

Structural and Functional Determinates of Metabolic Rate¹

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SYNOPSIS. Standard metabolic rates are principally determined by relatively few factors: temperature, mass, and phylogenetic affinities. 1) Temperature. Body temperature has pervasive effects on biological processes through the influence of temperature on the activity of metabolically important enzymes: metabolic rates double or triple when body temperature increases 10°C. The absolute levels of metabolism that any temperature establishes may be subject to acclimatory or evolutionary change by alteration of enzyme composition or structure. In endotherms, the effects of this basic thermal dependence may be overcome by the physiological regulation of body temperature, but such regulation is very energetically expensive. 2) Body mass. Metabolic rate scales interspecifically with body mass^{0.75}. We understand to a degree how animals are structured to produce this observed allometric dependence of metabolism on mass, principally by quantitative differences in cellular metabolism that can be attributed to differential mitochondrial content. But we do not understand why animals are so structured or what exactly is the reason for this particular mass exponent. 3) Phylogeny. Metabolic level varies among taxa, and the phylogenetic history and relative associations of an animal are important determinates of energy expenditure. Mammals and birds have substantially greater metabolic rates than do ectothermic vertebrates, even at common body temperatures. However, even within vertebrate classes, metabolic level varies among orders. The principle of symmorphosis has been proposed to describe the structural consequences of functional design and the morphogenetic response of biological systems to functional need.

INTRODUCTION: METABOLIC RATE

Metabolic rate is the pace at which energy is utilized by an organism. It is the integration of all catabolic energy transformations within the body and is an expression of the intensity and speed of life itself. Metabolism has been called the fire of life (Kleiber, 1961), and metabolic rate is the measure of the fuel consumed and heat evolved by that fire. Energetic transformations underlie all biological activities, from the molecular and biochemical level to the ecological, including processes of great evolutionary significance, such as growth and reproduction.

Metabolic rate is increased by a number of different processes of considerable ecological importance, such as physical activity, food processing, and tissue synthesis (Townsend and Calow, 1981). There is, however, a minimal level of metabolism that proceeds even in the absence of external stimulation, work, and growth (Brody, 1945; Kleiber, 1961). It is designated stan-

dard, basal, or maintenance metabolism and accounts for one-third to one-half of total energetic expenditure, even in free-living animals in natural environments (Nagy, 1987). It represents the costs of organismal maintenance, including such factors as protein turnover, ion pumping, blood circulation, and ventilation, although the magnitude of the energetic cost of these individual components is poorly understood. Standard metabolic rates of animals have been the subject of frequent investigation, and this paper will summarize the major generalizations of those studies and examine their morphological and physiological bases. Standard metabolic rates have been found to be highly predictable with relatively few factors, namely temperature, body mass, and phylogeny. Other variables, such as time of day or year (Aschoff and Pohl, 1970), also may influence metabolic rate to a lesser degree, but these three are the main determinates of the level of maintenance metabolism that will be discussed here. Some organisms may temporarily decrease metabolism below these levels or even enter ametabolic states in response to unfavorable environmental conditions (Hochachka and Guppy, 1987). However, they are not fully functional

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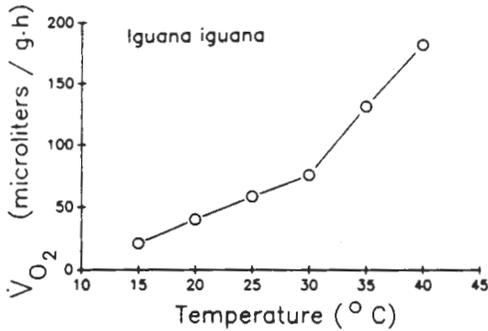


FIG. 1. Oxygen consumption by the lizard *Iguana iguana* at different body temperatures (data from Moberly, 1968).

organisms under these conditions and must return to normal metabolic levels to proceed with normal processes of life.

TEMPERATURE

Body temperature has pervasive effects on biological processes, greatly accelerating reaction rates with increasing temperature (Cossins and Bowler, 1987). An example of the thermal dependence of standard metabolic rate is given in Figure 1: in the lizard *Iguana iguana*, maintenance costs are over 700% greater at 40°C than at 15°C. This strong thermal effect cannot be accounted for on the basis of changes in mean kinetic energy of the system, which increases only 9% over this range. The theoretical basis of the strong thermal dependence of biological reaction rates was explained by Arrhenius (1915). He formulated the concept of activation energy, an absolute, high level of kinetic energy required for molecules to react to form products. Because the distribution of kinetic energy in a population of molecules is positively skewed, even minor shifts in mean kinetic energy due to increased temperature greatly increase the population of molecules exceeding activation energy. Commonly, reaction rates, including metabolic rates, double or triple when body temperature increases 10°C. This thermal dependence is expressed as the temperature coefficient or Q_{10} , defined as

$$Q_{10} = (R_2/R_1)^{10/(T_2-T_1)}$$

where R_2 is the rate at T_2 , R_1 is the rate at

T_1 , and $T_2 > T_1$. Q_{10} values for metabolic rate in *Iguana* (Fig. 1) are approximately 2.3 and are typical for most animals.

Variability in body temperature and thermoregulatory response varies greatly throughout the animal kingdom, and metabolic response varies with it. Most animals are poikilothermic, conforming to the temperature of their environment and changing body temperature with it. Some groups are homeothermic and maintain a relatively constant body temperature. The magnitude of metabolic rate determines whether it will be a significant factor in the establishment of body temperature. In ectothermic animals, metabolic heat production is so low in comparison to environmental heat flux that the latter predominates in thermoregulation. High body temperatures and thermal constancy may be obtained in ectotherms by the behavioral selection of appropriate microclimates, but it is still the environmental thermal conditions that determine body temperature. In endothermic animals, metabolic rate is high and is adjusted to establish body temperature. Endothermy and associated high metabolic capacity have evolved several times in animals (and even in plants, Nagy *et al.*, 1972). It occurs in many insect groups (Heinrich, 1981), tunas and some sharks (Carey *et al.*, 1971), and some snakes (Hutchison *et al.*, 1966). In all these animals, endothermy is myogenic; body temperature is raised by the contraction of skeletal muscle. When muscle activity ceases, body temperature declines to environmental levels and maintenance metabolic rates are indistinguishable from those of closely related but non-endothermic groups. In mammals and birds, however, endothermy is obtained by high metabolic rates in many body organs and continuously high standard metabolic rates. Under basal conditions, skeletal muscle metabolism plays a minor role in thermoregulation: it is used as a heat source only in relatively cold environments.

The maintenance of endothermic homeothermy in mammals and birds reverses the pattern of metabolic rate and environmental temperature seen in ectotherms. As environmental temperatures

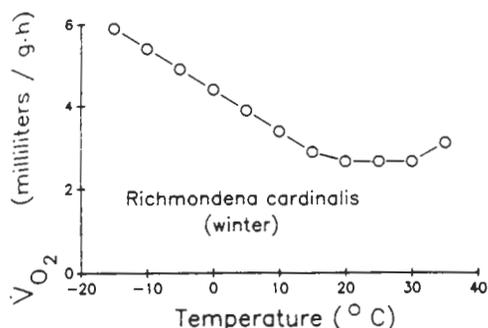


FIG. 2. Oxygen consumption of the cardinal (*Richmondia cardinalis*) during winter at different ambient temperatures (body temperature = 38.5–40°C) (data from Dawson, 1958).

decrease, metabolic rate increases rather than declining. As exemplified by a small bird in Figure 2, body temperature is stabilized by varying metabolic rate. Standard or basal metabolic conditions obtain only over a limited range of environmental temperatures, the zone of thermal neutrality (20 to 30°C in the example). The energetic cost of this sort of endothermy is very high, even in this thermal neutral zone, as will be discussed in the section on phylogenetic influences on metabolic rate. This type of thermoregulatory pattern obscures but does not negate the underlying thermal dependence of the metabolic systems of endotherms. If body temperature does vary, for example, during diurnal cycles in body temperature or in very cold environments where thermoregulatory capacity is overwhelmed, metabolic rates of birds and mammals have Q_{10} values of 2 to 3, as do their ectothermic relatives.

In ectotherms, changes in environmen-

tal temperature directly cause alterations in metabolic rate. This thermal dependence has both disadvantages and advantages for poikilothermic organisms. At low body temperatures, work, synthetic, and energy extraction capacities are greatly curtailed, but so is energy expenditure, resulting in great energetic economy (Pough, 1980). The lizard *Sceloporus occidentalis*, for example, behaviorally maintains body temperature at 35°C while diurnally active and assumes the temperature of its burrow (20°C) while inactive (Table 1) (Bennett and Nagy, 1977). Although 67% of the lizard's day is spent underground, it expends only 17% of its daily energy budget during this time.

During chronic exposure to a new temperature, metabolic rates of some ectothermic animals may be modified and return to their former levels, even as the new thermal regime persists. This process is termed acclimation (or acclimatization, in response to seasonal change), and reflects alterations in the underlying metabolic machinery of the cell. Modifications in enzyme concentration, isozyme composition, or membrane structure may be involved in this response (Hochachka and Somero, 1984). Recovery of original metabolic rate may be complete or only partial (Precht *et al.*, 1973). The result of acclimation is an alteration of the effect of temperature on the animal: at any common temperature, a cold acclimated animal of a species will have a higher metabolic rate than a warm acclimated animal (Fig. 3). Similar shifts in metabolic rate may occur among groups of species that occupy different thermal conditions. Metabolic rates

TABLE 1. A comparison of daily metabolic rates of rodents and lizards.^a

	T _a (°C)	Standard M.R.			Daily field-active M.R. (kJ/dav)
		Day (J/hr)	Night (J/hr)	Daily total ^b (kJ/dav)	
Rodent ^c	38	430	430	10.3	37.0
Lizard ^d	35 day, 20 night	64	16.4	0.77	1.53
Ratio		6.7:1	26:1	13:1	24:1

^a Body mass = 12 g.

^b Based on 8 hr day: 16 hr night.

^c Values from Lechner (1978) (wild mammal eq.) and Nagy (1987) (rodent eq.).

^d Values from Bennett and Nagy (1977) for lizard *Sceloporus occidentalis*.

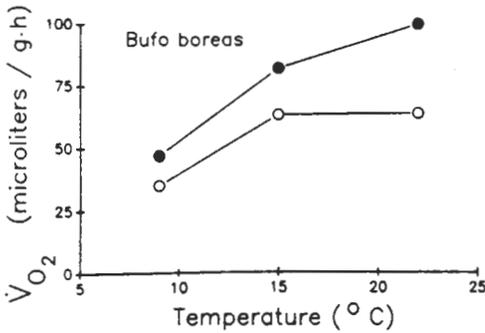


FIG. 3. Oxygen consumption of toads (*Bufo boreas*) acclimated for 15 to 20 days at 9°C (closed circles) and 31°C (open circles) and measured at different body temperatures (data from Bishop and Gordon, 1967).

of fish from temperate environments, for instance, are greater than those of tropical fish and less than those of polar fish, when measured at common body temperatures (Brett and Groves, 1979). Evolutionary changes in enzyme composition may underlie these differences.

Body temperature is thus seen to have a major determining effect on metabolic rate through its influence on enzymatic activity of metabolically important enzymes. Metabolic rate doubles or triples when body temperature increases 10°C. The absolute levels of metabolism that any temperature establishes may be subject to acclimatory or evolutionary change by alteration of enzyme composition or structure. In endotherms, the effects of this basic thermal dependence may be overcome by the physiological regulation of body temperature, but such regulation is very energetically expensive.

MASS

Body size clearly affects metabolic rate: a chihuahua eats and requires much less food than a Saint Bernard and produces much less heat. However, the quantitative relationship between body size and metabolism in animals is by no means straightforward and its nature is poorly understood.

If standard metabolic rates of animals of different body size are plotted as a function of body mass, a non-linear relationship is

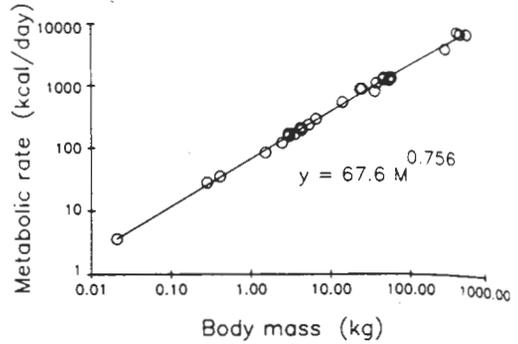


FIG. 4. Basal metabolic rates of representatives of 12 different species of mammals as a function of their body mass (data from Kleiber, 1961).

obtained. If one animal is twice as large as another, its metabolic rate is only 68% greater, not 100%. When such a non-linear association between a structural or functional relationship and body mass occurs, it is termed allometric and is usually best described by the power equation:

$$y = aM^b$$

where M is body mass and a and b are empirically fit constants. If metabolic rates of different species of mammals are fit to this relation, they are very well described with a mass exponent (b) of 0.75 (Fig. 4) (Kleiber, 1961). A similar mass dependence has been found generally throughout the animal kingdom (Hemmingsen, 1960; Schmidt-Nielsen, 1984).

The theoretical grounds for anticipating a mass-dependent exponent of 0.75 are obscure. One might expect a value of 1.00, in which case every increment in mass would be accompanied by a proportional increment in metabolic rate. On the other hand, one might expect that surface area rather than mass would determine metabolic rate (e.g., Heusner, 1982), as surface is important for the importation and exportation of materials and products of metabolism. Surface area scales to volume of an object with an exponent of 0.67, and this would be the anticipated relationship between metabolic rate and mass if surface area were the controlling variable. Intra-specifically, a diversity of mass-dependent exponents have been found, including some

equal to 0.67 and 1.00; however, interspecific comparisons have almost universally resulted in values approximating 0.75, significantly different from either of the former values. No convincing explanation has yet been advanced for this relationship. Hemmingsen (1960) considers it a compromise between mass and surface area factors but offers no consideration for why it should be set at this level. McMahon (1973) develops a theoretical argument for its dependence on muscle power output, but standard metabolic levels are not related to muscle activity.

Although we may not understand why animals are built with metabolic rates of this mass dependence, we do understand some aspects of how they are built with this attending result. The metabolic power exponent of 0.75 partially results from differential composition of inert structural material in larger animals. Structural support does scale allometrically; larger animals have relatively more support material than smaller ones. Bone is metabolically inert, and thus increments in size add disproportionate amounts of metabolically inert material and depress metabolic rate below that of strict mass dependence ($b = 1.00$). However, this effect is relatively small (b of skeletal mass on body mass = 1.08, Prange *et al.*, 1979) and cannot account for the magnitude of the observed mass dependence. Division of metabolic rate by mass suggests that each unit of mass from a smaller animal metabolizes more intensely than that derived from a larger animal. The implication is that mass-dependent effects reside at the cellular level and that cells of small animals are quantitatively different from those of large animals. Such differences do exist. Per gram metabolic rates of isolated tissues show significant inverse dependence on organismal mass (Fig. 5) (Krebs, 1950): cells from mice have higher metabolic rates than those from dogs or other larger animals. This differential is the result of greater concentrations of mitochondria, the machinery of aerobic metabolism, within the cells of smaller animals; both mitochondrial volume density and relative surface area are higher (Table 2) (Smith, 1956; Mathieu *et*

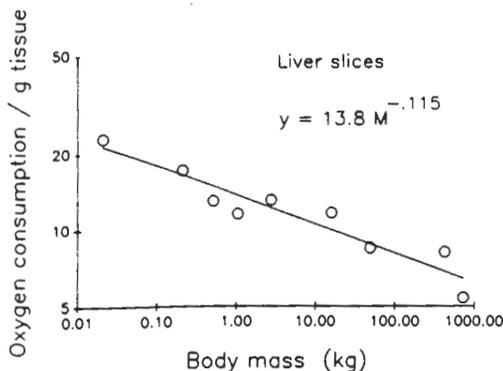


FIG. 5. Oxygen consumption (unspecified units per g tissue) of liver slices from nine different species of mammals as a function of body mass (data from Krebs, 1950).

al., 1981; Else and Hulbert, 1985). Thus, the allometric dependence of metabolic rate on mass resides in the structural and functional organization of the cells themselves.

The allometric dependence of metabolic rate on mass has pervasive consequences for many aspects of physiological and ecological function (Calder, 1984). For example, all rate processes affecting oxygen uptake and transport must be structured to take this dependence into account. In ventilation, oxygen transferred to the blood (and ultimately consumed) is the product of ventilation frequency, tidal volume, and percentage oxygen extraction. Tidal volume scales isometrically with body mass ($b = 1.00$) and percentage oxygen extraction is mass independent ($b = 0$); if oxygen consumption scales with $b = 0.75$, ventilation frequency must decline with $b = -0.25$. Larger animals must therefore breathe less frequently than smaller ones. Similar considerations apply to blood circulation, and consequently rate of heart beat is lower in larger animals. Because energy demand is not linearly dependent on mass, many ecological factors also vary allometrically, including volumes and rates of food consumption, home range size, growth rates, and reproductive outputs (Peters, 1983). Allometry of physiological and ecological factors is currently a very active area of study, but many investigations unfortunately involve only the gen-

TABLE 2. Allometry of mammalian mitochondrial morphology.^{a,b}

	Liver	Kidney	Cardiac muscle	Skeletal muscle
Mitochondrial volume density (% cell)	11.2M ^{-0.13}	14.4M ^{-0.14}	22.7M ^{-0.09}	4.4M ^{-0.09}
Mitochondrial membrane surface area (m ² /cm ³ tissue)	2.17M ^{-0.24}	4.75M ^{-0.22}	11.1M ^{-0.16}	2.53M ^{-0.23}

^a Equations in the form $y = aM^b$, where M is body mass in kg.

^b Data from Else and Hulbert (1985).

eration of allometric equations, rather than an experimental examination of the functional linkages among the variables investigated. Future studies need to be more analytical in uncovering the causes of mass dependence, not in simply describing it.

Metabolic rate scales with body mass^{0.75}. We understand to a degree how animals are structured to produce this observed allometric dependence of metabolism on mass, principally by quantitative differences in cellular metabolism that can be attributed to differential mitochondrial content. But we do not understand why animals are so structured or what exactly is the reason for this particular mass exponent.

PHYLOGENY

Metabolic level varies among taxa, and the phylogenetic history and relative associations of an animal are important determinants of energy expenditure.

Differences in metabolic rates are apparent even within classes of vertebrates. In birds, considerable diversity is apparent among orders (Table 3). Perching birds (Passeriformes) have metabolic rates 50 to 60% greater than those of other avian groups of similar body mass (Lasiewski and Dawson, 1967; Aschoff and Pohl, 1970). Even among the "non-passerine" group, some orders have lower metabolic rates (e.g., hawks and owls) and some higher (e.g., ducks and herons) (Zar, 1969). The functional basis of these differences is largely unknown: passerines have slightly higher body temperatures than other birds but this effect alone cannot account for the observed metabolic differential.

Considerable metabolic diversity is apparent among the subclasses of mammals, with monotremes and marsupials

having substantially lower metabolic rates than "advanced" eutherians (Table 4). These differences were originally taken as evidence of less developed metabolic systems in these so-called "primitive mammals" (Sutherland, 1897; Martin, 1903). However, these animals and some other groups of eutherians regulate body temperature at substantially lower levels than do most other mammals. Temperature effects apparently account for much of the diversity in metabolic rate among these groups (Table 4). Monotremes and marsupials are no longer viewed as having inferior or incompletely developed metabolic capacities, but simply lower thermoregulatory setpoints (Dawson and Hulbert, 1970).

Within certain taxa, clines in metabolic rate are apparent over environmental gradients. In both pigeons and heteromyid rodents, for instance, desert-dwelling species have lower basal metabolic rates than do more mesic forms (Dawson and Bennett, 1973; MacMillen, 1983). The low rates of desert animals are judged to be advantageous by restricting energy demand

TABLE 3. Metabolic rates of different orders of birds.

Order	Common name	Watts/ 1 kg bird	% predicted ^a
Anseriformes	Ducks	4.36	118
Ciconiiformes	Storks and herons	4.63	125
Columbiformes	Doves	3.95	107
Falconiformes	Hawks	2.30	76
Galliformes	Fowl	3.75	102
Passeriformes	Sparrows	5.47	148
Strigiformes	Owls	3.03	82

^a From Zar, 1969.

^b Predicted values are calculated according to Zar's general formula for nonpasserine birds, M.R. in Watts = 3.69M^{0.743}, where M is body mass in kg.

TABLE 4. Standard metabolic rates of mammals.*

	Metabolic rate (Watts/1 kg animal)	% advanced eutherian M.R.	T _b (°C)	M.R. at T _b = 38°C (Watts/1 kg animal)
Monotremes				
Echidnas	0.92	28	31	1.55
Platypus	2.21	66	32	3.45
Marsupials	2.37	71	35	3.00
Eutherians				
Insectivores	2.76	83	35	3.63
Edentates	1.69	51	33	2.66
Advanced eutherian	3.34	100	38	3.34

* From Hulbert (1978).

in environments of low productivity, conserving water, and producing less heat which must be dissipated in warm environments. Because these clines are found among closely related species, the interpretation that they represent specific environmental adaptations is probably secure. Care must be taken, however, not to neglect phylogenetic effects in the interpretation of adaptation (Huey and Bennett, 1986; Huey, 1987). For instance, original observations on metabolic rates of desert-dwelling poor-wills found exceptionally low basal metabolic rates in these caprimulgid birds (Bartholomew *et al.*, 1962). These low metabolic rates were interpreted as adaptations to a desert existence according to the above reasoning. However, subsequent measurements of metabolic rate in other caprimulgids from tropical rainforests found similarly low metabolic values (Lasiewski *et al.*, 1970). Low metabolic rate is apparently a general feature of the physiology of members of the order Caprimulgiformes. Although it may constitute a pre-adaptation to desert existence, it is not a specific adaptation of desert species of this group.

Among the vertebrate classes, indeed, among all groups of the animal kingdom, the largest differential in standard metabolic rates occurs between the mammals and birds on one hand and the ectothermic vertebrates on the other. These classes of endothermic animals were independently derived from reptiles. They attained metabolic levels that are very similar to each other and approximately six- to tenfold

greater than those of extant reptilian groups, even when body temperatures are equal (Bennett and Dawson, 1976). This greater level of maintenance metabolism is the source of heat for endothermic body temperature regulation. It is extraordinarily energetically expensive. Because high body temperature is maintained throughout the day in endotherms, the real metabolic differential between field active reptiles and birds or mammals is even greater, approximately 15- to 20-fold (Table 1) (Nagy, 1987). These differentials have profound consequences for the ecology of these groups. The amount of food required daily by a mammal can provision a reptile of equal size for nearly a month, or a given level of prey productivity could sustain many more reptiles than mammals in a community.

The selective features that occasioned the evolution of endothermy in mammals and birds are controversial and unresolved (*e.g.*, Heinrich, 1977; Crompton *et al.*, 1978; Bennett and Ruben, 1979). The structural and functional bases of its evolution are more clear. There has been an extensive reorganization of all systems involved in oxygen consumption and transport in accompaniment of greater metabolic rates. Lung structure has been modified (radically so in birds) with resulting greater surface area, and the ventilatory apparatus has been greatly altered. Blood hemoglobin concentration and hence oxygen carrying capacity was greatly increased, as was oxygen affinity of the hemoglobin. Four chambered hearts were independently evolved.

TABLE 5. A comparison of hepatic structure and functional capacity in a lizard and a mammal.*

	Units	Lizard	Mammal
Liver mass	% body mass	3.7	5.9
Cytochrome oxidase activity	nmol O ₂ mg liver ⁻¹ min ⁻¹ at 38°C	11.2	30.0
Mitochondrial volume density	% liver volume	12.4	16.0
Mitochondrial membrane surface area	m ² cm ⁻³ liver	0.79	1.34

* Data from Else and Hulbert (1981).

improving separation of venous and arterial blood, and blood pressure and tissue capillarity were increased greatly. Aerobic enzymatic capacity of the tissues was increased (Bennett, 1972), due largely to an increase in relative mitochondrial volume and membrane surface area (Table 5) (Else and Hulbert, 1981). In addition to these improvements in oxygen processing capacities, both groups developed insulatory layers (fur and feathers) that retain metabolically produced heat. The remodelling of the structure and functional capacities of the vertebrate body demanded by endothermy have thus been very extensive. The very great similarities between the independent avian and mammalian solutions to this evolutionary problem suggest that the developmental routes by which this endothermy could be attained were fairly circumscribed.

Phylogenetic affinities are thus seen to have strong influences on metabolic rate. Other factors such as adaptation to specific environmental circumstances may modify these levels, but investigations of these are best pursued within a phylogenetic context. The physiological basis and ecological implications of these observed differences are poorly investigated and understood.

STRUCTURAL IMPLICATIONS OF FUNCTIONAL DESIGN

We have seen that metabolic level is determined principally by only three factors: temperature, mass, and phylogeny. The specification of only these three items is in most cases adequate to produce a remarkably good prediction of metabolic rate. How then are morphological systems "designed" (structured) to meet these and other (e.g., physiological, developmental, ecological) constraints on metabolism?

The general principle of symmorphosis has been proposed by Taylor and Weibel (1981) to describe structural consequences of functional design. Symmorphosis is defined as "... a state of structural design commensurate to functional needs resulting from regulated morphogenesis, whereby the formation of structural elements is regulated to satisfy but not exceed the requirements of the functional system." Briefly stated, symmorphosis predicts that excess structural capacity does not exist, that it is sufficient for maximal demand and no more. This principle has three corollaries: 1) Structural design is rate limiting for flow at each level of a multi-compartmental system, 2) Structural design is optimized, and 3) Structural design is adaptable (Taylor and Weibel, 1981). In an ambitious and pioneering set of studies (summarized in Weibel *et al.*, 1981), Taylor, Weibel, and their co-workers conducted allometric studies on oxygen transport systems of mammals. On the basis of this work, they concluded that the principle of symmorphosis was not well supported by the structural design of these systems.

The concept of symmorphosis is not without its detractors, on both theoretical and empirical grounds. It is an exceptionally forthright statement of the adaptationist program, that animals are built rationally and economically. This view of panadaptationism has been explicitly criticized for failing to recognize phylogenetic and developmental constraints on adaptation (Gould and Lewontin, 1979; Lewontin, 1979). Further, it is very difficult in practice to specify a single function for any structural element in an animal. Most perform multiple functions and are subject to multiple, sometimes contradictory selec-

tion pressures. What might appear to be excess capacity and a violation of symmorphosis from one viewpoint might in fact be just adequate from another. Empirically, reanalysis of Taylor and Weibel's original and subsequent data on oxygen transport systems with mass corrected residuals failed to support the concept (Garland and Huey, 1987). To what extent the principle of symmorphosis will be found to be generally applicable is at this time unclear. However, even if it is ultimately disproved, it has been a valuable statement of a particular philosophical view of animal design and has and will continue to stimulate research in this area. Functional and structural studies have produced relatively few such generalities and their emergence is to be welcomed.

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