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ANAEROBIC THRESHOLD OF ANURAN AMPHIBIANS¹

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The metabolic responses to graded levels of exercise were determined for three species of anuran amphibians (*Bufo americanus*, *Hyla crucifer*, and *Rana sylvatica*). Both oxygen consumption ($\dot{V}O_2$) and lactate production were measured at low, moderate, and high levels of mechanically stimulated activity. Significant elevations in whole-body lactate content were observed in all three species during moderate exercise. Anaerobic threshold, defined as the $\dot{V}O_2$ above which metabolic acidosis occurs, was estimated to be 0.47 ml $O_2/(g \cdot h)$ for *B. americanus* (45% of maximum oxygen consumption, $\dot{V}O_{2 \max}$), 0.56 ml $O_2/(g \cdot h)$ for *H. crucifer* (54% of $\dot{V}O_{2 \max}$), and 0.47 ml $O_2/(g \cdot h)$ for *R. sylvatica* (63% of $\dot{V}O_{2 \max}$). These values are consistent with data for other vertebrates, suggesting that anaerobic threshold is a relatively constant percentage of aerobic capacity.

INTRODUCTION

Studies of the exercise physiology of anuran amphibians generally deal with the performance of animals at maximum levels of activity (e.g., Bennett and Licht 1974; Carey 1979; Taigen, Emerson, and Pough 1982). The methods used to stimulate exercise vary, but in most cases the result is an extended bout (3–10 min) of intense exercise. The activity of the animal under these conditions is supported metabolically by a combination of aerobic and anaerobic ATP production, and both processes are presumed to be functioning at their maximum rates. Metabolic data generated in this way are thought to represent fixed, readily reproducible characteristics of species and have been investigated for their association with a variety of behavioral, ecological, morphological, and physiological features. Maximum activity metabolism of anuran amphibians has been correlated with defensive mechanisms (Bennett and Licht 1974), mode

of locomotion (Seymour 1973; Taigen et al. 1982), foraging behavior (Taigen et al. 1982), prey preference (Taigen and Pough 1983), habitat (Hutchison and Miller 1979), thermal history (Carey 1979), cardiac muscle mass (Hillman 1976), resting metabolism (Taigen 1983), physical training (Miller and Camilliere 1981), ontogeny (Taigen and Pough 1981), and method of stimulation (Hillman et al. 1979). While some of these generalizations have recently been reevaluated (e.g., Miller and Hutchison 1980; Taigen et al. 1982), expansive evolutionary and ecological inferences continue to be drawn from data of this sort (Bennett 1980; Taigen 1983).

Our concern with these studies is that the animals are forced to extreme activity levels quite unlike those that they normally experience in the field (e.g., Heatwole 1961; Pough et al. 1983). In fact, elevated lactate levels in unrestrained animals under field conditions appear in general to be a rare occurrence for terrestrial ectotherms (Seymour 1979; Gatten 1980, 1981; Gleeson 1980). The lack of demonstrated ecological relevance in studies of anuran exercise physiology makes the use of these data to formulate ecological or evolutionary generalizations questionable. This consideration impelled us to investigate the metabolic responses of anurans to submaximal levels of exercise that involve normal locomotor behavior. The results indicate that significant anaerobic metabolism occurs during moderate exercise at levels of stimulation well below maximum. This

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finding is consistent with data for other vertebrate species, both ectothermic and endothermic, and may be an important consideration in evaluating the role of anaerobic metabolism in the activity of free-ranging animals.

MATERIAL AND METHODS

Wood frogs (*Rana sylvatica*), American toads (*Bufo americanus*), and spring peepers (*Hyla crucifer*) were collected within 5 km of Ithaca, New York, in March, April, and May 1980. Only males in good health were used in this study. Following transport to the laboratory, the animals were kept in plastic boxes with a damp paper towel and maintained at 20 C in a constant-temperature cabinet on a 12-h photoperiod. After 3 days of acclimation, resting metabolism and activity metabolism were measured using a technique described in detail elsewhere (Taigen and Pough 1981; Taigen et al. 1982). Each animal was placed inside a cylindrical, airtight metabolic chamber fashioned from clear Plexiglas tubing. The metabolic chambers were held inside a darkened constant-temperature cabinet at 20 C and vented to air in the cabinet through a two-way stopcock. Rates of oxygen consumption were determined from analysis of gas samples withdrawn from the chambers before and after a precisely timed bout of quiescence (for resting metabolism) or exercise (for activity metabolism). Resting oxygen consumption ($\dot{V}O_2$ rest) was measured between 1300–1400 hours EST, 6–8 h after the animals had been placed in the metabolic chambers.

Immediately after $\dot{V}O_2$ rest was determined, the animals were mechanically stimulated to exercise by rotating the chambers, using an electric motor (see Seymour [1973] for description). The exercise regime imposed on each animal was immediate in onset and constant in intensity. Intensity of exertion was varied among individuals by altering chamber rotation rates with a motor speed control. The linear velocity experienced by an animal inside its chamber was used as an indicator of level of stimulation and was calculated from the diameter and rotation rate of the chamber. Animals were randomly assigned to one of three levels of exertion: low

(<0.5 body lengths/s), moderate (0.5–1.5 body lengths/s), and high (>1.5 body lengths/s). These levels of stimulation were chosen on the basis of preliminary experiments and produced graded work loads for all three species. The behavior of the exercising animals was observed through a window in the side of the environmental cabinet.

After 4 min of exercise, gas samples were withdrawn from the chambers and the animals were immediately frozen in liquid nitrogen. The bodies were then assayed for total lactate content by colorimetric analysis of whole-body homogenates (Taigen and Pough 1981). Lactic acid assay kits (Sigma) and a Beckman DU spectrophotometer with a Gilford photometer were used for this analysis. Resting lactate levels were determined from a group of undisturbed animals that were removed from their chambers and frozen in liquid nitrogen immediately after measurement of $\dot{V}O_2$ rest.

STATISTICS

Means and 95% confidence intervals of resting lactate content (mg/g) and $\dot{V}O_2$ rest (ml O_2 /[g · h]) were calculated for each species and used to assess aerobic and anaerobic responses during exercise. We evaluated the relationships between oxygen consumption and lactate content of exercising animals with least-squares regression analyses. These analyses were used to estimate the anaerobic threshold for each species, functionally defined as the rate of oxygen consumption above which lactate levels are significantly elevated (Wasserman et al. 1973). The anaerobic threshold was taken as the point at which the regression line intercepted with the upper bound of the 95% confidence interval of resting lactate content (see figs. 2, 3, and 4). We calculated standard errors for anaerobic threshold from the confidence limits of the regression statistics, following the procedure of Sokal and Rohlf (1969, pp. 424–426).

RESULTS

Behavioral responses of the animals during exercise varied with the intensity of stimulation. At low (<0.5 body lengths/s) and moderate (0.5–1.5 body lengths/s)

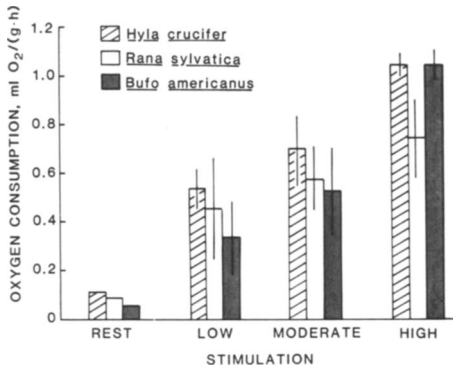


FIG. 1.—Rates of oxygen consumption of three anuran species at low (<0.5 body lengths/s), moderate (0.5–1.5 body lengths/s), and high (>1.5 body lengths/s) levels of stimulation to exertion in rotating chambers. Vertical bars represent 95% confidence intervals. Confidence intervals for resting metabolism are given in table 1.

levels of stimulation, all three species walked or hopped, generally keeping pace with the rotating chamber. These locomotor activities were similar to those observed of free-ranging animals. In contrast, the high (>1.5 body lengths/s) level of stimulation resulted in constant, vigorous flexion of the limbs as the animals continuously attempted to maintain an upright position in the rapidly rotating chambers.

Rates of oxygen consumption increased with intensity of stimulation for all three species (fig. 1). Aerobic capacity ($\dot{V}O_2$ max), computed as the mean rate of oxygen consumption at the high level of exertion, differed significantly among the three species ($F_{2,11} = 39.1, P < .001$), with *Rana sylvatica* lower than both *Hyla crucifer* and *Bufo americanus* (table 1).

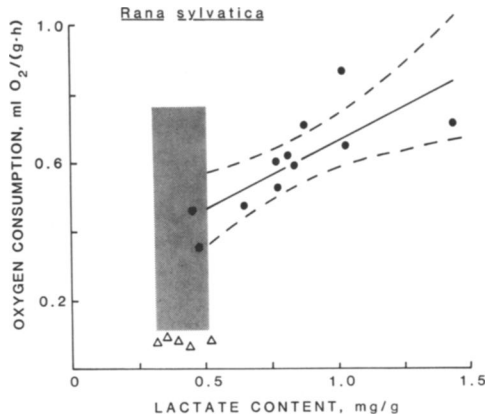


FIG. 2.—Oxygen consumption versus lactate content for resting (Δ) and exercising (\bullet) *Rana sylvatica*. The stippled region represents the 95% confidence limits for resting lactate content. The results of a regression analysis of data from exercising animals are shown. Dashed lines represent 95% confidence limits of the regression line.

Animals with low rates of oxygen consumption had lactate contents that were within the 95% confidence interval of resting values (figs. 2, 3, and 4). Higher $\dot{V}O_2$'s, however, were associated with elevated whole-body lactate levels. As animals were exercised more vigorously, oxygen consumption increased (fig. 1), and, above the anaerobic threshold, lactate levels increased as well (figs. 2, 3, and 4). Anaerobic thresholds, estimated from regression analyses of these data, were 45%, 54%, and 63% of $\dot{V}O_2$ max for *B. americanus*, *H. crucifer*, and *R. sylvatica*, respectively. Differences among species in relative (% of $\dot{V}O_2$ max) and absolute (ml O₂/[g·h]) anaerobic threshold were not significant (table 1).

TABLE 1
RESTING AND ACTIVITY METABOLISM OF THREE SPECIES OF ANURANS

SPECIES	RESTING O ₂ CONSUMPTION [ml O ₂ /(g·h)]	RESTING LACTATE (mg/g)	MAXIMUM O ₂ CONSUMPTION [ml O ₂ /(g·h)]	ANAEROBIC THRESHOLD	
				[ml O ₂ /(g·h)]	(% of capacity)
<i>Rana sylvatica</i>085 ± .011 (4)	.41 ± .10 (5)	.745 ± .148 (4)	.472 ± .103	63.3 ± 13.8
<i>Hyla crucifer</i>111 ± .018 (5)	.48 ± .10 (6)	1.043 ± .037 (5)	.560 ± .113	53.7 ± 10.9
<i>Bufo americanus</i>051 ± .009 (5)	.22 ± .07 (4)	1.039 ± .050 (5)	.465 ± .076	44.8 ± 7.3

NOTE.—Results are given as means ± 95% confidence intervals. Numbers in parentheses are sample sizes.

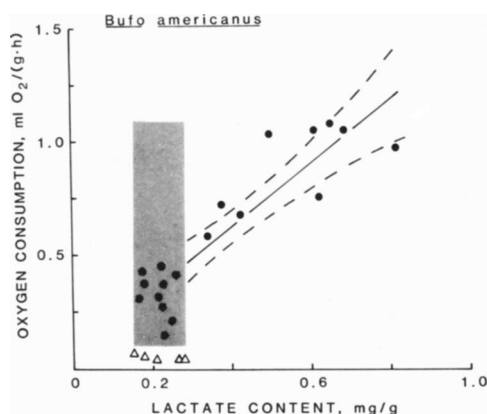


FIG. 3.—Oxygen consumption versus lactate content for *Bufo americanus*. Symbols and legend as in fig. 2.

DISCUSSION

COMPARATIVE DATA

The accumulation of lactic acid we observed in frogs exercising at submaximal levels presumably results from an inadequate delivery of oxygen to working muscles at the beginning of the exercise period (Hill and Lupton 1923). Locomotor activities entailing $\dot{V}O_2$'s less than 45%–63% of $\dot{V}O_2$ max do not result in elevations of lactate. Our results are consistent with the data available for reptiles, fishes, and other amphibians. Monitor lizards (*Varanus salvator*) rely on anaerobic energy production to support the initial phase of activity when forced to run at 85% of $\dot{V}O_2$ max (Gleeson and Bennett 1982). Transitory respiratory quotients greater than one, indicating significant anaerobiosis, are also reported for whiptail lizards (*Cnemidophorus murinus*) exercised at 73% of $\dot{V}O_2$ max (Bennett and Gleeson 1979). In contrast, lactate values of burrowing spadefoot toads (*Scaphiopus hammondi*) exercising at 30% of $\dot{V}O_2$ max were not significantly different from resting values (Seymour 1973). Wokoma and Johnston (1981) found resting lactate levels in slowly swimming (0.9 body lengths/s) rainbow trout (*Salmo gairdneri*), but large increases in lactate concentration occurred when swimming speed was increased to 3.5 body lengths/s (judged by Wokoma and Johnston to be between 60% and 100% $\dot{V}O_2$ max).

Data for mammals (pigs, dogs, lions, and horses) exercised on a treadmill indicate that blood lactate levels are elevated when $\dot{V}O_2$ is greater than 50% $\dot{V}O_2$ max (Seeherman et al. 1981). Further, it is well known among human exercise physiologists that lactate accumulates in exercising individuals at work loads well below maximum. The work load at which anaerobiosis contributes significantly to total power input is variable, depending on factors such as the type of exercise (Davis et al. 1976; Withers et al. 1981), training schedule (Williams et al. 1967; Davis et al. 1979), and whether the work load is constant or incremental during exercise (Wasserman, Van Kessel, and Burton 1967; Wasserman et al. 1973). The point at which lactate levels are elevated above resting ranges from 46.5% of $\dot{V}O_2$ max during arm cranking (Davis et al. 1976) to 75% during exercise on a treadmill (Withers et al. 1981). Lower values (40% of $\dot{V}O_2$ max) are reported for untrained individuals performing unfamiliar tasks (Williams et al. 1967; Senay, Rogers, and Jooste 1980).

DETERMINANTS OF ANAEROBIC THRESHOLD

At low levels of exertion, the oxygen deficit that occurs before steady-state $\dot{V}O_2$ is achieved can be accommodated by any of the following mechanisms: (1) desaturation of oxymyoglobin, (2) reduction in venous oxygen content, (3) utilization of ATP, creatine phosphate, or other high-

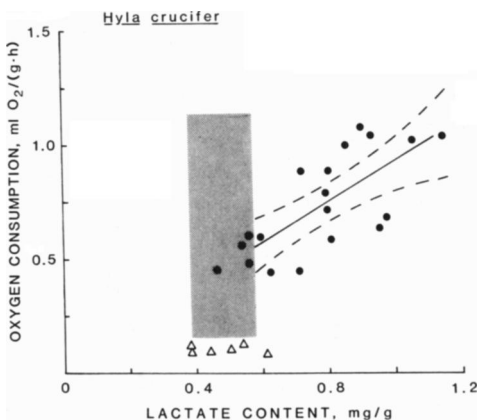


FIG. 4.—Oxygen consumption versus lactate content for *Hyla crucifer*. Symbols and legend as in fig. 2.

energy substances, (4) reduction of oxidized coenzymes, and (5) decreased dissolved oxygen in body fluids (Wasserman et al. 1967). The anaerobic threshold occurs, and pyruvate is converted to lactic acid, when these mechanisms combined cannot meet the oxygen deficit. Consequently, variation in blood hematocrit, cardiac output, and intracellular myoglobin and phosphogen concentration may all affect anaerobic threshold. Other factors may also be important, including the respiratory capacity of the exercising muscle (Ivy et al. 1980) and the condition of intracellular glycogen stores (Hughes, Turner, and Brooks 1982). These factors presumably also affect aerobic capacity, thereby linking these physiological characteristics. These considerations are consistent with the observation that anaerobic threshold appears to be a relatively constant percentage of aerobic capacity.

ECOLOGICAL CONSIDERATIONS

Data from field studies of several species of amphibians and reptiles suggest that the energetic demands of daily activities do not exceed the anaerobic threshold and are not accommodated by anaerobic metabolism. Marine iguanas do not have elevated blood lactate levels when basking, foraging, swimming, or diving (Gleeson 1980). Oxygen consumption rates of these animals during foraging appear to be 60%–80% of their $\dot{V}O_2$ max (Bennett, Dawson, and Bartholomew 1975; Gleeson 1979). A similar observation was obtained for whiptail lizards; average foraging velocities entail rates of oxygen consumption that are 60%–65% of $\dot{V}O_2$ max, presumably at or below the anaerobic threshold (Bennett and Gleeson 1979). Unrestrained, voluntary dives by sea snakes and freshwater turtles are supported entirely by aerobic metabolism (Seymour 1979; Gatten 1980, 1981). Whole-body lactate levels of free-ranging anoline lizards did not vary during a 24-h period, although they were higher than laboratory resting values (Bennett, Gleeson, and Gorman 1981). These data suggest that, while anoles may periodically engage in activities that require anaerobiosis (e.g., territorial defense), there is no regular anaerobic contribution to daily activities.

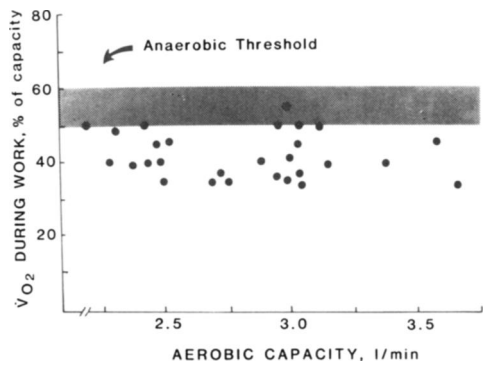


FIG. 5.—Oxygen consumption (% of $\dot{V}O_2$ max) of human workers during voluntary manual labor vs. $\dot{V}O_2$ max. The anaerobic threshold was estimated from several references (see text for details).

Acoustic communication is an especially prominent activity for many anuran species and appears to have high energetic costs. The maximum rate of oxygen consumption during calling in a Neotropical frog (*Physalaemus pustulosus*) is 1.00 ml $O_2/(g \cdot h)$ (Bucher, Ryan, and Bartholomew 1982), a value corresponding to 55% of $\dot{V}O_2$ max (Ryan, Bartholomew, and Rand 1983). Lactate levels of calling frogs are not significantly elevated above resting, although animals forced to exercise at 64% of $\dot{V}O_2$ max do experience a significant increase in lactate (Ryan et al. 1983). The threshold for anaerobic metabolism appears to lie between 55% and 64% of $\dot{V}O_2$ max and is not exceeded by calling animals. In contrast to these results, recent studies of vocalization energetics in *Hyla versicolor* and *Hyla crucifer* indicate that calling in these two species entails very high rates of oxygen consumption, exceeding even the rates measured during forced locomotor exercise (Taigen and Wells [1984] and unpublished data). This metabolic performance is associated with exceptionally high activities of catabolic enzymes in the trunk muscles involved in sound production (Taigen, Wells, and Marsh, unpublished). Hence, the trunk muscles appear to be operating at well below their full oxidative capacity, even at very high calling rates.

Our prediction that the anaerobic threshold correlates with the demands of daily activities is further corroborated by

data on the energetics of human behavior. Rates of oxygen consumption of manual laborers, estimated from cardiac contraction rates, were monitored during an 8-h shift (Astrand 1967). Individuals with high aerobic capacities had high levels of activity and high rates of oxygen consumption, whereas individuals with low aerobic capacities had low oxygen consumption rates.

Hence, all workers maintained levels of oxygen consumption during their voluntary labor at 40%–60% of $\dot{V}O_2$ max, just below the anaerobic threshold (fig. 5). In fact, if manual laborers are forced to work at levels greater than 60% of $\dot{V}O_2$ max, they are unable to maintain their strength and are eventually incapacitated by fatigue (Astrand 1960).

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