplexing questions in biology. The intercept values vary from <1 to $>400 \text{ J hr}^{-1}$, with a mean of 3 for ectotherms (at 20° C), 116 for mammals, and 139 for birds. Why there is such a variation in intercept values is a little easier to explain than the value of the slope.

Unicells, Ectotherms, and Endotherms. There is a profound consistency in the relationship between metabolic rate and body mass for animals of varying taxonomic position.

There are three major "grades" of animals, based on the allometry of their metabolic rates. This is apparent from the relationship between log metabolic rate and log mass observed for virtually all kinds of animals, as is apparent from a reanalysis (Phillipson 1981) of the classical studies of Hemmingsen (1950) and Zuethen (1953) for unicellular ectotherms, multicellular ectotherms, and endotherms (Figure 4-9). The data for ectotherms are corrected to a body temperature of 10° C (the approximate mean annual temperature for these animals), and for endotherms the data are corrected to a body temperature of 39° C .

A number of salient features are illustrated by Figure 4-9. First, there is considerable overlap in

body mass for unicellular and multicellular ectotherms. Second, the relationships for the three grades of organisms are fairly discrete. Third, the slopes of the three relationships are not equal to one for any grade of organism. The \log_{10} -transformed relationship between VO_2 ($\mu\text{l O}_2 \text{ hr}^{-1}$) and mass (g) for unicellular ectotherms (bacteria, fungi, flagellates, ciliates, rhizopods) has a slope of 0.66 (with 95% confidence limits of ± 0.09) and an intercept of $0.59 \mu\text{l O}_2 \text{ hr}^{-1}$ (0.012 J hr^{-1}). The relationship for multicellular ectothermic animals (see legend for Figure 4-9) has a higher slope (0.88 ± 0.00002) and intercept value of $14.8 \mu\text{l O}_2 \text{ hr}^{-1}$ (0.297 J hr^{-1}). The relationship for endotherms has a slope of 0.69 (± 0.0017) and an intercept of $2630 \mu\text{l O}_2 \text{ hr}^{-1}$ (52.9 J hr^{-1}). Finally, the major metabolic step between unicellular and multicellular ectotherms is about three times, and the metabolic step between multicellular ectotherms (at 10° C) and endotherms (corrected to 10° C) is even larger, at about eight times.

Why are there three metabolic grades of animals? The metabolic step from unicellular ectotherm to multicellular ectotherm has been explained by their differing surface areas (Phillipson 1981). Consider a theoretical single-celled, cuboidal animal with cell dimensions $1\mu \times 1\mu \times 1\mu$; the surface area is $6 \mu^2$ ($6 \times 1 \times 1$). If a multicellular animal of the same mass had 1000 cubic cells, then the total cellular surface area would be $60 \mu^2$ ($1000 \times (6 \times 1/10 \times 1/10)$), i.e., $10 \times$ the area of the unicell. The metabolic rate of the multicellular animal might be expected to be $10 \times$ that of the unicell if adequate

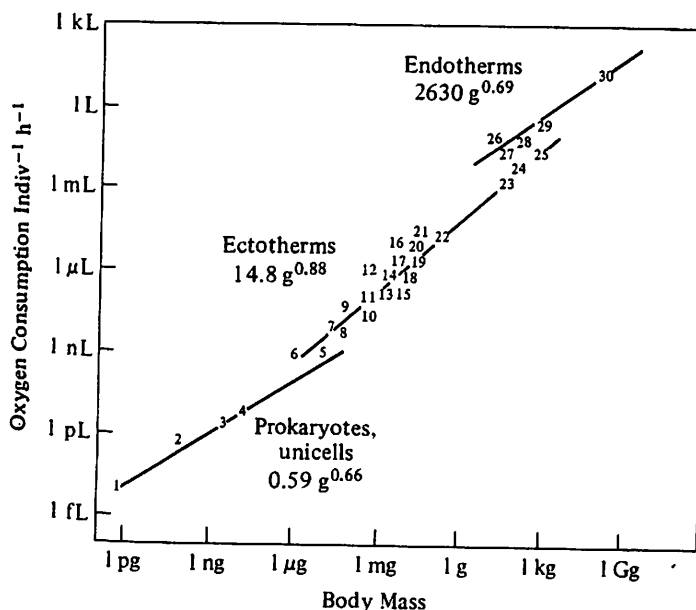
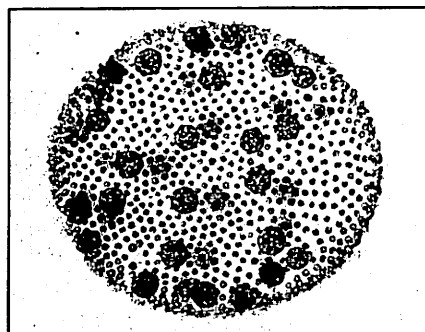


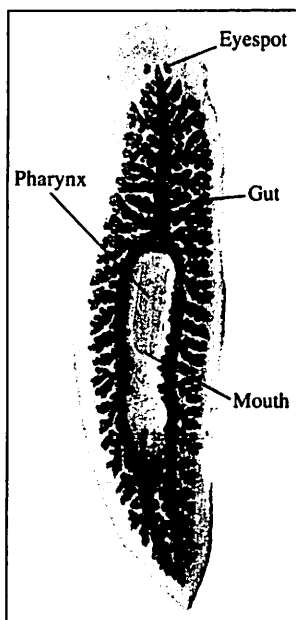
FIGURE 4-9 \log_{10} transformed relationship between rate of oxygen consumption (from 1 femtoliter to 1 kiloliter hr^{-1}) and body mass (from 1 picogram to 1 gigagram) for prokaryote and unicellular eukaryote organisms, multicellular ectothermic animals, and endothermic animals. Numbers indicate the pivotal point for the regression line for the following taxa: 1 bacteria; 2 fungi, 3 flagellates, 4 ciliates, 5 rhizopods, 6 nematodes, 7 microcrustaceans, 8 acari, 9 collembolans, 10 isopteran larvae, 11 enchytraeids, 12 coleopteran larvae, 13 isopteran adults, 14 formicid workers, 15 lumbricid cocoons, 16 phalangiids, 17 diplopods, 18 araneans, 19 isopods, 20 mollusks, 21 coleopteran adults, 22 lumbricid adults, 23 macrocrustaceans, 24 fish, 25 reptiles, 26 small mammals, 27 chiropterans, 28 birds, 29 primitive mammals, and 30 large mammals. Data for unicells are corrected to 10° C , and data for endothermic animals are corrected to 39° C . (From Phillipson 1981.)



A



B



C

TABLE 4-6

Comparison between a dragon lizard and a mouse for the following: body temperature; organ weights; standard/basal metabolic rate of whole animal; *in vitro* metabolic rate of liver; component of *in vitro* metabolic rate of liver for Na⁺ transport (*i.e.* blocked by ouabain); and mitochondrial volume, surface area and enzyme activity. The ratio of the mammalian to lizard value (M/L) is also given. (Modified from Else and Hulbert 1981.)

	LIZARD <i>Amphibolurus nuchalis</i>	MOUSE <i>Mus musculus</i>	M/L
Body weight (g)	34.3	32.1	1
Body temperature (°C)	37.0	36.8	1
Liver mass (% total)	10.7	20.7	1.9
Kidney mass (% total)	1.9	5.9	3.1
Heart mass (% total)	1.1	2.8	2.5
Brain mass (% total)	1.7	5.5	3.3
VO₂ (ml O₂ g⁻¹ h⁻¹)			
<i>In Vivo</i> —whole animal	0.20	1.62	8.1
<i>In Vitro</i> ¹ —liver	0.90	4.59	5.1
<i>In Vitro</i> ¹ Na ⁺ transport	0.22	1.97	9.0
% Mitochondrial volume	12.4	16.0	1.3
Mitochondrial Surface Area			
Cristae (m ² g ⁻¹)	15.5	22.9	1.5
Inner (m ² g ⁻¹)	0.79	1.34	1.7
Total area (m ²)	3.4	10.2	3.0
Cytochrome oxidase (nmol O ₂ mg ⁻¹ min ⁻¹)	11.2	30.0	2.7

¹Per gram dry weight.

O₂ could be delivered to the entire cellular surface area. An alternative argument is to assume that the metabolic rate of a cell in a multicellular animal is equal to that of a unicell of the same size as that cell. The multicellular animal would then have a higher metabolic rate than the same-sized unicell. If the multicellular animal again has 1000 cells, then each cell would have a metabolic rate not 0.001 × that of the unicell but about 0.0098 ×, if the slope of the allometric relationship is 0.67. The total metabolic rate of the multicellular animal would

FIGURE 4-10 The protozoan *Amoeba proteus* (A), the colonial protozoan *Volvox* (B), and a planarian flatworm (C) illustrate the possible evolutionary sequence from a unicellular organism to a multicellular animal, via a colonial intermediate form. (Photographs A and C, Courtesy of Carolina Biological Supply Co., Inc.; B Courtesy of Richard Starr.)

therefore be $9.8 \times$ that of the same-sized unicell. Such arguments may provide a plausible explanation for the metabolic grade between unicells and multicellular animals, particularly if the intermediate evolutionary stage was a colony of small unicells (Figure 4-10).

The metabolic grade between ectotherms and endotherms cannot be so easily explained by surface area effects, since the total cellular surface area is presumably similar for ectothermic and endothermic multicellular animals. The difference might be attributed to differences in cellular metabolic machinery. For example, the scaling of $VO_{2,rest}$ and $VO_{2,max}$ in mammals is closely related to the scaling of their visceral and total mitochondrial surface areas respectively (Figure 4-11). There is a similar relationship for reptiles. The mitochondria of endotherms are similar in morphology and biochemistry to those of ectotherms, although mammalian mitochondria have slightly greater membrane areas (both cristae and inner membrane). Endotherm tissues also have

slightly greater mitochondrial volumes, due to greater numbers of mitochondria and/or larger mitochondria. Consequently, endothermic tissues have greater mitochondrial enzyme activity than ectotherm tissues, hence a potentially higher metabolic rate. The significant difference between *in vivo* and *in vitro* metabolic rates for tissues of house mice and similar-sized lizards (at the same body temperature) are explained by the summed effects of a number of small differences, including minor differences in mitochondrial morphology, numbers of mitochondria, mitochondrial enzyme activity (cytochrome oxidase), and the greater mass of internal organs: liver, kidneys, heart, and brain (Table 4-6). The visceral mass of endotherms provides a major fraction of the resting metabolic requirements, disproportionate to their mass (72% and 8% respectively in humans).

The metabolic differences between ectotherms and endotherms are apparent for whole animals and for *in vitro* homogenates or tissue slices. The scaling

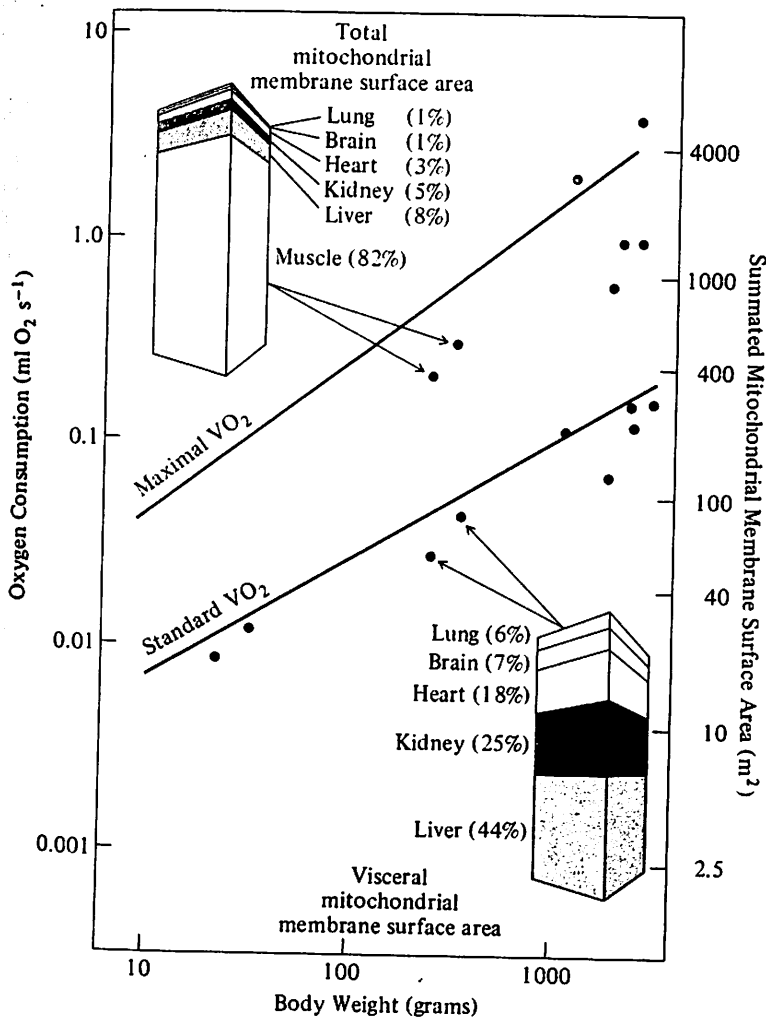


FIGURE 4-11 Relationship between \log_{10} -transformed resting oxygen consumption rate and body mass for a mammal (solid line), and between visceral organ mitochondrial surface area (liver + brain + kidney + heart) and body mass (\bullet). Shown also is the relationship between maximal oxygen consumption rate (colored line) and total mitochondrial surface area (visceral organs + skeletal muscle; \bullet) with body mass. The mitochondrial surface for visceral organs and skeletal muscle is shown. (Modified from Else and Hulbert 1981.)

relationships observed *in vivo* for whole animals are sometimes, but not always, observed *in vitro* with tissue slices or homogenates. For example, mammalian liver slices show the same systematic increase in metabolic rate with body weight (the exponent is about 0.75; Kleiber 1945) but fish organs and tissue homogenates do not (Vernberg 1954).

Why Isn't Metabolism Proportional to Mass? Why is the slope about 0.75 for the relationship between log metabolic rate and log body mass for virtually all animal taxa? This is a fundamental question in biology, but unfortunately we lack a convincing answer to this question. There are, however, a number of hypotheses to explain why the slope is about 0.75.

Geometric Similarity. Geometric similarity predicts a slope of 2/3, or 0.67, for the metabolic rate–mass

relationship. Consider a sphere of radius r ; its surface area is $4\pi r^2$ and volume is $4/3 \pi r^3$. If the density of the sphere (ρ) is independent of its size, then its mass is $4/3 \pi \rho r^3$, i.e., its weight is proportional to r^3 and r is proportional to $\text{mass}^{1/3}$. The surface area, which is proportional to r^2 , is therefore proportional to $\text{mass}^{2/3}$. This relationship between mass and surface area is found not only for spheres, but for any geometrically similar (i.e., same-shaped) animal. For example, a small cockroach is geometrically similar to a large cockroach that might weigh 100 or even 1000 times more, and their surface area/mass is proportional to $\text{mass}^{2/3}$. For many species of mammal, the slope is about 0.67, although the inter-specific slope is about 0.75 (Figure 4–12).

Metabolic rate should be proportional to surface area, or $\text{mass}^{2/3}$, if an important metabolic process is dependent on surface area. Many important meta-

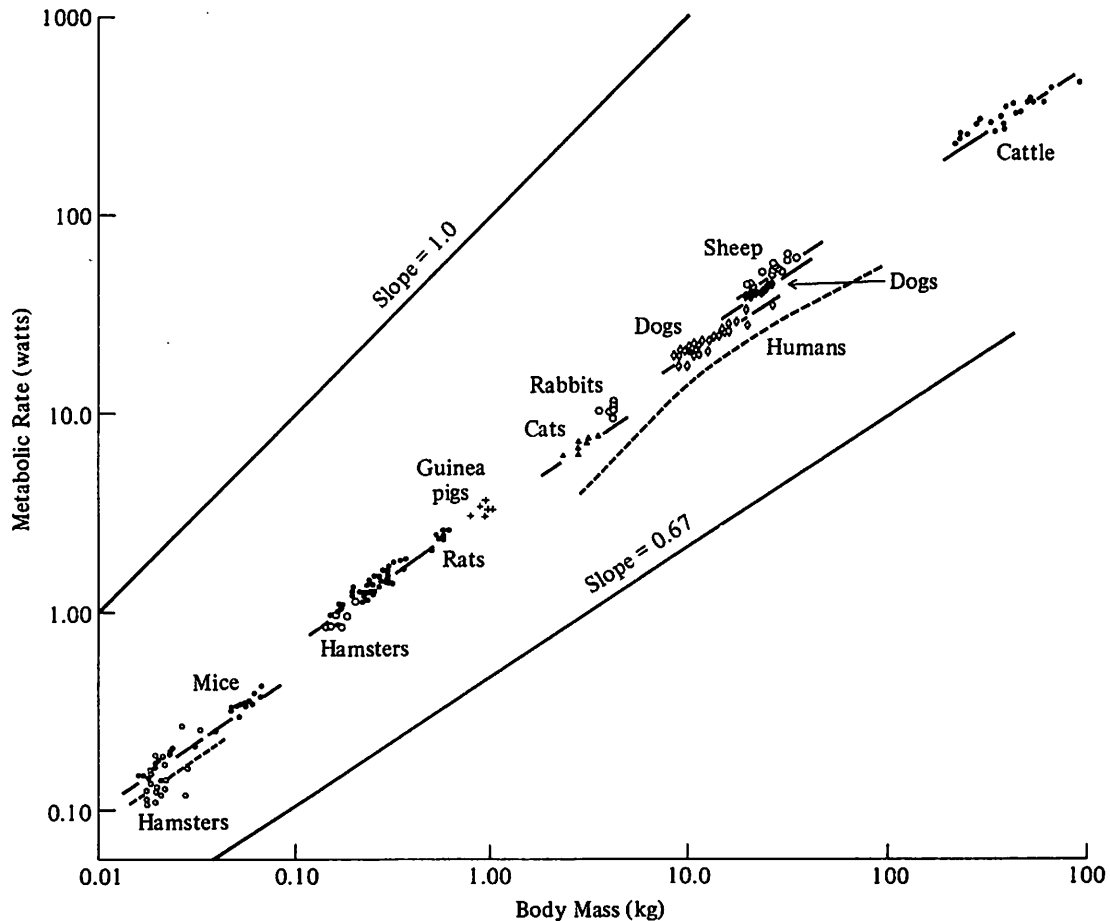


FIGURE 4–12 Log_{10} -transformed relationship between metabolic rate and body mass for a variety of mammals, showing the lower generally intraspecific scaling relationship (slopes from 0.51 to 0.91) compared to the interspecific scaling relationship (slope of 0.776). (From Heusner 1982; Hill and Rahimtulla 1965.)

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bolic processes, such as O₂ and CO₂ exchange and digestive absorption, are dependent either on the surface area of the animal or other internal surface areas, such as the lung surface or digestive tract surface. Thus, we might expect metabolic rate to be proportional to mass^{2/3} for geometrically similar animals; for example, based on a relationship between respiratory surface area and mass (Hughes 1984). The heat loss of endothermic animals is a function of their surface area, not their volume. Since the metabolic rate of endotherms is essentially proportional to the rate of heat loss, then metabolic rate might be expected to be proportional to mass^{2/3}.

The metabolic rate of unicellular organisms (which tend to be geometrically similar) is proportional to mass^{0.66} (see Figure 4-9, page 99), which is essentially the slope expected if metabolism is proportional to surface area, for geometrically similar animals. For multicellular ectotherms, which are generally not geometrically similar, metabolic rate is not proportional to mass^{0.67}, but the slope is 0.88 (±95% confidence limits of 0.00002). However, the slope for endotherms is 0.69, which is again similar to the 2/3 value expected from geometric similarity.

Structural Support. The structural support properties of materials influence body shape, muscle size, and power output (McMahon 1973). The ability of a cylinder to resist bending or buckling depends on its length, radius, and elastic properties. The critical length at which a cylinder will buckle (l_{crit}) is proportional to $r^{2/3}$. Consequently, r^2 is proportional to l_{crit}^3 . The weight of the cylinder of critical length is equal to $\pi r^2 \rho l_{crit}$ since weight = volume × density (ρ). The cylinder weight is thus proportional to $r^2 \cdot r^{2/3}$, or $r^{8/3}$, and r is proportional to weight^{3/8}. The maximal force exerted by a muscle is proportional to its cross-sectional area (see Chapter 9) and the maximal energy expenditure of a muscle is therefore proportional to r^2 or weight^{3/4}. There appears to be a fairly consistent proportionality between resting and maximal metabolic rate and so resting metabolism is also proportional to mass^{0.75}.

This hypothesis predicts the allometric relationship for the metabolic rate of animals that might experience buckling deformation, but it is unlikely to be universally applicable to all animals, from aquatic unicells to terrestrial endotherms.

Additive Scaling. The metabolic scaling relationship may be the additive result of two different influences (Swan 1972; Yates 1981), a surface-area specific effect ($VO_2 \propto \text{mass}^{0.67}$) and a mass-specific effect ($VO_2 \propto \text{mass}^{1.0}$).

$$VO_{2,\text{total}} = k_1 \text{mass}^{0.67} + k_2 \text{mass}^{1.0} \quad (4.7)$$

$$\propto k_3 \text{mass}^{0.75}$$

Complex explanations based on heat exchange have been presented to account for the slope of 0.75 for mammals (Swan 1972; Gray 1981). The minimal, and essential, energy requirement for cells (M_{cer}) is assumed to be proportional to mass, i.e., $M_{cer} = e \text{Mass}^{1.0}$ where e is a constant. An additional energy production is required by endotherms for regulation of body temperature, since M_{cer} is too low; the metabolic rate for obligate heat production (M_{ohp}) is proportional to surface area because heat loss is proportional to surface area, i.e., $M_{ohp} = h \text{Mass}^{2/3}$ where h is a constant. The total metabolic rate is $M_{tot} = M_{cer} + M_{ohp}$. Larger endotherms are not geometrically similar to small endotherms, and they have a higher proportion of supporting tissues with lower metabolic requirements than other tissues, i.e., the values of e and h are mass-dependent. Appropriate values for e and h as a function of mass closely predict the observed relationship between M_{tot} and body mass for mammals, i.e., $M_{tot} = a \text{Mass}^{0.75}$.

Unfortunately for the above argument, ectothermic animals also have b values similar to 0.75 but do not have a functional relationship between body temperature, heat exchange, and surface area. Either there are different explanations for the allometry of metabolic rate for endotherms and ectotherms resulting in similar predicted b values, or there is a single explanation and the above thermal argument for mammals is irrelevant. An obsession with "Ockham's razor" entices comparative physiologists to seek for the single, unifying theory of metabolic allometry. Ockham's doctrine of nomination suggests that explanations should not be unnecessarily complex.

Four-dimensional Scaling. Another explanation for a slope of 0.75 is afforded by considering area in four dimensions rather than the three dimensions we are used to (Blum 1977). In n -dimensional space, the surface area/volume is proportional to radius^{($n-1$)/ n} . Surface area/volume $\propto r^{2/3}$ for three dimensions (as we saw above) and $\propto r^{3/4}$ for four dimensions, i.e., metabolic rate $\propto \text{mass}^{3/4}$ if metabolic rate is proportional to four-dimensional surface area.

This is a relatively straightforward derivation of the 3/4 slope, but what is the fourth dimension? Time is one suggestion, especially as the life span of animals is proportional to mass^{0.25} (Calder 1984). Thus, the total energy expended by an animal over its entire life span is proportional to metabolic

rate \times life span, or mass^{1.0}. But, is time as important a determinant of metabolic rate as the linear dimensions of an animal? Another suggestion for the fourth dimension is a ratio of quantities required for mechanical stability, such as the ratio of energy cost of ion pumps per unit area/energy cost of assembling/maintaining metabolic machinery per unit volume.

Fractal Scaling. Fractal dimensional analysis has also been applied to metabolic scaling. In essence, the fractal dimension is a scaling exponent that alters, depending on the scale of the measurement (see Chapter 13). For metabolic scaling, $VO_2 = aM^b - f$, where b is the normal scaling exponent and f is a fractal scaling exponent, which may change with the value of M (Sernetz, Gelleri, and Hoffman 1985). Fractal scaling may provide yet another procedure for fitting a curve to the metabolic mass data, but unfortunately it does not provide a fundamental insight into the reason for the scaling relationship.

The best summary for the allometry of metabolic rate that seems possible at present is that metabolic rate increases with body mass at less than direct proportionality (i.e., $b < 1.0$), sometimes in accord with surface area proportionality (i.e., $b = 0.67$), but generally with an intermediate proportionality (i.e., $b = 0.7$ to 0.8). Different explanations for b may be required for interspecific and intraspecific analyses and for different taxonomic groups of animals (Economos 1982). It seems highly unlikely at present that there is any "universal b value" for all animal groups.

Mass-Specific Metabolism. The slope for the scaling of mass-specific metabolic rate with body mass (b') is different from that for absolute metabolic rate (b); $b' = 1 - b$. The intercept value a is the same. For example, Kleiber's mouse-to-elephant equation for mass-specific metabolism of mammals is as follows.

$$\begin{aligned} VO_2 &= 3.2 \text{ g}^{-0.24} \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1} \\ &= 64 \text{ g}^{-0.24} \text{ J g}^{-1} \text{ hr}^{-1} \end{aligned} \quad (4.8)$$

The allometry of mass-specific metabolism illustrates the energetic constraints of small size for endotherms. The mass-specific metabolic rate of a small mammal is substantially greater than that for a large mammal. For example, a 2 g shrew has a mass-specific metabolism of $141 \text{ J g}^{-1} \text{ hr}^{-1}$, whereas a 4 tonne elephant has a mass-specific metabolic rate of about $1.66 \text{ J g}^{-1} \text{ hr}^{-1}$. The shrew expends in one hour about 1% of its total body energy, whereas an elephant expends 1% of its total body energy in about 5 days. Obviously, the rate of food consump-

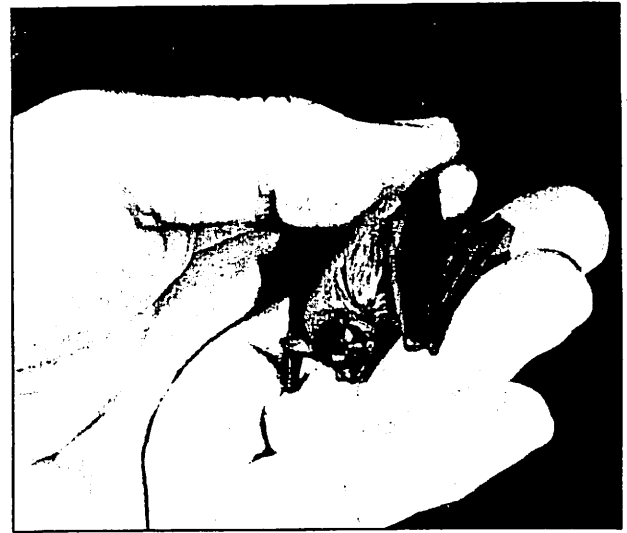


FIGURE 4-13 The adult bumblebee bat weighs only 2 grams. Its size is about the minimum lower limit for an endothermic mammal or bird. (Photograph courtesy of Bat Conservation International, Merlin D. Tuttle, BCI.)

tion has to match the energy expenditure, and so the shrew has to eat almost continuously to support its high mass-specific metabolism, whereas the elephant could starve for many days or weeks without severely depleting its body energy stores.

A body mass of 1 to 2 grams would appear to be an energetic lower limit to size for endotherms. The smallest adult mammals (bumblebee bat and Etruscan shrew) and bird (bee-hummingbird) weigh about 2 g (Figure 4-13). There are many extremely small endothermic invertebrates (e.g., moths weighing only a few mg), but these insects are intermittent rather than continuous endotherms. The largest size of terrestrial animals (African elephant, about 5000 kg) is probably determined by strength and mechanical constraints, rather than by metabolic effects of size. Marine animals can attain much larger sizes than terrestrial animals. For example, the largest mammal is the blue whale, which weighs about 150000 kg.

Temporal and Geographic Effects

Most animals have a pronounced circadian (daily) cycle in activity. Nocturnal animals are active at night and sleep during the day, whereas diurnal animals are active during the day and sleep at night. Crepuscular animals are active near dawn and dusk. The minimal metabolic rate measured for mammals and birds during their active phase of the circadian cycle (called the α phase) is typically 25 to 30%