The Metabolic Foundations of Vertebrate Behavior

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The disciplines of physiology and morphology have often emphasized design constraints and the working limits of functional systems. This method provides information concerning the possible range of function within which normal activity must occur. Such an approach may also prove useful for the study of behavior, since behavior relies on the coordinated interplay of the nervous and muscular systems. These rely, in turn, on the provision of adequate amounts of fuel and materials to support their function.

The metabolic design and capacities of an organism determine what levels and types of behavior are feasible. Certain forms of animal activity have limits, sometimes surprisingly short limits, imposed by the physiology and morphology of the organism, and behavior can proceed only within those constraints. This article examines some aspects and examples of the metabolic support of activity and behavior among vertebrates and indicates the consequences and limitations of their metabolic design.

LIMITATIONS OF AEROBIC & ANAEROBIC METABOLISM

The muscle activity involved in vertebrate behavior may be supported by either aerobic or anaerobic metabolism. Aerobic metabolism supplies resting energy requirements and sustains certain types of low-intensity behaviors. It employs the complete oxidation of a variety of fuels—fats, carbohydrates, and amino acids—with molecular oxygen. The process is highly efficient at trapping bond energy in fuel molecules and converting it to a more biologically useful form. However, aerobiosis relies upon a continuous supply of oxygen from outside the organism.

Environmental oxygen is far from its eventual site of use within the cells, and there has been an elaborate development of the respiratory and cardiovascular systems in vertebrates for oxygen procurement and supply. Oxygen molecules must first be brought to the site of the respiratory surface, generally by active ventilation. They then diffuse across several barriers, combine with hemoglobin, which transports them in bulk to distant portions of the body. After being released within the tissues, they traverse several different cell membranes to the final site of use within the mitochondria.

Because of the numerous systems and distances involved and the necessity of diffusion across several barriers, significant time lags may occur between metabolic demand and oxygen supply. The development of maximal levels of oxygen supply requires 1 to 2 minutes (Hickson et al. 1978), a long time in terms of rapid behavioral requirements. Consequently, there may be a significant temporal displacement between metabolic demand and aerobic energy supply. In addition, each functional system involved in oxygen procurement has a maximal transport rate due to physical considerations alone, such as the amount of blood that the heart can pump per unit time.

The system limiting maximal oxygen transport has not been determined (Holloszy 1973, Keul 1973), but the transport capacity of each system will probably not greatly exceed that of the others. In general, the maximal level of oxygen uptake in vertebrates exceeds the minimal (resting) level by only a factor of 10 at any particular body temperature (Bennett 1978, Bennett and Ruben 1979). Thus, vertebrate aerobic metabolism is not greatly expandable, and animals with low resting metabolic rates—such as the poikilothermic vertebrates—have very low powers of maximal oxygen transport.

The vertebrate plan is certainly not the only feasible design for oxygen transport. In insects, for instance, oxygen can be delivered through the tracheal system directly to the cells without the intermediate position of elaborate ventilatory and circulatory systems. Oxygen uptake in some insects may exceed resting levels by 100- to 200-fold during activity, achieving levels sufficient to sustain vigorous activity without supplementary anaerobic metabolism (Kalmius and Heinrich 1970). Although the basic design of the vertebrate body has been very successful in view of the diversity of vertebrates and the numerous environments they occupy, it places severe limits on the ability to sustain behavior aerobically.

The lags and limits of oxygen consumption are not the final determinants of vertebrate behavioral capacities. Vertebrates also have well-developed capacities for anaerobic metabolism (Gołnick and Hermansen 1973). Although these are occasionally useful in tolerating temporary circumstances of low environmental oxygen availability, such as during asphyxia or diving, their primary use is in supporting short-term or very intense activity. The catabolism of high-energy phosphate compounds (ATP and creatine phosphate) is sufficient to support activity for several seconds.

Beyond this, however, the principal anaerobic pathway in vertebrates is anaerobic glycolysis—the conversion of larger carbohydrates to lactic acid. This catabolism occurs primarily in skeletal muscle and has the significant advantage of having both the fuels (in the form of muscle glycogen and glycolytic enzymes) already located within the muscle.

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cells. No external transport is required; hence, the energy demands of intense activity can be met immediately without the lags associated with aerobic metabolism.

However, anaerobic metabolism has several important drawbacks (Lehninger 1973). It is only about one-tenth as efficient per molecule catalyzed as is aerobic metabolism in trapping bound energy, so that much more fuel is required to sustain comparable levels of exertion. In a moderately strong acid (pK ≈ 3.9), and its production can cause a large depression in cell and blood pH, with attendant effects on enzymatic activity and hemoglobin function. And, although the mechanism is not yet understood, significant lactic acid production is generally associated with rapid tiring and exhaustion, and recovery can involve long time periods.

Lactic acid is rarely found as a significant anaerobic end-product in vertebrates (Hochachka and Somero 1973, Saz 1971). In particular, it is not formed in animals that tolerate long periods of anaerobiosis, such as some invertebrate mollusks. Only among the decapod crustaceans has it been reported as an important by-product of muscular activity (Phillip et al. 1977).

This dual metabolic support of muscle activity and behavior arises from the phylogenetic origin of the vertebrates. Lactic acid formation during vigorous activity has been demonstrated in mammals, reptiles, amphibians, teleosts, elasmobranchs, and extant agnathans. At least two mechanisms are involved. Firstly, the metabolic production of lactic acid is anaerobic, yielding less energy per molecule of ATP when catalyzed by anaerobic enyzmes than by their aerobic counterparts. Secondly, the energy demands of intense activity can usually be met immediately by anaerobic metabolism, whereas aerobic metabolism can only respond after an initial lag period. For most vertebrates, the energy demands of intense activity exceed aerobic energy output per unit of time significantly.

The escape behavior of the frog relies upon anaerobic metabolism and that of the toad is aerobic. This differential dependence is apparent in their relative abilities to consume oxygen and produce lactic acid (Table 1). Anaerobic scope, the maximal rate of lactic acid formation, is more than three times as great in the frog as in the toad. This corresponds to a similar differential in performance during the first 30 seconds of activity. The greater stamina of the toad is reflected in its substantially greater levels of maximal oxygen consumption. The amount of energy made available by these two pathways may be directly compared by calculation of the ATP-equivalents generated by each. The production capacity of each mode is similar in the toad, whereas the frog's capacity for anaerobically produced power input exceeds aerobic power input by more than sevenfold. Thus, even if maximal levels of oxygen transport could be activated immediately upon activity, nearly 90% of the supporting energy would be anaerobically supplied in the frog. Due to the lags in development of active oxygen consumption, the percentage contribution will, in fact, be even greater. The explosive jumping activity of the frog, with its high performance and rapid exhaustion, demonstrates well the advantages and disadvantages of anaerobic metabolism. Although the aerobically fueled performance of the toad cannot be sustained, it is relatively low level and lacks the ability for rapid evasive maneuvers.

Other amphibians exhibit a wide diversity of escape behaviors and metabolic support for their behaviors. Generally, a species emphasizes either aerobic or anaerobic capacities, but this is not a necessary relationship (Bennett and Licht 1973). Rapid escape capacity, however, is thought to be provided only with the activation of extensive anaerobic metabolism. This leads to the interesting behavioral problem of how slow-moving amphibians without this anaerobic escape response are able to deter predators, since they cannot flee from them.

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### TABLE 1. Aerobic and anaerobic metabolism during intense activity at 20°C in a frog and a toad

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<thead>
<tr>
<th>Category</th>
<th>Rate</th>
<th>Butto</th>
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<tbody>
<tr>
<td>Maximal oxygen consumption (μl O2/g × min)</td>
<td>12.7</td>
<td>4.0</td>
</tr>
<tr>
<td>Maximal lactic acid formation (mg lactate/g × min)</td>
<td>0.24</td>
<td>0.08</td>
</tr>
<tr>
<td>ATP equivalents generated (μmoles ATP/g × min)</td>
<td>3.7</td>
<td>0.81</td>
</tr>
<tr>
<td>Aerobic</td>
<td>1.8</td>
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</tr>
<tr>
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<tr>
<td>Seymour 1973</td>
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**Figure 1. Distance traversed during pursuit escape by leopard frogs (Rana pipiens, closed circles) and western toads (Bufo boreas, open circles) in 20°C C. Frogs are exhausted at 5 min. (Putnam and Bennett, unpublished data)**
havioral deterrent occur among these species. Many of their slow-moving anoma-

mals secrete poisons or noxious fluids from their skin when provoked (e.g.,
Bufo, Scaphiopus, Taricha). The various compounds that they secrete (e.g., bufo-
toxin, tetradotoxin, curare) can induce effects ranging from irritation to death. 
Other mucous secretions produced by some species (e.g., Anolis, Ensatina)
are so copious and sticky that they glue the mouths of predators shut or stick
them to the ground (Arnold 1980).

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TABLE 2. ATP-equivalents produced
during 5 min of activity in four species of
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characteristic of most birds is far beyond the aerobic metabolic limits of modern
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port and utilization capacities was neces-
sary to make this type of behavior fea-
sible. Its evolution permitted new modes
of escape and foraging, as well as move-
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of anaerobic apply even at comparatively low levels of exertion in poikilotherms and have therefore strongly shaped the behavior of these animals.

**BODY TEMPERATURE, METABOLIC CAPACITY, AND BEHAVIOR**

Body temperature exerts a controlling influence on physiological rate processes and may consequently have a significant impact on behavior and reaction speed. Homeotherms stabilize their body temperature with high metabolic rates and controlled heat loss, thereby avoiding thermal perturbation of many physiological and behavioral processes. Most vertebrate poikilotherms do not; they must assume the temperature of their environment or seek out microenvironments in which an appropriate temperature can be attained. Unlike mammals and birds, the poikilotherms must cope with the effects of low and varying body temperature on their activity and behavior.

The biochemical rate processes which underly physiological processes usually have a pronounced thermal dependence. Biochemical reaction rates commonly double or triple as the temperature of the system increases 10°C (Q10 = 2-3); they likewise show a similar degree of depression as temperature is lowered. It might be expected that various types of behavior would show a similar thermal dependence and, the influence of body temperature on activity capacity would be both significant and very apparent. For instance, an animal at 30°C might be able to run only one-third to one-half as fast as an animal at 40°C. The influence of temperature on many physiological rate processes has been measured, but very few data have been collected concerning behavioral performance of poikilotherms in spite of its importance to their survival. Is behavior as temperature dependent as might be expected on physiological or biochemical bases?

Aerobic metabolism, both resting and maximal, is markedly temperature dependent in vertebrate poikilotherms (Bennett 1978). Temperature coefficients (Q10) are normally within the anticipated range of 2-3. In some species, maximal oxygen consumption will stabilize or even decline with increasing body temperature, but these plateaus are generally associated with temperatures above those normally attained by the species. There is little or no maintenance of high aerobic metabolic rates at lower temperatures. Consequently, sustained behaviors supported through aerobic metabolism should be similarly thermally dependent.

The few data available suggest that this is indeed the case. The stamina of walking guppies increases with increasing temperature up to 35°C and declines at higher temperatures (Moerbit 1968). This performance exacts parallels maximal net oxygen transport in these lizards. In salmon, even after groups of animals have been acclimated to test temperatures, sustained swimming performance follows the thermal dependence of maximal oxygen consumption (Brett 1974). Hence, the thermal sensitivity of sustained behavior in poikilotherms may depend directly upon that of oxygen-transporting capacities.

Anaerobic metabolism may be more thermally independent than aerobic, with Q10 values of 1.1-1.3, particularly at temperatures in excess of 20°C (Bennett and Licht 1972, 1974). These values indicate thermal independence of anaerobic energy-generating capacity. The physiological or biochemical basis of this independence is unknown, but its behavioral implications are clear: Rapid activity and behavior may also be relatively insensitive to body temperature.

Observations on lizards and anurans amphibians show a coincidence of thermal independence of anaerobic metabolism and burst activity (Bennett 1980, Price and Bennett, unpublished data). For instance, distance hopped by Rana pipiens at 20°C is nearly temperature-independent between 20 and 30°C (Q10 = 1.0), as is anaerobic metabolism (Q10 = 0.9-1.1). Below 20°C, lactic acid generation and performance show similar declines with decreasing temperature (Q10 = 2-3.5), and at 10°C these do not differ much from those normally attained by the species. Burst performance at high body temperatures may also be relatively temperature-insensitive for small lizards. The western fence lizard (Sceloporus occidentalis, closed circles) measured at a running speed of 5 m from a standing start. Hatched area indicates anticipated running speed based on Q10 = 2 (upper boundary) and Q10 = 3 (lower boundary) based on performance at 40°C. (Adapted from data in Bennett 1980)
Maximal behavioral capacity is attained only at the highest temperatures tolerated, which are rarely if ever attained under natural conditions. Thus, complete compensation and thermal independence of activity is not normally attained. Poikilotherms operating at low temperatures have burst behavioral capacity significantly retarded by the effects of low and variable body temperature. The former appears more susceptible than the latter.

The mammals and birds have much greater rates of aerobic metabolism and can sustain behavioral performance that is impossible for the lower vertebrates. In addition, their homeothermic condition, with its high and stable body temperature, avoids the retarding effects of low temperature on metabolic supply and performance.

ACKNOWLEDGMENTS
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