

# **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 entails 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 limited 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 interposition 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 (Kammer and Heinrich 1978). 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 (Gollnick 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 1975, Simonson 1971). It is only about one-tenth as efficient per molecule catabolized as is aerobic metabolism in trapping bond energy, so that much more fuel is required to sustain comparable levels of exertion. It is 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 invertebrates (Hochachka and Somero 1973, Saz 1971). In particular, it is not formed in animals that tolerate long periods of anoxia, such as some bivalve mollusks. Only among the decapod crustaceans has it been reported as an important by-product of muscular activity (Phillips 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 (hagfish and lampreys) (Bennett 1978, Ruben and Bennett, unpublished data). Because of its persistence in the latter jawless vertebrates, it may have been

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

Category	<i>Rana</i>	<i>Bufo</i>	Reference
Maximal oxygen consumption [ $\mu\ell$ O <sub>2</sub> /(g mass × min)]	6.2	12.7	Seymour 1973 Carey 1979
Maximal lactic acid formation [mg lactate/(g mass × min)]	0.81	0.24	Bennett and Licht 1974
ATP equivalents generated [ $\mu$ moles ATP/(g mass × min)]			Bennett and Licht 1972
Aerobic	1.8	3.7	
Anaerobic	13.5	4.0	

present among the primitive ostracoderms, which were the first vertebrates.

Consequently, the dual reliance on aerobic and anaerobic metabolism, with their advantages and disadvantages, has affected the course of vertebrate development and evolution from the beginning. Vertebrate behavior is based on an interplay of these two metabolic modes. Activated sequentially, they can supplement each other; however, different groups of vertebrates often emphasize one or the other in their normal behavioral repertoire.

#### ANAEROBIC AND AEROBIC ACTIVITY PATTERNS

A familiar example of this differential metabolic reliance is found in the escape behavior of anuran amphibians. A fail-proof classroom demonstration of interspecific differences in activity capacity involves the simultaneous release of a frog (*Rana pipiens*) and a toad (*Bufo boreas*). The frog leaps about with an explosive burst of activity and is genuinely difficult to catch. The toad is considerably slower and is easily retrieved. Distance traversed as a function of time after release is shown in Figure 1. Although the frog can cover three times the distance as can the toad in the first 30 seconds of activity, this performance cannot be maintained. Its behavioral capacity for escape is nearly over after 2 min, and the animal is completely exhausted by 5 min. The toad, on the other hand, maintains a constant walking speed of 6-7 m/min (at 20° C) and can sustain it almost indefinitely. Consequently, the total distance traversed by the toad is greater, and the race is not always to the swift.

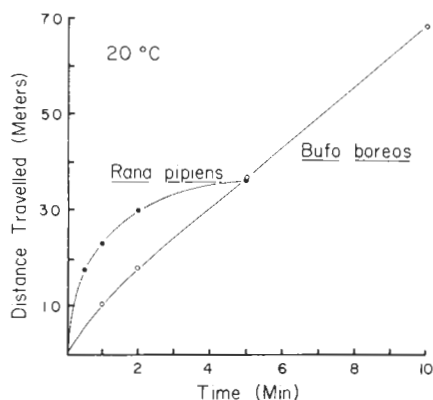
The escape behavior of the frog relies upon anaerobic metabolism and that of the toad is aerobic. This differential dependence is apparent in their relative abilities to consume oxygen and produce

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 can 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.

At least three different modes of be-



**Figure 1.** Distance traveled during pursued escape by leopard frogs (*Rana pipiens*, closed circles) and western toads (*Bufo boreas*, open circles) at 20° C. Frogs are exhausted at 5 min. (Putnam and Bennett, unpublished data)

havioral deterrence occur among these species. Many of these slow-moving animals secrete poisonous or noxious fluids from their skins when provoked (e.g., *Bufo*, *Scaphiopus*, *Taricha*). The various compounds that they secrete (e.g., bufotoxin, tetrodotoxin, curare) can induce effects ranging from irritation to death. Other mucous secretions produced by some species (e.g. *Aneides*, *Ensatina*) are so copious and sticky that they glue the mouths of predators shut or stick them to the ground (Arnold 1980).

A second avoidance behavior involves the adoption of inedible postures. Several species inflate their lungs and become almost spherical when disturbed (*Bufo*) or become very rigid with an arched back and protruding limbs (*Taricha*)—shapes that prevent ingestion by certain small predators, particularly snakes (Arnold 1980).

Finally, some amphibians will counterattack and defend themselves with small but very sharp teeth (*Aneides lugubris*, *Lepidobatrachus llanensis*).

The metabolic capacities of amphibians permit only certain types of behavior and preclude other types. The behavioral differences are not simply volitional but reside within the structure and functional capacities of each species. For example, the limb muscles of *Rana* are considerably larger than those of *Bufo* and have substantially greater activities of rate-regulating glycolytic enzymes (Bennett 1974). The oxygen-transporting abilities of the cardiovascular system, including heart size, oxygen capacity of the blood, and blood volume, are much better developed in *Bufo* than *Rana* (Hillman 1976). Major modifications of these respiratory, cardiovascular, and muscular systems are possible only in evolutionary time; each species is now constrained in its behavioral capacities by prior canalization and differential development of these structures and their functional capacities.

Snakes also have very different behavioral types and activity capacities. Recent studies (Ruben 1976a, b, 1977) have compared the metabolic physiology and anatomy with the activity response of racers and coachwhips, rattlesnakes, and boas. Racers and coachwhips (*Masticophis*, *Coluber*), as their names imply, are very fast, active snakes that attain and sustain high speeds during prey pursuit and escape. Rattlesnakes (*Crotalus*) do not sustain great speeds and lie quietly in ambush for prey. They are capable, however, of intense struggling and striking behavior for short periods of time.

Rosy boas (*Lichanura*) are sluggish, slow-moving snakes that rely on constriction to immobilize and kill their prey. After initial attempts at escape, they roll into a ball shape and exude a nauseating secretion from their cloacas.

The prey pursuit and escape behaviors of these species depend on very different metabolic capacities (Table 2). In these instances, aerobic and anaerobic abilities are directly, not inversely, related. Both oxygen consumption and lactic acid production attain very high levels in the racer and coachwhip, are of intermediate capacity in rattlesnakes, and are only modestly developed in boas. The range of energy use in both metabolic modes is five-fold between coachwhips and boas.

These differences also depend on structural and physiological differences between the species. High activities of glycolytic enzymes and myoglobin occur in the skeletal muscles of the more active snakes, and their lungs are better developed and more complex. The skeletal muscles of racers are unusually long and extend over many vertebrae; those of boas are much shorter. Although greater speeds of contraction can be obtained with the former arrangement, this type of muscle organization precludes tight coiling and constriction. Racers do not have the flexibility of boas. Thus, metabolic adaptation and specialization have restricted the range of potential behavioral response in these animals.

#### ACTIVITY METABOLISM IN HOMEOTHERMS AND POIKILOOTHERMS

The differences between the metabolic capacities of the homeothermic and poikilothermic vertebrates overshadow the differences found within each group. Aerobic capacity was greatly expanded during the evolution of birds and mammals. Both resting and maximal rates of oxygen consumption are nearly an order of magnitude greater in homeotherms than in poikilotherms of equal size and body temperature (Bennett and Ruben 1979). Consequently, the stamina and range of aerobically supported work outputs are much greater in homeotherms.

The evolution of this expanded aerobic capacity may have been a key selective feature in the evolution of homeothermy, since it opened a broad new array of possible behaviors that could not be supported by the metabolic pattern of the poikilothermic vertebrates (Bennett and Ruben 1979). For instance, the energy required for flapping flight

**TABLE 2.** ATP-equivalents produced during 5 min of activity in four species of snakes. (After Ruben 1976a)

Species	μmoles ATP/mass		
	Aerobic	Anaerobic	Total
<i>Coluber</i> & <i>Masticophis</i>	23.0	29.1	52.1
<i>Crotalus</i>	10.6	16.2	26.8
<i>Lichanura</i>	4.6	5.0	9.6

characteristic of most birds is far beyond the aerobic metabolic limits of modern reptiles. Thus, expansion of oxygen transport and utilization capacities was necessary to make this type of behavior feasible. Its evolution permitted new modes of escape and foraging, as well as movement over much greater distances, since the distance moved per unit energy expended is substantially less for flying organisms than for walkers or runners (Schmidt-Nielsen 1972).

Terrestrial homeotherms likewise are afforded a greatly expanded behavioral repertoire by their greater aerobic capacity. Mammals can sustain running speeds far in excess of those possible for lizards, which fatigue at velocities of only 0.5–1.0 km/h. Various sets of behaviors requiring endurance, such as certain types of courtship and hunting, are available to mammals but not to reptiles. However, the energetic costs of homeothermy and this increased behavioral capacity are very high, even for resting animals.

Anaerobic capacities did not achieve a similar expansion with the evolution of homeothermy. Thus, the capacity for rapid, burst-like behavior, which is supported principally through anaerobic sources, is not greatly different in poikilothermic and homeothermic vertebrates. Burst speeds of small mammals and lizards, for instance, are both approximately 8–12 km/h (Bennett 1980, Layne and Benton 1954). The total metabolic power input to burst activity is very similar in small rodents and reptiles (Ruben and Battalia 1979), which explains why many lower vertebrates appear so fleet and are difficult to capture.

Poikilothermic vertebrates depend on anaerobic metabolism more heavily than do homeotherms. In the former animals, it provides a very broad range of possible speeds, metabolic power inputs, and work outputs, even though they cannot be sustained. Running speed can be increased 10- to 30-fold in lizards through the activation of anaerobic metabolism. In humans, a similar increment is only two- to three-fold. Thus, the limitations

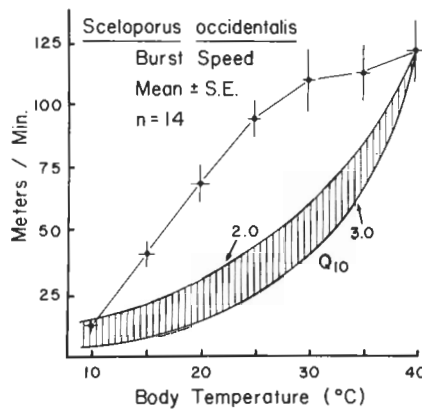
of anaerobiosis apply even at comparatively low levels of exertion in poikilotherms and have therefore strongly shaped the behavior of these animals.

## 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 ( $Q_{10} = 2-3$ ); 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 ( $Q_{10}$ ) 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 levels of aerobic metabolism at lower temperatures. Consequently, sustained behaviors supported through aerobic



**Figure 2. Burst running speed of western fence lizards (*Sceloporus occidentalis*, closed circles) measured during a run of 2 m from a standing start. Hatched area indicates anticipated running speed based on  $Q_{10} = 2$  (upper boundary) and  $Q_{10} = 3$  (lower boundary) based on performance at 40° C. (Adapted from data in Bennett 1980)**

metabolism should be similarly thermally dependent.

The few data available suggest that this is indeed the case. The stamina of walking iguanas increases with increasing temperature up to 35° C and declines at higher temperatures (Moberly 1968). This performance exactly 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 1964). 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  $Q_{10}$  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.

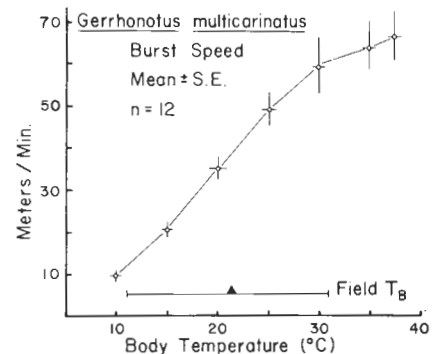
Observations on lizards and anuran amphibians show a coincidence of thermal independence of anaerobic metabolism and burst activity (Bennett 1980, Putnam and Bennett, unpublished data). For instance, distance hopped by *Rana* is nearly temperature-independent between 20 and 30° C ( $Q_{10} = 1.1$ ), as is anaerobic metabolism ( $Q_{10} = 0.9-1.1$ ). Below 20° C, lactic acid generation and performance show similar declines with

decreasing temperature ( $Q_{10} = 2-3.5$ ), and at 10° C are only 35-38% of capacity at 20° C.

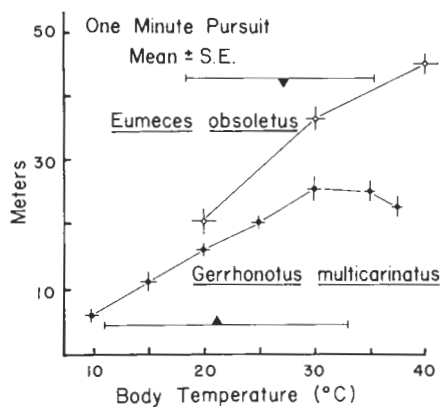
Burst performance at high body temperatures may also be relatively temperature-insensitive for small lizards. The western fence lizard (*Sceloporus occidentalis*) can run as fast at 30° C as at 40° C (Figure 2), a performance much greater than that anticipated for normal temperature dependence. The normal temperature regulated by this animal while active in the field is 35° C. Burst activity capacity remains substantially above anticipated levels down to temperatures as low as 10° C.

Although a considerable degree of thermal independence can be obtained in anaerobic energetics and capacity for rapid activity, thermal performance is not completely temperature independent. For thermophilic animals, such as *Sceloporus*, which normally are active only at high body temperatures, maximal behavioral capacity and normally experienced body temperatures coincide. The animals run fastest and longest at the body temperatures they normally maintain in nature.

However, poikilotherms that are active at lower temperatures do not necessarily attain maximal behavioral levels at normally encountered temperatures. Burst speed and escape capacities are reported in Figures 3 and 4 for the alligator lizard (*Gerrhonotus multicarinatus*) and the Great Plains skink (*Eumeces obsoletus*). The former forages in leaf litter, and the latter is principally fossorial; both have a relatively low and broad range of activity temperatures averaging 22 and 27° C, respectively. Escape and pursuit capacity are greatly restricted by these low body temperatures.



**Figure 3. Burst running speed of alligator lizards (*Gerrhonotus multicarinatus*, open circles) measured as in Figure 2. Horizontal line indicates range and mean (triangle) of temperatures of lizards active under natural field conditions (Brattstrom 1965). (Adapted from data in Bennett 1980)**



**Figure 4. Distance run during 1 min of pursuit by two species of lizards (*Gerrhonotus multicarinatus*, closed circles, and Great Plains skink, *Eumeces obsoletus*, open circles). Thermal data for each species is reported as in Figure 3. (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 those temperatures experienced normally under field conditions.

Thus, both aerobically sustainable behavior and anaerobic burst behavior can be retarded by the effects of low and variable body temperature. The former appears more susceptible than the latter, although the data deal only with maximal locomotory speeds and endurance capacities. The influence of temperature on performance requiring more careful behavioral discrimination, such as is required for prey capture or predator avoidance, is not known. However, the ability of a gopher snake to capture prey successfully, for example, has a much greater thermal dependence than does its striking speed ( $Q_{10} = 2.4$  vs 1.4, respectively, at 18–27°C); consequently, the snake is much less accurate at lower temperatures even though strike velocity is little affected (Greenwald 1974). The influence of body temperature on behavior of poikilotherms will doubtless be an area of considerable research interest in the future.

## CONCLUSIONS

Behavioral capacities are based upon the physiology and morphology of neuromuscular systems. Understanding the limits of these systems, particularly

those of the fuel and support capacities of skeletal muscle, can provide a framework for understanding the limitations of behavioral performance.

Among the poikilothermic vertebrates, the ability to support and sustain activity by aerobic metabolism is limited. Consequently endurance is low, and performance requiring moderate or high levels of activity depends heavily on anaerobic metabolism and results in fairly rapid exhaustion.

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.

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