Anaerobic Metabolism during Activity in Lizards

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Summary. A new technique developed for the determination of total lactate production in small animals was used to evaluate the role of anaerobiosis during activity at different temperatures in lizards. Measurements on six species of small lizards indicate little interspecific variation or thermal effect in resting lactate levels (0.35 mg lactate/g body weight) or maximal lactate levels achieved at exhaustion (1.4 mg lactate/g). Normally active *Anolis* in captivity had a lactate content of 0.5 mg lactate/g. Rates of lactate formation were most rapid during the first 30 sec of activity and had a low thermal dependence ($Q_{10}=1.1$—1.3 above 20° C). The lactate formed during activity persists for long periods; e.g., for 30 to 60 min between 20 and 37°C in *Anolis carolinensis* (Fig. 1). Recovery rate generally increases with temperature. Muscle lactate concentrations peak at the end of activity, but liver and blood lactate are not maximal until 10 and 30 min, respectively, after activity (Fig. 2). The decrease in the blood lactate is shown to be a poor estimator of total recovery. An estimated 80—90% of the total energy utilized during initial vigorous activity comes from anaerobic sources. Because of its low thermal dependence, anaerobiosis permits high levels of activity in lizards at all body temperatures without requiring high levels of aerobic resting metabolism.

Introduction

The concept of metabolic scope, the maximum potential increment in metabolic rate above standard metabolic levels, has been proposed as a general metabolic index of the capacity for activity in an organism (Fry, 1947). This metabolic scope has generally been equated with the increment that occurs in the rate of oxygen consumption during activity. However, aerobic processes clearly represent only one aspect of the total metabolic expenditure. Moberly's studies (1968a, b) in the lizard *Iguana iguana* suggest that anaerobic metabolism, i.e., the degradation of glycogen or glucose to lactic acid, may be particularly important in reptiles. The energetic yield of this process is relatively low compared to aerobic pathways and it can have disruptive effects on blood pH and oxygen transporting ability (see Bennett, 1971). However, it has the advantage of providing a rapid energy mobilization, and has the capacity for generating relatively large continuous energetic output because it is independent of supplies of material external to the muscle, i.e., it is free of lags inherent in the general transport systems of the body.

A variety of evidence indicates that reptiles rely heavily upon anaerobic metabolism and thus represent an interesting group for an examination of this metabolic process. The activities of the regulatory enzymes of glycolysis are particularly high in the muscles of iguanid lizards (Bennett, 1972a), and plasma levels of lactate dehydrogenase are ten- to twenty-times greater in reptiles than in mammals (H. Pough, pers. comm.). Reptiles tolerate high levels of anaerobiosis in anoxic situations and can survive extended exposure to pure nitrogen (Belkin, 1963). Blood lactate reaches extremely high levels during or after diving in turtles (Johlin and Moreland, 1933; Robin *et al.*, 1964), lizards (Moberly, 1968b), snakes (Murdaugh and Jackson, 1962), and crocodilians (Andersen, 1961). Even in non-hypoxic situations, most reptiles examined appear to depend upon anaerobic metabolism during activity. Blood lactate reaches high levels after struggling in iguanid and agamid lizards (Moberly, 1968a, b; Bennett, 1971; Wilson, 1971) and crocodilians (Dill and Edwards, 1931). Analysis of oxygen debts following struggling in *Sauromalus hispidus* also suggest high levels of anaerobic metabolism during activity (Bennett, 1972b). Varanid lizards appear exceptional in their ability to minimize reliance on anaerobiosis (Bennett, 1971, 1972b).

Despite the apparent importance of anaerobic pathways, it has formerly been impossible to quantify accurately the metabolic contribution of anaerobiosis to total energy utilization. During activity, lactate is produced in the muscles, transported in the blood, and catabolized in the liver. Due to the dynamic and compartmental nature of these processes, analysis of any single component cannot yield total lactate production. Standard techniques such as measurement of blood lactate can only indicate the general level of anaerobiosis and cannot be used to estimate anaerobic scope. A complete compartmental analysis requires large numbers of organisms and is hampered by the non-uniform distribution of lactate production in the various muscles. We have developed a new technique for the determination of total lactate production during activity. In the present investigation, this technique has been employed to evaluate the anaerobic contribution to activity in different species of lizards and to determine the thermal dependence of this process.

Materials and Methods

Analysis of Total Lactate. Total lactate levels were determined by analysis of whole body homogenates. Animals are homogenized in perchloric acid and the lactate content of the supernatant fluid is then determined with an enzymatic test kit. Since all body compartments are analyzed simultaneously, total lactate content is thus obtained. The variability between individual organisms in any given activity state has proved to be small, and only a few specimens are consequently required for analysis. Since only small volumes are necessary for lactate determination by this

technique, it is possible to measure anaerobiosis in animals smaller than 1 g. This analytical technique is applicable to any organism within a reasonable size range. Using this method, it is possible to examine the effects of various factors on anaerobiosis in the same manner as their influence on aerobic metabolism has been examined in the past.

Chemical analysis. Animals were decapitated and homogenized on ice at maximum speed in 4- to 10-times their weight in 0.6 N perchloric acid for 1 min in a Servall Omnimixer or an Osterizer. A sample of the homogenate was centrifuged for 10 min at 3000 rpm on a bench centrifuge. The supernatant fluid was filtered and recentrifuged at 10000 rpm (12000 g) at 4°C for 10 min. The resulting supernatant was analyzed for lactate with an enzymatic test kit (No. 15972, Lactate—UV method, Boehringer and Soehne). Occasional precipitates formed by the addition of the supernatant to the test buffer solution were removed by bench centrifugation immediately before spectrophotometric analysis. All samples were read on a Beckman DB spectrophotometer at 366 nm.

Effects of Temperature and Activity on Lactate Production. Adults of the following species of lizards were obtained from commercial animal dealers: *Anolis carolinensis* (mean weight = 4.5 g), *Dipsosaurus dorsalis* (33.4 g), *Lygosoma laterale* (1.7 g), *Phrynosoma platyrhinos* (18.5 g), *Uta stansburiana* (4.0 g), and *Xantusia vigilis* (1.16 g). Mixed sexes were used in all cases except for *Anolis*, in which only males were employed. The animals were fasted for at least two days but had water up to the time of experimentation. They were weighed, put in small individual containers, and placed in the dark in a large temperature cabinet, which was regulated at 12, 20, 30, or 37°C (± 0.5°C). The animals were left undisturbed overnight for at least 18 hr. A sample of individuals was then either analyzed immediately (resting controls) or subjected to stimulation for either 30 sec or 90 sec or until exhaustion. The latter was judged by the inability of the animal to right itself when placed on its back; this condition was accompanied by eye closure and extreme muscular weakness. Stimulation consisted of chasing the unrestrained animal about a plastic container within the temperature cabinet by prodding the legs and tail. This stimulation was sufficient to produce violent running and struggling behavior, equivalent to the response obtained by electrical stimulation.

A separate experiment was performed with *Anolis* to estimate lactate levels during daytime activity. Animals were maintained in a vivarium for several weeks; this container was then transferred to the temperature cabinet, which was set at 30°C and illuminated on a 12 hr photoperiod. The following day, animals were sampled periodically without regard to previous activity.

Recovery from Activity. To determine the time course of lactate removal after stimulation, individual *Anolis*, held at 20, 30, or 37°C, were stimulated to exhaustion and then permitted to rest undisturbed for various time periods. The animals remained completely quiescent during this recovery period. They were then removed, homogenized, and analyzed as described previously.

Compartmentalization of Lactate. An experiment was performed on *Anolis* at 30°C to determine the amount of lactate in different body compartments during rest, and its transfer between these during and after activity. Groups of five animals were analyzed after rest, exhaustion, or 10, 30, or 90 min recovery after exhaustion. Samples of blood, liver, and leg from all the animals within each experimental group were pooled in iced perchloric acid, weighed, homogenized, and analyzed as previously described. The intestinal tracts were also removed and pooled from the resting group to determine whether detectable amounts of lactate occur within the guts of these animals.

Results

Lactate Production during Activity

To facilitate discussion, we have adopted the following terminology. In accordance with Fry's concept (1947) of metabolic scope, the term *anaerobic scope* is defined as the maximal rate of lactic acid production during activity. In the present study, this rate was estimated from the lactate generated during the first 30 sec of activity, because these were the maximal rates observed (Table 1) and they coincided with the highest levels of activity. The term *anaerobic capacity* is defined as the total amount of lactate produced during activity to exhaustion, i.e., the maximum increment over resting levels. Anaerobic capacity is taken as an estimate of the total anaerobic energy which an animal is capable of generating for activity.

Behavioral responses to stimulation underwent a similar sequential pattern in all species. At 20°C and above, there was always an initial burst of violent activity characterized by continuous running which lasted 1 to 1.5 min. This behavior probably corresponds to the high speed flight observed in most of these animals. Thereafter, animals became sluggish and generally unresponsive to further stimulation of any type: activity became much more episodic and was never sustained until complete exhaustion occurred. At 12°C, the initial burst of activity was essentialy absent; animals tended to be sluggish throughout the period of stimulation. Variation in behavior and in time to exhaustion between individuals of a species at each temperature was low (Table 1). Time to exhaustion is inversely proportional to temperature, but in general all animals except *Dipsosaurus* exhausted rapidly, i.e., in about 5 min. *Dipsosaurus* at 37°C was not completely exhausted after 10 min of activity, but was very sluggish and unresponsive to stimulation.

Lactate production paralleled these changes in behavior. More than half of the total lactate produced during activity to exhaustion is formed during the first 30 sec and about 90% of the total, in the first 90 sec of activity (Table 1). There appears to be little difference in resting lactate levels either between species or within a species at different temperatures; these concentrations approximate 0.35 mg lactate/g body weight. Likewise, the lactate concentrations at exhaustion, averaging about 1.4 mg lactate/g, are remarkable in their homogeneity among species and in their thermal independence (Table 1). Thus, these animals have an anaerobic capacity of approximately 1.1 mg lactate/g (Table 2).

Anaerobic scope has a surprisingly low thermal dependence (Table 2). The Q_{10} values for this process above 20°C were approximately 1.15 for *Anolis*, 1.3 for *Uta*, and 1.2 for *Xantusia*. The higher Q_{10} of 3.1 between 12 and 20°C in *Xantusia* reflects the relative inactivity of these animals at the colder temperature (see above).

Table 1. Lactate content of lizards during rest and activity. Mean values with standard errors are reported; number of animals is given in parentheses

Species	Temperature °C	Lactate Concentration mg lactate/g body weight				Time to exhaustion min
		Rest	30 sec	90 sec	Exhaustion	
Anolis carolinensis	20	0.35±0.01 (3)	0.97±0.03 (8)	—	1.37±0.09 (4)	5.34±0.58
	30	0.39±0.02 (3)	1.06±0.06 (4)	1.33±0.05 (4)	1.46±0.04 (3)	4.94±0.29
	37	0.36±0.02 (3)	1.13±0.06 (4)	—	1.55±0.04 (4)	4.66±0.50
Dipsosaurus dorsalis	37	0.31±0.03 (3)	1.16±0.11 (3)	1.75±0.06 (4)	1.87±0.08 (5)	—[a]
Lygosoma laterale	12	0.19±0.03 (5)	—	—	1.32±0.05 (3)	9.42±0.74
	20	0.34±0.04 (5)	—	—	1.28±0.03 (5)	5.73±0.15
	30	0.49±0.02 (4)	—	—	1.37±0.04 (6)	4.61±0.26
Phrynosoma platyrhinos	37	0.27±0.04 (3)	0.76±0.03 (4)	1.20±0.04 (4)	1.43±0.05 (4)	5.01±0.13
Uta stansburiana	20	0.33±0.06 (3)	0.92±0.05 (3)	—	1.45±0.04 (3)	4.67±0.13
	37	0.37±0.02 (3)	1.26±0.07 (4)	—	1.49±0.08 (5)	3.25±0.54
Xantusia vigilis	12	0.27±0.02 (3)	0.54±0.05 (5)	—	1.42±0.07 (4)	8.05±0.64
	20	0.23±0.01 (3)	0.89±0.06 (5)	—	1.42±0.07 (4)	6.02±0.49
	30	0.34±0.02 (3)	1.12±0.03 (5)	1.63±0.04 (3)	1.66±0.06 (5)	5.68±0.40

[a] Experiment terminated after 10 min of activity.

Anolis which were permitted free mobility in a vivarium at 30°C were fairly quiescent; they had an average lactate content of 0.50 (± 0.03 S. E.) mg lactate/g ($n = 8$). This is about 30% above strictly resting diurnal lactate levels at this temperature (Table 1) but represents only 10% of the possible anaerobic capacity.

Recovery from Exhaustion

The rate of disappearance of lactate formed during activity to exhaustion in *Anolis* at different temperatures is shown in Fig. 1. There does not appear to be continued lactate production after the cessation of

Table 2. Anaerobic capacity and anaerobic scope in small lizards

Species	Temperature °C	Anaerobic capacity[a] mg lactate/g	Anaerobic scope[b] mg lactate/(g × min)
Anolis carolinensis	20	1.02	1.24
	30	1.07	1.34
	37	1.19	1.54
Dipsosaurus dorsalis	37	1.56[c]	1.70
Lygosoma laterale	12	1.13	—
	20	0.94	—
	30	0.88	—
Phrynosoma plathyrhinos	37	1.16	1.00
Uta stansbutiana	20	1.12	1.16
	37	1.12	1.78
Xantusia vigilis	12	1.15	0.54
	20	1.19	1.32
	30	1.32	1.54

[a] Total lactate produced during activity to exhaustion.

[b] Rate of lactate formation during first 30 sec of activity.

[c] After 10 min of activity.

activity, since lactate levels do not rise after termination of stimulation. The presistence of the lactate is impressive, especially at the coolest temperature: insignificant amounts have been catabolized after 15 min at 30°C, 30 min at 37°C, and 60 min at 20°C. Overall recovery rates are generally temperature dependent, being slowest at 20°C and most rapid at 37°C.

Compartmentalization of Lactate

The distribution of lactate within the body before and after activity in *Anolis* is shown in Fig. 2. Lactate levels are high in leg muscle tissue even during rest. Blood, liver, and gut have lactate contents of 0.1–0.2 mg lactate/g tissue (10–20 mg-%). These values are similar to those reported for blood lactate in other resting lizards (Dill *et al.*, 1935; Edwards and Dill, 1935; Moberly, 1968a; Bennett, 1971; Wilson, 1971). The low gut lactate content indicates that there is no significant exogenous lactate production by the gut biota after two days of fast.

Of the three compartments examined, only muscle lactate levels have reached their highest values at the time of exhaustion. We determined that muscle constitutes approximately 60% of the total leg weight. Assuming that the skin and bone of the leg contain insignificant amounts
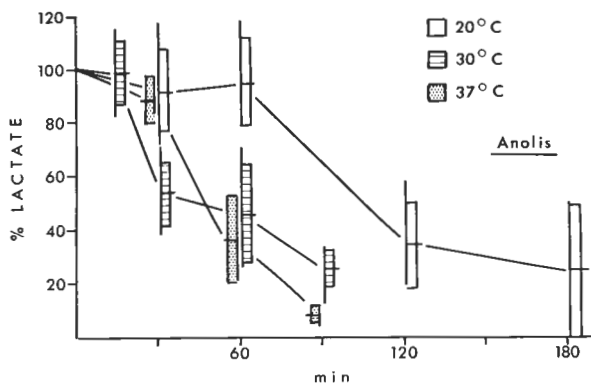
Fig. 1. Removal of lactate produced during activity to exhaustion in adult male *Anolis carolinensis*. Animals were stimulated and allowed to recover at the same temperature. The ordinate shows percentage of lactate increment due to activity which remained after intervals. The abscissa indicates the time after exhaustion. Each sample consisted of 5–10 animals. Values for mean, twice the standard error, and range are given by horizontal line, vertical bar, and vertical line
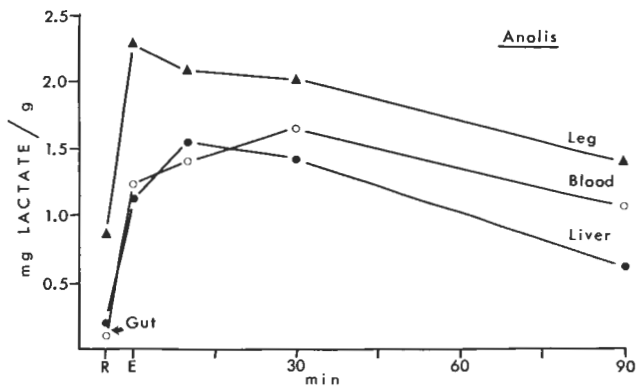

Fig. 2. Compartimentalization of lactate in *Anolis carolinensis* at 30°C before activity (*R*), at the time of exhaustion (*E*), and at various times after exhaustion. Gut samples were run only on resting animals. Each value represents pooled samples of tissue from five animals

of lactate, muscle tissue at exhaustion would contain about 3.8 mg lactate/g. Moberly (1968a) measured 2.5 mg lactate/g of leg muscle during activity in *Iguana iguana*. Liver and blood lactate concentrations increase considerably during activity but do not reach peak values until 10 and 30 min, respectively, after activity. Peak values of blood lactate

are similar to maximal values reported for *Iguana* and *Sauromalus* (Moberly, 1968a, b; Bennett, 1971). After 30 min, the rates of elimination [mg lactate/(g × min)] are approximately equal, indicating that an equilibrium between these compartments has been established.

Discussion

These data represent the first measurements of total anaerobic energy utilized during activity. As such, no strictly similar data are available for comparison. From separate measurements of lactate concentrations in muscle, blood, and liver in *Iguana iguana*, Moberly (1966) estimated a total body concentration of 1.64 mg lactate/g after 5 min of activity. This estimate agrees well with the whole body lactate concentrations measured here. The recovery times from lactacid debt for *Anolis* are over twice as great as those for *Sauromalus hispidus*, calculated on the basis of post-activity oxygen consumption (Bennett, 1972b). Moberly (1968a) measured a more rapid rate of removal of lactate from the blood of adult *Iguana iguana* than we found in *Anolis* (70% recovery after 90 min compared to 38% for *Anolis*). These two species, however, are considerably larger than *Anolis*, and size may be an important factor in the rate of debt repayment. There is a good correspondence between the maximal level of blood lactate after activity (1.64 mg/ml) and that of total lactate production during activity (1.46 mg/g). For some species, it may be possible to establish an equivalence between maximal blood and whole body lactate concentrations, so that the former sampling technique may be used to estimate total anaerobic energy production. However, the rate of removal of blood lactate appears to be a poor estimate of recovery from lactate debt. Recovery is commonly estimated as a percentage of lactate remaining compared to the total formed during activity. On this basis, blood lactate levels remain much higher than those of either muscle or liver and do not correspond well with removal from the entire body. For example, calculations based on blood lactate levels indicate only 38% recovery 90 min after activity in *Anolis* at 30°C (Fig. 2), whereas whole body lactate determinations show a recovery of 74% (Fig. 1).

This study suggests little variation in anaerobic abilities between species of lizards. The anaerobic scope of *Phrynosoma* is lower than that of other species. However, this is probably the result of the locomotory patterns of these animals. Unlike the other species examined, its body structure is rigid and does not participate in forward propulsion; consequently the legs are responsible for nearly all the muscular activity. Anaerobic capacity, however, in *Phrynosoma* is similar to that of other species. The highest anaerobic capacity was measured in *Dipsosaurus*

at 37°C, the only temperature at which the species was examined. It is noteworthy that *Dipsosaurus* was also less prone to exhaustion than the other species examined. A more detailed study of lactate generation during activity in *Dipsosaurus* has been made (Bennett and Dawson, 1972). Lactate production during a 2-min activity period at 25, 30, 35, and 45°C is similar to the anaerobic capacity reported for species in the present study: 1.3 mg lactate/g. But lactate generation is significantly higher within the range of normal activity temperatures, e.g., 1.8 mg lactate/g at 40°C. *Dipsosaurus*, therefore, appears to possess exceptional powers of anaerobiosis in comparison to other lizards in this study. Preliminary experiments of *Cnemidophorus tigris* suggest an anaerobic capacity and resistance to exhaustion comparable to *Dipsosaurus*. *Varanus* appears to possess an even greater resistance to exhaustion than all other species of lizards examined, probably due to its superior aerobic capacities (Bennett, 1971, 1972b).

The thermal independence of anaerobic scope and capacity in the species examined is one of the most interesting aspects to emerge from this study. These species have diverse thermal preferenda and activity temperatures: *Anolis*, 31°C (Licht, 1968); *Dipsosaurus*, 40°C; *Lygosoma*, 29°C; *Phrynosoma*, 36°C; *Uta*, 35°C; *Xantusia*, 30°C (Brattstrom, 1965). With the exception of *Dipsosaurus*, there is no indication that lactate production at preferred body temperature is significantly greater than at other body temperatures. The very low thermal dependence of anaerobiosis in these animals (e.g., $Q_{10} = 1.1$–1.3 over a wide temperature range) is in distinct contrast to that of aerobic metabolism: Q_{10} values for active oxygen consumption and scope are generally greater than 2.0 at body temperatures below preferred levels (Dawson, 1967; Asplund, 1970; Wilson, 1971; Bennett, 1972b). Also, recent data indicate that aerobic scope is generally maximal at preferred body temperature in reptiles (Wilson, 1971; Bennett and Dawson, MS in press). It is, therefore, to be expected that the relative contribution of aerobic metabolic processes to activity would be greatest at preferred temperatures and that anaerobiosis would be especially important at other temperatures.

It is possible to estimate the percentage contribution of anaerobic and aerobic energy sources to total energy utilized during activity from measurements of oxygen consumption and lactate production. The amounts of ATP generated from these two processes are:

$$1.0 \text{ mg lactate formed} = 0.0167 \text{ millimoles ATP};$$
$$1.0 \text{ cc } O_2(\text{STP}) \text{ consumed} = 0.290 \text{ millimoles ATP}.$$

The first equation assumes that glycogen is the only substrate catabolized; blood glucose levels do not change during activity in *Iguana iguana* and all lactate formation can be accounted for by the decrement in muscle

glycogen (Moberly, 1968a). The second equation assumes a P/O ratio of 3.0; the latter has been determined in turtle heart mitochondria (Privitera and Mersmann, 1966).

The only aerobic scopes reported for small lizards are 0.47–0.76 cc $O_2/(g \times hr)$ at 15–35°C for *Uta stansburiana* (Alexander and Whitford, 1968) and 0.36–1.75 cc $O_2/(g \times hr)$ at 20–40°C for *Cnemidophorus tigris* (Asplund, 1970). Assuming average aerobic scopes of 0.5 and 1.5 cc $O_2/(g \times hr)$ at 20 and 37°C, respectively, and an average total production of 1.1 and 1.25 mg lactate/g at these same two temperatures, then anaerobic sources account for 60% at 20°C and 36% at 37°C of the total energetic production over a 5-min period. These values of oxygen consumption probably overestimate the aerobic component because of contamination by oxygen debt repayment. Moberly (1968a) estimated that at least 77% of the total energy utilized by *Iguana iguana* during a 5-min struggle is anaerobically derived. Moberly did not, however, take into account the lactate content of the animals before activity. Assuming that distribution of lactate in *Iguana* is similar to that in *Anolis*, his estimate should be corrected to yield 64% anaerobic energy generation. Between 60–80% of the energy utilized during a 2-min burst of activity by *Dipsosaurus* between 25 and 45°C is anaerobically produced (Bennett and Dawson, 1972).

Lizards are rarely active for periods as long as 5 min. As reported previously, violent, sustained struggling is only maintained for 1.0–1.5 min. We may calculate a more meaningful ratio of the sources of energy production by estimating expenditures during the first 30 sec of activity, the critical period for escape or chase. Assuming rates of 0.60 and 0.80 mg lactate/$(g \times 30$ sec) at 20 and 37°C, respectively, and the same aerobic rates as above, the anaerobic component constitutes 90% of the total energy production at 20°C and 80% at 37°C. It is improbable that oxygen consumption reaches the maximal values utilized in these calculations during the first 30 sec of activity. These figures indicate that during the initial stages of activity, these lizards are relying almost exclusively on anaerobic sources of energy.

Anaerobiosis appears to constitute the ideal solution to the energetic problems posed by activity to small behaviorally-thermoregulating poikilotherms. Such animals are forced to contend with a wide range of body temperatures over the course of a day, even though the behaviorally-regulated thermal range may be quite narrow. A capacity for a rapid activity response is desirable at all body temperatures. Due to the complexity of oxygen transport, aerobic systems cannot be mobilized rapidly. In order to process large amounts of substrate rapidly, oxygen utilization would have to be maintained at high levels continuously and thus would require a continuously high metabolic rate. Anaerobiosis is a potential

system of energy generation that requires maintenance without the need for a continuous flow of substrate. Since the capacity for anaerobic energy generation is essentially temperature independent in reptiles, it permits activity at all body temperatures and does not require high levels of resting metabolism. Its disadvantages, i. e., the formation of a large amount of lactate with its disruptive physiological effects, appear to be outweighed by the rapid activity responses which the system permits.

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