

FIGURE 4-5 Relationship between production ($\text{J m}^{-2} \text{ year}^{-1}$) and metabolic rate ($\text{J m}^{-2} \text{ year}^{-1}$) for populations of a variety of animals: the number next to each regression line is the mean value for net production efficiency (100 P/A). (Modified from Humphreys 1979.)

siderably higher net production efficiency than endotherms.

A statistical summary of a large amount of data for production and metabolism for populations of various animals indicates that the ratio 100 P/M is independent of body mass, but varies dramatically from <1% for insectivorous mammals to >40% for nonsocial insects (Figure 4-5). There is a linear relationship between $\log_{10} P$ and $\log_{10} M$, with slopes not significantly different from 1.0 for animals divided into seven groupings (based on P and M), i.e., there is no effect of mass on 100 P/M or $P/(P + M)$. However, for a given production level (e.g., $50 \text{ J m}^{-2} \text{ year}^{-1}$) there is a dramatically lower M for nonsocial insects (about $72 \text{ J m}^{-2} \text{ y}^{-1}$) compared with insectivorous mammals (about $5050 \text{ J m}^{-2} \text{ y}^{-1}$), with these figures corresponding to net production efficiencies of about 41% and 1% respectively.

Aerobic Metabolism

Metabolic rate is one of the most commonly measured physiological variables; there is an immense body of information concerning metabolic rates for

many different animals under a wide variety of conditions. Metabolic rate measurements invariably fall in a range between a minimal value, called the standard metabolic rate or basal metabolic rate, and an upper value, often called summit metabolic rate or maximal metabolic rate. A number of different levels can be distinguished within this range.

Standard metabolic rate (SMR) is the value measured when an ectothermic animal is quiet, inactive, not digesting a meal, and not experiencing any stress (either physical, thermal, psychological, etc). **Basal metabolic rate (BMR)** is the equivalent minimal metabolic rate measured for an endothermic animal. The distinction between the terms standard and basal is necessary because the metabolic rate of ectotherms is temperature dependent, and so the SMR is the minimal metabolic rate at a particular temperature. The basal metabolic rate of an endotherm is measured within a range of ambient temperatures that is thermally neutral (the thermoneutral zone) to avoid temperature stress (see Chapter 5).

Resting metabolic rate (RMR) is somewhat similar to standard, or basal, except that the animals are simply perceived to be "resting," whereas the conditions for standard or basal metabolic rate are more stringently defined. RMR may be substantially higher than standard/basal, e.g., up to two times standard or basal. For example, the resting metabolic rate of a standing human is about 440 kJ hr^{-1} , whereas basal metabolic rate is about 270 kJ hr^{-1} . The metabolic rate even lying still but awake is about 322 kJ hr^{-1} and "at rest" is about 420 kJ hr^{-1} . Resting metabolic rate is measured with uncontrolled, but minimal, activity. **Average daily metabolic rate (ADMR)** is the metabolic rate averaged for the routine activities of a 24 hour period.

Activity metabolic rate is that measured during some form of activity, ranging from slight, to moderate, to intense, to the highest metabolic rate, summit or **maximal metabolic rate (MMR)**. This can be determined for animals during intense physical exercise, locomotion at high speeds, or with extreme cold stress for endotherms. However, it is difficult to show that the highest metabolic rate measured is actually the highest achievable metabolic rate for an animal. Furthermore, no activity requires the simultaneous activity of all muscles, and so the maximal metabolic rate for one activity (e.g., locomotion) is not necessarily the same as for other activities (e.g., thermoregulation). Motivation is another factor that makes the estimation of maximal metabolic rate difficult.

The metabolic rate of animals is determined not only by their physiological state and level of activity, but also by a multitude of other factors, including

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

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

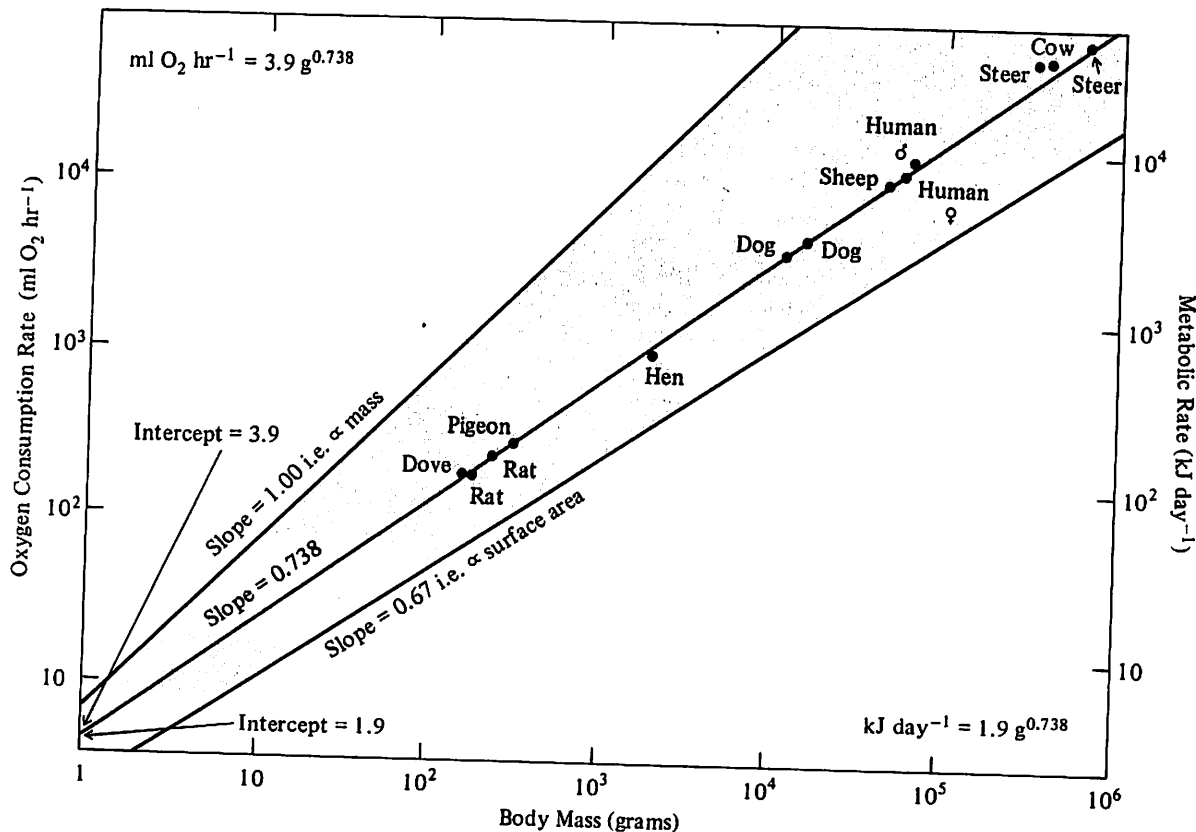


FIGURE 4-6 Relationship between \log_{10} metabolic rate and \log_{10} body mass for mammals and birds. (Modified from Kleiber 1932.)

TABLE 4-7

Variation of basal metabolic rate (BMR) for various mammals and birds in their activity phase (α) and inactivity phase (ρ) of the photoperiodic cycle. Regression equations are of the form $BMR = aM^b$, where M is mass in grams. (From Aschoff 1981; Kenagy 1982; Aschoff and Pohl 1970.)

	α	ρ	α/ρ
Mammals			
Primates	$285 M^{0.51}$	$158 M^{0.56}$	$1.80 M^{-0.05}$
Nonprimates	$402 M^{0.53}$	$268 M^{0.49}$	$1.50 M^{0.04}$
Small mammals	$143 M^{0.61}$	$112 M^{0.61}$	$1.28 M^{0.00}$
Birds			
Passerines	$190 M^{0.70}$	$133 M^{0.73}$	$1.23 M^{-0.01}$
Nonpasserines	$103 M^{0.73}$	$81 M^{0.73}$	$1.24 M^{0.00}$

higher than the minimal values during the inactive (ρ) phase (Table 4-7). There are some exceptions to this general trend among small mammals. Continuously fossorial mammals (e.g., gophers) and herbivorous species that consume low-quality food (e.g., voles) do not have day-night activity cycles, and exhibit smaller (5 to 10%) differences in day-night metabolic rates (Kenagy and Vleck 1982). Very small mammals (e.g., shrews), which must continuously feed day and night to support their high mass-specific metabolic rate, also have small (about 7%) differences between day and night minimal metabolic rates.

There are undoubtedly seasonal and geographic variations in basal metabolic rate for individual species and for groups of similar species (e.g., passerine birds), but it is not clear how general these variations are. Altitude, season, and latitude can influence the basal metabolic rate of some birds by about 20%, with higher rates in colder conditions, i.e., high altitude, winter, high latitude (Weathers 1979). Similarly, some desert mammals and birds have low basal rates of metabolism, perhaps as a consequence of their thermal environment.

Food and Oxygen Availability

The standard/basal metabolic rate of an animal reflects its minimal energy requirement for the steady-state maintenance of necessary metabolic processes. The rate of a biochemical reaction is dependent on the concentration of substrates and end products, but we might not expect in an analogous manner that the availability of oxygen or metabolic substrates would influence the standard or basal metabolic rate of animals. However, the

availability of oxygen or metabolic substrates does influence the standard/basal metabolic rate for some animals under nonsteady-state conditions. For example, some animals often have a reduced standard/basal metabolic rate during partial or complete O_2 deprivation (hypoxia or anoxia) or food deprivation (food restriction or starvation).

There are two basic patterns for the effect of O_2 availability on standard/basal metabolic rate. Many animals, called **metabolic regulators**, maintain their normal standard/basal metabolic rate as pO_2 is reduced, down to some critical value (P_{crit}) below which the standard/basal metabolic rate declines markedly (often in direct proportion to the pO_2). The P_{crit} depends on many variables, including temperature, acclimation state, body mass, and standard/basal metabolic rate (see also Chapter 12). Many protozoans, annelids, mollusks, crustaceans, and vertebrates are metabolic regulators; a typical example is the worm *Lumbricus* (Figure 4-14). The critical pO_2 for metabolic regulators is elevated at metabolic rates above resting values; hovering honeybees have a much higher metabolic rate than resting honeybees, and their critical pO_2 is much higher than at rest. In other animals, called **metabolic conformers**, the standard/basal metabolic rate is directly proportional to ambient pO_2 . Many invertebrates and some aquatic vertebrates are **metabolic conformers**; a typical example is the pycnogonid crustacean *Decolopoda*. Some animals have responses intermediate to metabolic regulators and metabolic conformers.

Starvation depresses basal metabolic rate in a wide variety of animals (Table 4-8). Absolute metabolic rate (i.e., $ml O_2 hr^{-1}$) often declines dramatically with starvation, but a decline in body mass complicates the analysis of starvation effects. A decline in mass should slightly increase the mass-specific metabolic rate (i.e., $ml O_2 g^{-1} hr^{-1}$), based on the allometry of metabolic rate. However, mass-specific metabolic rate tends to decline during starvation, although not by so much as absolute metabolic rate.

Short-term starvation can markedly reduce many avenues of energy expenditure, such as activity and food processing, and may reduce the standard/basal metabolic rate. In the white rat, for example, 24 hr starvation reduces total daily metabolic rate by 10%; there is a 12% increase in nonfeeding activity, an 87% decline in metabolic energy expended on feeding, and an 8% reduction in basal metabolic rate (Morrison 1968). Prolonged starvation results in a greater depression of basal metabolic rate in rats (Westerterp 1978). The badger has a reduced metabolism when starved, due to diminished activity, reduced food processing, and lowered maintenance

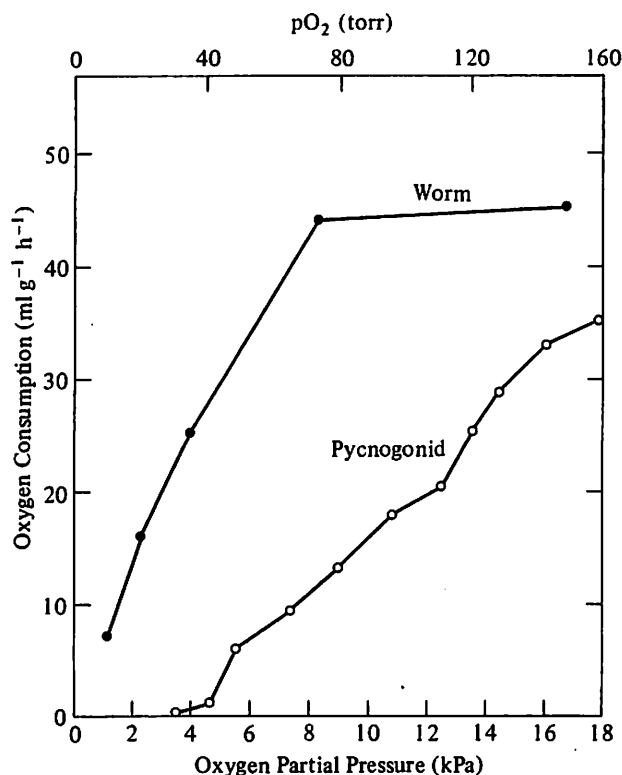


FIGURE 4-14 Relationship between oxygen consumption rate and ambient pO_2 for metabolic conformers and metabolic regulators. The pycnogonid (*Decolopoda*) is a typical metabolic conformer whose resting oxygen consumption rate depends on ambient pO_2 from 0 to 21.3 kPa; there is no critical pO_2 . The earthworm (*Lumbricus*) is a typical metabolic regulator whose resting oxygen consumption rate is independent of ambient pO_2 at high values (10.6 to 21.3 kPa) but not at lower pO_2 's; the critical pO_2 is about 10.6 kPa. (Earthworm data from Johnson 1942; pycnogonid data from Davenport et al. 1987.)

costs (Figure 4-15). A fraction of the decrease in basal metabolic rate during starvation can be attributed to a lower body temperature and its effect on metabolic rate; this is significant to the basal energy savings of starving rats and badgers.

Animals that consume food of low nutritive value or widely spaced and scarce food items may be regarded, in a sense, as experiencing chronic "partial starvation." For example, many spiders are "sit-and-wait" predators and therefore prone to extended periods between meals; spiders have a lower metabolic rate than is expected (Anderson 1970). There is a general relationship for mammals between diet and the allometry of metabolic rate. Frugivorous bats have higher basal metabolic rates than insectivorous bats; blood- or nectar-feeding bats have intermediate metabolic rates (McNab 1983). The insectivorous bats are probably more influenced by seasonal abundance of their food than fruit-eating bats.

Temperature

Body temperature has a marked effect on metabolic rate, just as temperature affects chemical and biochemical reaction rates. In general, there is an exponential relationship between metabolic rate and temperature, with a 2 to 3 \times increase in VO_2 per $10^\circ C$ increase in body temperature, i.e. the Q_{10} is 2 to 3.

Ambient temperature has a profound effect on the standard metabolic rate of ectotherms because their body temperature is often the same as ambient temperature. Typical examples of the relationship between metabolic rate and body temperature are illustrated in Figure 4-16A for a variety of ectotherms. The VO_2 does not rise as rapidly, and may even decline, at high ambient temperatures,

TABLE 4-8

Species	Absolute Metabolism			Mass-Specific Metabolism		
	Normal	Starved	N/S	Normal	Starved	N/S
Spider	0.002	0.001	0.35	0.21	0.08	0.41
Mussel	0.03	0.019	0.63	0.021	0.024	1.14
Spider	0.057	0.021	0.37	0.061	0.026	0.43
Sparrow	58	32	0.56	2.14	1.5	0.7
Sand rat	70	50	0.65	0.33	0.27	0.81
Rat	162	67	0.41	0.56	0.35	0.62
Badger	244	136	0.56	0.03	0.02	0.73
Goose	984	577	0.59	0.53	0.37	0.70
Human	6347	4414	0.79	0.1	0.09	0.85

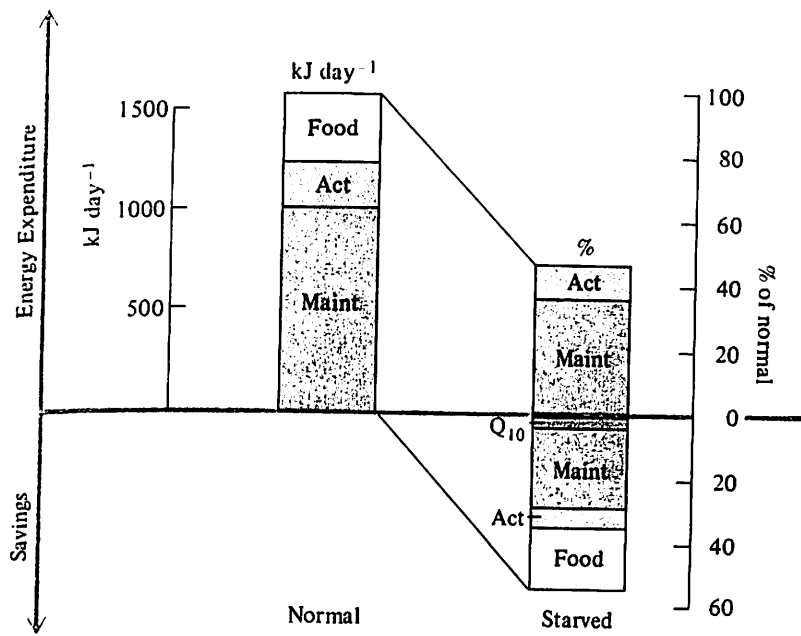


FIGURE 4-15 Effects of starvation on metabolic rate (kJ day^{-1}) and the partitioning of metabolic rate between food acquisition (Food), activity (Act), and maintenance (Maint) for a badger (starved for 30 days). The percentage decline in metabolic rate is primarily due to reduced maintenance metabolism, part of which reflects the reduced body temperature (Q_{10}). (Data from Harlow 1981.)

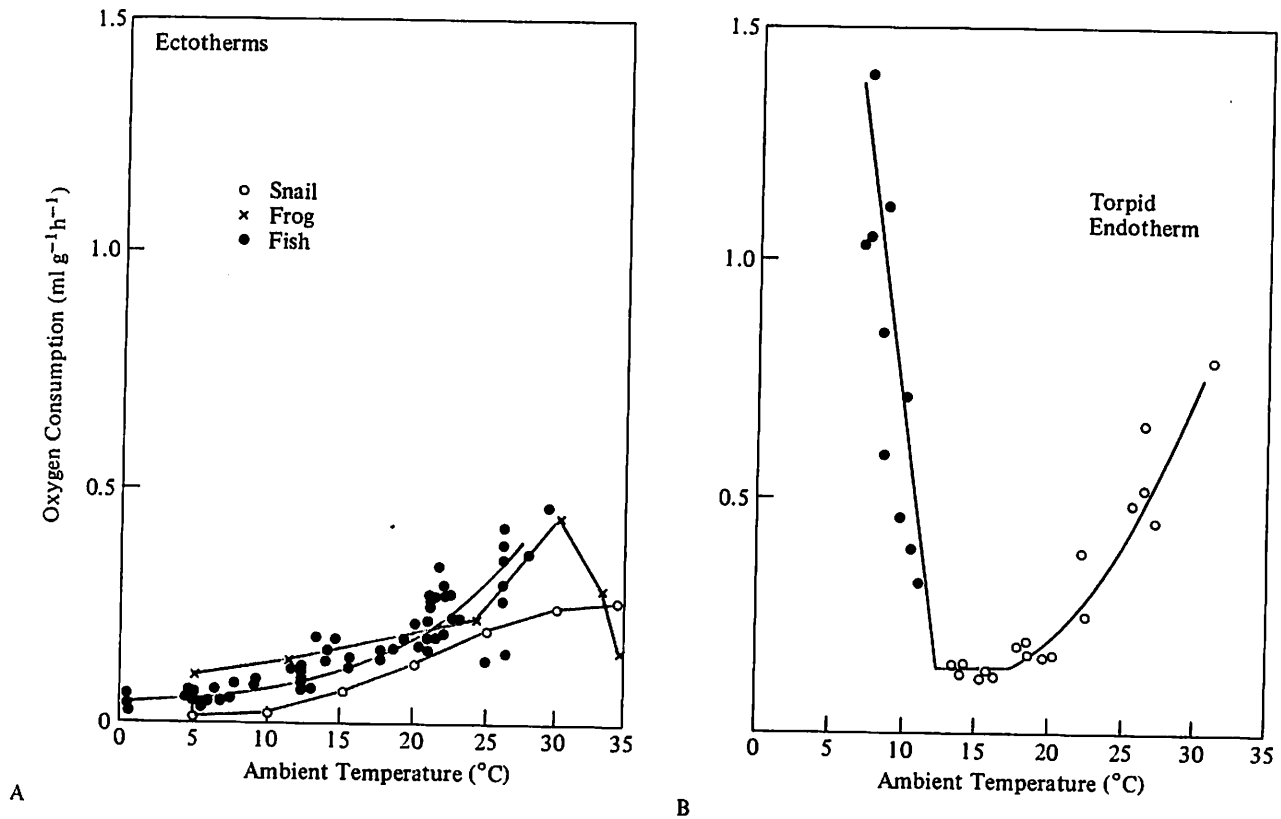


FIGURE 4-16 (A) Exponential relationship between metabolic rate and ambient temperature (body temperature) for ectotherms (snails, frog, and fish). The metabolic rate plateaus or even declines at high ambient temperatures, indicating thermal inhibition of metabolism. **(B)** There is a complex relationship between metabolic rate and ambient temperature for an endotherm, such as the marsupial mouse *Antechinomys*, when torpid. There is an exponential relationship between metabolic rate and ambient temperature, except at ambient temperatures less than about 10°C , when the marsupial mouse thermoregulates to prevent body temperature from dropping below 10°C . (Snail data from Santos, Penteado, and Mendes 1987; frog data from Jusiak and Poczopko 1972; fish data from Haugaard and Irving 1943; marsupial mouse data from Geiser, 1986.)

indicating thermal inhibition of metabolism by enzyme inactivation.

The metabolic rate of endotherms is also dependent on body temperature, but this effect is generally obscured by their precise regulation of body temperature. However, many endothermic mammals and birds hibernate, estivate, or become torpid (see Chapter 5) and then the exponential effect of body temperature on metabolic rate becomes apparent (Figure 4-16B). The metabolic rate of a hibernating mammal, corrected to a body temperature of 10° C, is 3.09 g^{0.69} J hr⁻¹, which is about 50 × lower than the metabolic rate of mammals at 37° C (157 g^{0.62} J

hr⁻¹; Malan 1986). The metabolic rate of a large hibernating endotherm is similar to that expected for an ectotherm, but small hibernating mammals have a higher metabolic rate than expected for an ectotherm.

The taxonomic differences in the basal metabolic rates of animals are partly due to differences in body temperature (Table 4-9). For example, the differences in basal VO₂ for the platypus, marsupials, primitive insectivorous mammals, "general" mammals, and nonpasserine birds are reduced when corrected to a body temperature of 38° C, i.e., the corrected metabolic rate is 3 to 4 watts kg^{-0.75}. However, the substantial differences in basal metabolic rates of other endotherms, e.g., shrews and passerine birds (which have high VO₂'s) and the monotremes and ratite birds (which have a low VO₂) are not eliminated by correction to a body temperature of 38° C. Reptiles and amphibians have substantially lower standard VO₂ values at, or when extrapolated to, body temperatures of 38° C (0.3 to 1.1 watts kg^{-0.75}).

TABLE 4-9

Basal and standard metabolic rates of ectothermic and endothermic vertebrates, measured at their body temperature and corrected to a body temperature of 38° C. All values are expressed as watts kg ^{-0.75} . A Q ₁₀ of 2.5 was assumed for temperature correction unless a different Q ₁₀ was cited in the original reference.			
	Normal T _b (°C)	Normal Metabolic Rate	Metabolic Rate at (38° C)
Mammals			
Monotreme <i>Zaglossus</i>	32	0.86	1.53
Monotreme <i>Tachyglossus</i>	32	0.98	1.81
Edentates	33	1.69	2.66
Marsupials	35	2.37	3.00
General	38	3.34	3.34
Primitive insectivores	35	2.76	3.63
Golden mole	35	2.86	3.76
Monotreme			
<i>Ornithorhynchus</i>	32	2.21	3.80
Crocidurine shrews	36	6.7	8.0
Soricine shrews	38	13.4	13.4
Birds			
Ratites	37	2.10	2.31
Nonpasserines	40	4.05	3.37
Passerines	41	7.40	5.62
Reptiles			
Turtles	20	0.15	0.58
Lizards	30	0.40	1.02
Snakes	30	0.48	1.02
Crocodiles	23	0.29	1.06
Amphibians			
Apoda	25	0.15	0.25
Salamanders	20	0.06	0.33
Lungless salamanders	20	0.07	0.36
Anurans	20	0.21	1.07

Specific Dynamic Effect

Lavoisier found that the metabolic rate of a human subject was increased after a meal to about 150% of their fasting metabolic rate. He explained this increase as the "work of digestion." Many different terms have been subsequently used to describe the observed increase in metabolic rate as a consequence of a meal. "Work of digestion" is unsuitable because it implies an incorrect digestive origin for the metabolic increase (as we shall see below). The term **specific dynamic effect (SDE)** was used by Rubner; the similar term specific dynamic action (SDA) is a poor translation of his original German term "spezifisch-dynamische Wirkung." Numerous other terms also have been used, e.g., heat of nutrient metabolism, postprandial thermogenesis, calorigenic effect, and dietary-induced thermogenesis.

The specific dynamic effect is of varying magnitude for a wide variety of animals. Rubner's classical studies indicated that the fasting metabolic rate of a dog (about 3105 kJ day⁻¹) was increased by 1272 kJ (41%) after ingestion of 2 kg meat. The magnitude of the SDE accounted for 15.8% of the metabolic energy content of the ingested meat. For man, the SDE is often a 30% increase in metabolic rate after a meal, which is sustained for a few hours. Fish (plaice) have a twofold increase in metabolic rate for 1 to 3 days after feeding (Figure 4-17). In many instances, the magnitude of a SDE is greatest for a high protein meal, and is often proportional to the

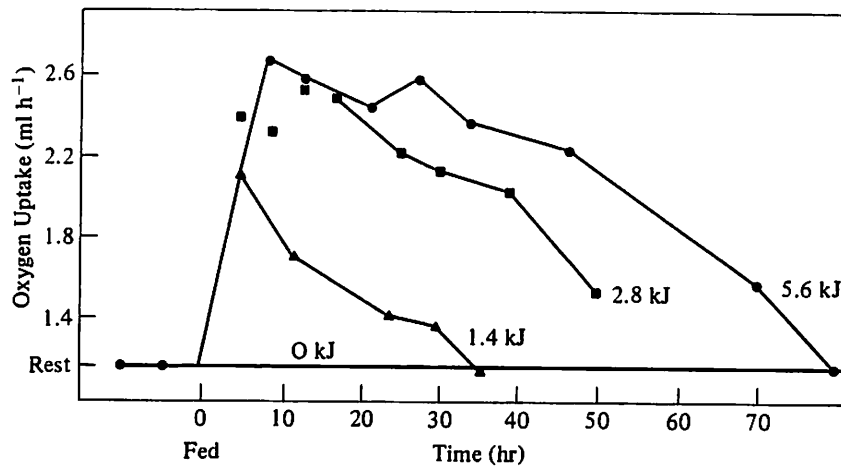


FIGURE 4-17 Specific dynamic effect of three levels of energy consumption by the plaice. Numbers indicate the energy content of the meal. (From Jobling and Davis 1980.)

amount of protein ingested. Many invertebrates have an SDE. In general, the SDE is proportional to the amount of food ingested, as seen for the plaice. An SDE of 494 J per mmol N ingested (about 35 kJ g N⁻¹) has been reported for frogs. Many factors contribute to the wide range of observed SDE values, including whether a fasting or maintenance ratio is used as the baseline metabolic state, how much of the additional nutrient is metabolized or stored, the ambient temperature, etc.

The history of the study of the “work of digestion” has been long and complex, and there still is not a universally accepted explanation for its mechanism. This probably is because there is not a single explanation for this complex phenomenon. Original notions regarding the “work of digestion” were that SDE represented mastication, muscle movements for food transport through the gut, the cost of secretion of digestive fluids and enzymes, and the metabolic cost of active nutrient absorption from the gut. However, the lack of a metabolic effect of feeding bones to dogs and the increase in metabolic rate after injection of amino acids into the blood stream argue against this “work of digestion” theory. The “plethora” theory advocates a generalized metabolic stimulation after a meal by the presence of high concentrations of metabolites; similar theories advocate a metabolic stimulation by specific nutrients. The metabolic basis for SDE has also been attributed to a surge of metabolic synthesis, particularly protein synthesis, after a meal and to the metabolic cost of amino acid deamination. Ruminant and pseudoruminant mammals may also have a

significant component of SDE due to the “microbial fermentative costs of digestion” (see Chapter 18).

The metabolic cost of SDE can be separated into a mechanical component that is due to physical processing and movement of food through the digestive tract, anabolic and catabolic biochemical processes, and metabolic pathways for nitrogen excretion. The mechanical component of SDE has been estimated for fish to be from 10 to 30% of the total SDE, depending on the meal size (Tandler and Beamish 1979). The energy released by hydrolysis of glucosidic bonds (about 14 to 18 kJ mole⁻¹), peptide bonds (10 to 24), and ester bonds (10) is so low (about 1/2%) compared to the chemical energy content of foodstuffs that SDE does not reflect the costs of hydrolysis or resynthesis of macromolecular bonds. The possible contribution of the biochemical costs of nitrogen excretion to SDE merit detailed examination.

Early studies indicated that the SDE for dogs was about 31% of resting metabolism for meat, 13% for lipid, and 6% for carbohydrate (Brody 1945). The SDE was also reported to be proportional to the amount of nitrogenous waste excreted. For example, the urinary nitrogen excretion of dogs closely parallels the SDE (Figure 4-18) and indicates a conversion factor of about 46 J g N⁻¹ between SDE and urinary N excretion. The SDE component of the increased metabolism of mussels after feeding corresponds to the observed rate of nitrogen excretion; the conversion factor is about 94 kJ g N⁻¹ (Bayne and Scullard 1977). The metabolism of alanine provides a typical example of the energy

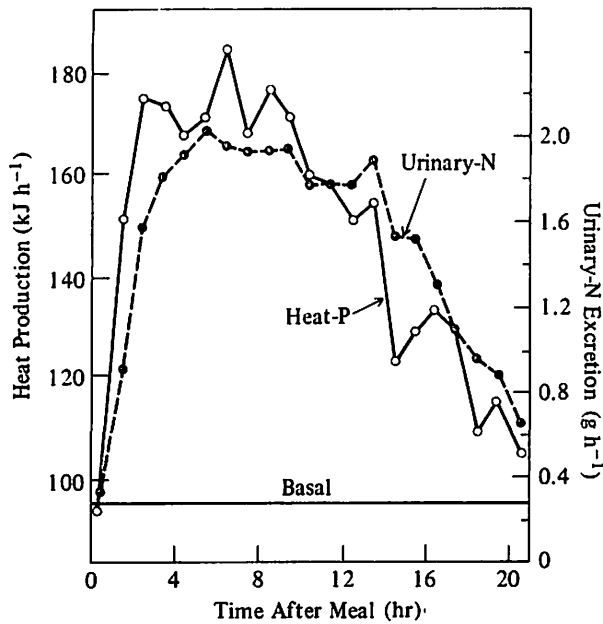


FIGURE 4-18 Relationship between increment in metabolic rate (kJ hr^{-1}) and urinary nitrogen excretion (g N hr^{-1}) for a fasting dog after being fed 1200 g meat. (Modified from Brody 1945.)

requirements for amino acid metabolism. The overall reaction



yields about $17 \text{ kJ heat g N}^{-1}$. The conversion of NH_3 to urea releases about 17 kJ g N^{-1} , and the renal excretion of urea releases perhaps a further 4 to 8 kJ g N^{-1} . The total energy released by deamination and urea excretion is therefore about $40 \text{ kJ heat g N}^{-1}$. About 126 kJ of potentially useful energy is yielded by oxidation of the deaminized alanine fragment. Thus, heat equivalent to about 28% of the energy content of alanine is liberated by deamination and urea excretion.

The metabolic expenditure due to SDE may be of no value to the metabolic processes of animals, but the energy of SDE may be of physiological consequence to endotherms. The magnitude of SDE appears to depend on the ambient temperature; the fasting rate of heat production increases by 50% for dogs after feeding at an ambient temperature of 30°C but does not increase at 7°C . This is because the heat production of SDE substitutes for the thermoregulatory increase in metabolic heat production of a cold-stressed endotherm. The magnitude of SDE appears to decline at ambient temperature

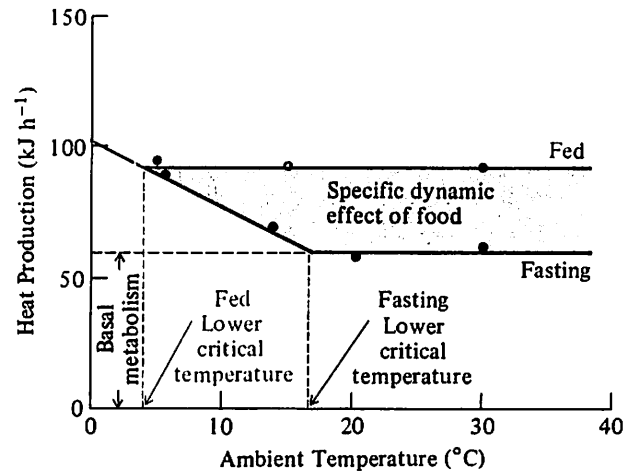


FIGURE 4-19 Schematic diagram of the increment in metabolic heat production for fasting dogs and for dogs fed 320 g meat, showing the substitution by heat of specific dynamic effect for thermoregulatory heat production. There appears to be no specific dynamic effect at low ambient temperatures. (Data from Rubner 1902.)

below the critical thermal minimum temperature and is absent when SDE equals or is less than the thermogenic heat requirement (Figure 4-19; see Chapter 5).

In summary, SDE reflects the energetic requirements of many processes that occur as a consequence of food digestion, including mechanical processing, energy exchange through catabolic and anabolic biochemical pathways, and amino acid deamination and nitrogen excretion.

Activity

Activity is probably the most important determinant of metabolic rate for an animal. There is a continuum of activity levels from none to maximal (or summit) and the level of activity determines the elevation of metabolic rate above the basal value.

The metabolic cost of graded activity has been most thoroughly documented for humans; a typical range of metabolic rates from minimal values to maximal values is summarized in Table 4-10. Similarly detailed compilations are not possible for animals, but one commonly measured metabolic rate is the rate during maximal activity or cold stress. The maximal metabolic rate sustained by aerobic metabolism is generally about 5 to $10 \times$ the resting, basal, or standard metabolic rate. The

TABLE 4-10

Human basal metabolic rate and metabolic rate with various forms of graded activity. Values are J min^{-1} . (Data from Passmore and Durnin 1955.)	
Basal	4.2
Lying at ease	6.3
Sitting at ease	6.7
Standing at ease	7.1
Walking: 1 km hr ⁻¹	8.4
Driving car	11.7
Walking: 4 km hr ⁻¹	14.2
Walking: 6 km hr ⁻¹	20.9
Cricket batting	25.1
Walking: + 15% incline/3 km hr ⁻¹	26.4
Tennis	29.7
Walking: 8 km hr ⁻¹	33.5
Rapid marching	40.6
Squash	42.7
Climbing vertical ladder	48.1
Walking in loose snow: 20 kg load	84.5
Ax work: 51 blows min ⁻¹	100.9
Carrying 60 kg upstairs	128.4

ratio $\text{VO}_{2,\text{max}}/\text{VO}_{2,\text{basal}}$ is the **factorial aerobic scope**, whereas $\text{VO}_{2,\text{max}} - \text{VO}_{2,\text{basal}}$ is the **absolute aerobic scope**.

The maximal metabolic rate of small mammals (<4 kg) is proportional to $\text{mass}^{0.72}$ with an intercept value (at 1 gram) of 602 J hr^{-1} ; this is $8.3 \times$ the intercept for basal metabolic rate of 72.6 J hr^{-1} (Lechner 1978). Larger mammals, dogs, humans, and horses appear to have higher maximal rates ($\text{VO}_{2,\text{max}} = 789 \text{ mass}^{0.79}$) and high factorial scopes of $11.5 \times$ basal (Pasquis, Lacaille, and Dejours 1970). Wild and domesticated mammals appear to have slightly different scaling relationships for $\text{VO}_{2,\text{max}}$ (Taylor et al. 1981). Dasyurid marsupials have a factorial scope of $8.7 \times$ basal despite their lower basal VO_2 of $2.45 \text{ ml O}_2 \text{ hr}^{-1} \text{ mass}^{-0.82}$ and lower $\text{VO}_{2,\text{max}}$ of $21.2 \text{ ml O}_2 \text{ hr}^{-1} \text{ mass}^{-0.95}$ (MacMillen and Nelson 1969; Baudinette, Nagle, and Scott 1976).

Factorial metabolic scopes during activity for other animals are generally of similar magnitude, about 5 to 10. Anuran amphibians demonstrate similar metabolic scopes for activity, even with a single species, over a wide range of body masses; *Bufo boreas* ranging in mass from 1 to 69 g have almost parallel allometric relationships for resting VO_2 , with an almost constant factorial scope of $10 \times$ (Figure 4-20).

Insects and crustaceans have aerobic scopes for walking and running that are similar to vertebrates.

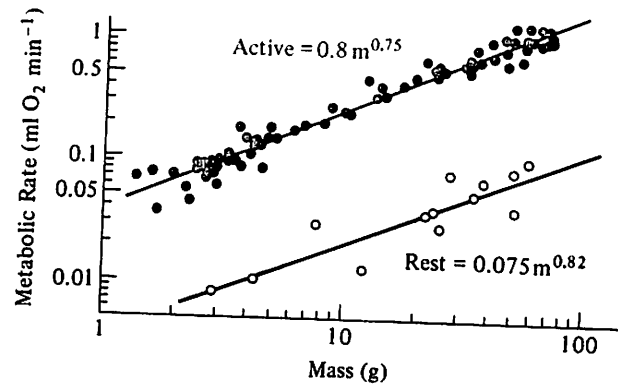


FIGURE 4-20 Relationship between metabolic rate (MR; ml min^{-1}) for the toad *Bufo boreas* at rest and during activity. (From Hillman and Withers 1979.)

For example, beetles have a factorial scope ranging from 8.0 times (0.1 g) to 33.3 times (10 g) due to a differing allometric relationship for resting VO_2 ($\text{ml O}_2 \text{ hr}^{-1} = 0.23 \text{ mass}^{0.86}$) and active VO_2 ($37.6 \text{ mass}^{1.17}$; Bartholomew and Casey 1977). This size dependence of factorial scope is due to the larger beetles having higher body temperatures than the smaller beetles. Cockroaches, tarantula spiders, and land crabs have aerobic scopes of two to ten times resting during locomotion (Herreid 1981; Full 1987).

Flying insects have much larger factorial metabolic scopes than other animals because of the high metabolic cost of flight, particularly hovering (Figure 4-21). Hovering honeybees have a factorial



FIGURE 4-21 A hovering honeybee has an extremely high metabolic cost. (Photograph courtesy of C. Ellington and A. R. Thomas.)

scope of up to $40 \times$ rest ($VO_{2, \text{hov}} = 120 \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$; $VO_{2, \text{rest}} = 3 \text{ ml O}_2 \text{ g}^{-1} \text{ hr}^{-1}$). An elevation of body temperature during hovering is not a major contributing factor to this high factorial scope (Withers 1981). Hovering sphingid moths have a $172 \times$ increase in VO_2 over rest, but part of this immense factorial scope is due to a substantial elevation of thoracic temperature from 23° to 42° C (Bartholomew and Casey 1978). The factorial scope is still high, about $29 \times$ rest when $VO_{2, \text{rest}}$ is corrected to 42° C assuming a Q_{10} of 2.5. Similar scopes for saturniid moths are $127 \times$ total factorial scope, and 29 times when resting VO_2 is corrected to the same thoracic temperature as hovering moths. These factorial scopes are not necessarily the maximal values, since hovering VO_2 is probably not the maximal rate.

Free-Living Metabolism

One aspect of animal metabolism that has proven very difficult to measure is the average daily metabolic rate of animals under natural conditions, i.e., **field metabolism**. However, the measurement of isotopic turnover of doubly labelled water has recently allowed the determination of field metabolic rate for many animals, primarily terrestrial vertebrates.

The field metabolic rate of terrestrial vertebrates is typically two to three times the basal metabolic rate (of endotherms) or standard metabolic rate (of ectotherms at the appropriate body temperature). Field metabolic rate (FMR) often scales with body mass in a similar fashion as BMR or SMR. For example, the *b* value for FMR (0.749) is similar to *b* for BMR of nonpasserine birds (Nagy 1987). However, the allometric relationships are not always similar; for example, the *b* value for FMR is greater than that for BMR in placental mammals and passerine birds, and *b* is less for FMR than BMR in marsupial mammals. Because of variation in *b* the intercept *a* values are not necessarily two to three times higher for FMR than BMR. The ratio of *a* for FMR/BMR varies from 1.2 (nonpasserine birds), 1.8 (passerine birds), and 1.9 (placentals) to 10.3 (marsupials). For iguanid lizards, field and standard values for *b* are virtually the same, and $FMR = 9.3 M^{0.799}$ and $SMR = 1.5M^{0.80}$ (at 20° C). The high ratio of *a* for FMR/SMR of 6.2 is due in part to field body temperature exceeding 20° C . The expected difference in *a* for ectotherms and endotherms is also apparent for FMR. For example, the ratio of *a* for eutherian mammals to iguanids is 15.1, and for passerine birds to iguanids the ratio is 39.8.

Anaerobic Metabolism

The biochemical details of anaerobic metabolism were discussed in Chapter 3, but the energetic significance of anaerobic metabolism to animal energetics will be discussed here.

Invertebrates

The resting metabolic rate of many bivalve mollusks is only partly supported by aerobic metabolism (Table 4-11). The ratio of aerobic heat production (Q_{ox}) to total heat production (Q_{tot}) varies from 0.5 to 0.7 for many pelycopods but is about 1 for *Mya* and many other marine invertebrates.

Metabolic responses to environmental anoxia are well documented for intertidal mollusks (de Zwaan 1983; Schick, de Zwaan, and de Bont 1983; Livingston and de Zwaan 1983; de Zwaan and van den Thillart 1985; de Zwaan and Putzer 1985). For

TABLE 4-11

	HEAT PRODUCTION ($\text{J g}^{-1} \text{ h}^{-1}$)		
	Aerobic (Q_{ox}) ¹	Total (Q_{tot})	Ratio Q_{ox}/Q_{tot}
Pelecypods			
<i>Mytilus</i>	1.18	1.59	0.74
<i>Crassostrea</i>	7.26	14.03	0.54
<i>Mya</i>	1.85	1.90	0.97
<i>Mercenaria</i>	0.66	1.02	0.65
<i>Modiolus</i>	1.39	2.10	0.66
<i>Petricola</i>	3.13	5.15	0.61
Gastropods			
<i>Littorina</i>	1.75	1.65	1.08
<i>Nucella</i>	2.77	2.74	1.01
<i>Biomphalaria</i>	3.16	2.66	1.19
Oligochetes			
<i>Lumbricus</i>	3.20	3.10	1.03
Crustaceans			
<i>Libinia</i>	1.18	1.24	0.95
<i>Asellus</i>	2.45	2.23	1.10
Echinoderms			
<i>Asterias</i>	1.28	1.25	1.02

¹ Assuming 1 ml O_2 is equivalent to 20.1 kJ.