

# 1 Ecological Consequences of Activity Metabolism

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LIZARDS EXHIBIT LOW RESTING levels of oxygen consumption and energy utilization compared to mammals and birds. Their rate of resting metabolism is similar to that of other reptiles and other ectothermic vertebrates and invertebrates of similar temperature and size (Hemmingsen, 1960; Bennett and Dawson, 1976). This low rate of energy turnover is insufficient to provide substantial physiological thermoregulation, and lizards must consequently thermoregulate behaviorally or assume the temperature of their environment. Such a low rate of energy demand has obvious advantages in permitting lizards and other ectotherms to survive on very little food, to tolerate periods of limited food availability or unpredictability of food resources, and to convert a large fraction of ingested food into biomass. The thermal and energetic consequences of low metabolic rate in lizards are fairly familiar to ecologists and have been summarized elsewhere (Dawson, 1967; Tucker, 1967; Templeton, 1970; Bennett and Dawson, 1976; Bennett, 1978, 1982; Pough, 1980). However, there are apparently other consequences associated with this low level of energy metabolism and oxygen consumption, among which is the fact that maximal levels of oxygen consumption for lizards are also relatively low compared to those of endotherms. Since sustained activity requires increased oxygen utilization, behavioral capacities of lizards are curtailed by low absolute levels of available aerobic power. These behavioral constraints structure interactions between lizards and both their biotic and abiotic environments. Thus lizards' physiological capacities for activity have direct effects on both their behavior and ecology.

## **Aerobic Power Input**

Power inputs from aerobic metabolism available to lizards during activity have been examined in different ways. One method is the determination of maximal oxygen consumption and calculation of maximal aer-

obic power input on that basis. The implicit assumption that all this oxygen consumption can be diverted to physical activity is incorrect since many processes besides contraction of skeletal muscle are maintained during exercise. Although this method yields an overestimate, it is at least relatively simple to perform. Another metric, the scope for activity, was proposed by Fry (1947) as a measure of work capacity and was defined as the difference between maximal and resting rates of oxygen consumption. But use of aerobic metabolic scope assumes that physiological processes continue at the resting level even during activity. This assumption is also almost certainly incorrect since some "maintenance" functions will be augmented and some will decrease during activity. This measure has the advantage, however, of recognizing that a portion of aerobically derived energy is not available for physical activity.

Aerobic power capacities of lizards have been summarized in a series of mass-dependent power expressions. For lizards, the following relationships describe aerobic metabolic power input at 35 °C (Bennett, 1982):

$$\begin{aligned} \text{resting oxygen consumption: } y &= 2.51 m^{0.78}, & (1.1) \\ \text{maximal oxygen consumption: } y &= 16.3 m^{0.76}, & (1.2) \\ \text{aerobic metabolic scope: } y &= 13.8 m^{0.76}, & (1.3) \end{aligned}$$

where  $y$  is aerobic power input in mW (divide by 5.6 to obtain values in ml O<sub>2</sub> h<sup>-1</sup>) and  $m$  is body mass in g. Thus, a 100-g lizard would have a maximal aerobic power input of 540 mW and an aerobic metabolic scope of 460 mW at 35 °C. Similar relationships have been derived for lizards at other body temperatures as well (Wilson, 1974; Bennett and Dawson, 1976; Bennett, 1982). These levels of resting and active metabolism are similar to those of fish and amphibians but are substantially less than those of mammals or birds of equal size (Table 1.1).

The maximal aerobic metabolic power input of which lizards are capable is quite low. Additionally only a small portion of this power input appears as power output (work involved in activity), because organisms are not completely efficient in energetic conversions. As lizards rarely do work in the sense of moving objects from one place to another, their low work capacities may not appear to be important. However, low aerobic power inputs have severe effects on locomotor capacities, and these effects underlie all of the behavioral repertoire of these animals. The consequences of such limited capabilities may be best envisioned in an examination of locomotor energetics.

### **Locomotor Energetics and Limitations**

The energetics of quadrupedal terrestrial locomotion have been measured in a variety of animals, including lizards, and theoretical discussions and summaries are available elsewhere (Taylor, Schmidt-Nielsen,

Table 1.1 Maximal aerobic power input during activity in small vertebrates (data summarized in Bennett and Ruben, 1979).

Species	Mass (g)	Aerobic power input (mW/g)
<b>Lizards</b>		
<i>Dipsosaurus dorsalis</i>	35	11
<i>Iguana iguana</i>	800	3
<i>Varanus gouldii</i>	674	6
<b>Other reptiles, amphibians, and fish</b>		
<i>Bufo cognatus</i>	40	9
<i>Carassius auratus</i>	66	2
<i>Pituophis catenifer</i>	548	3
<i>Pseudemys scripta</i>	305	6
<i>Rana pipiens</i>	38	3
<i>Salmo gairdneri</i>	66	3
<b>Mammals and birds</b>		
<i>Larus atricilla</i>	322	71
<i>Melopsittacus undulatus</i>	35	171
<i>Mus musculus</i>	34	52
<i>Pteropus gouldii</i>	779	60

and Raab, 1970; Tucker, 1970; Schmidt-Nielsen, 1972; Taylor, 1973). Aerobic power input (oxygen consumption) is measured as a function of locomotor speed, which is set by a motor-driven treadmill. As speed increases, oxygen consumption increases approximately linearly. The slope of the line is designated the net cost of transport, is expressed in units of ml O<sub>2</sub>/(g · km) or J/(g · km), and is independent of speed. From one point of view, this number may be interpreted as the amount of work required to move a unit of body mass over a unit distance. However, since this function does not have an intercept of zero, there are other costs in addition to those represented by the net cost of transport. These are accounted for by dividing total oxygen consumption by speed, yielding a value termed the cost of transport (Tucker, 1970) or the total cost of locomotion (Schmidt-Nielsen, 1972). This value is expressed in identical units, J/(g · km), but is dependent on speed and decreases as speed increases. Consequently, the total cost of moving a unit of mass over a unit distance decreases as speed increases. This relationship has obvious energetic consequences for locomotor activity. Both net and total cost of transport are useful in assessing locomotor costs in energy budgets, but it is important to distinguish between them because they are easily confused. The intercept of the metabolism-speed curve also merits some comment since it has been commonly observed that it exceeds the value of resting metabolic rate, often by a factor of 1.5 to 2.0. The significance of this relation is unclear. However, it does indicate that locomotion and activity, even at very slow speeds, almost always

involve substantial increments in metabolic rate. Locomotion and activity are expensive and can represent a major portion of the energy budget of an animal, even if activity is infrequent or low level.

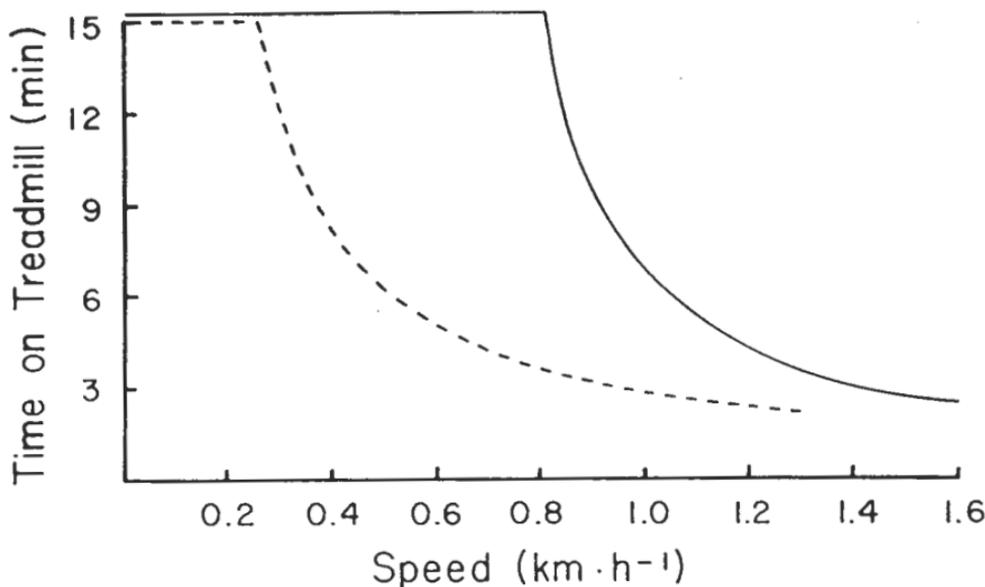
The relationship of aerobic metabolic rate to speed does not increase indefinitely. Oxygen consumption increases linearly with speed up to the point at which maximal oxygen consumption is attained (the maximal aerobic speed). Maximal oxygen consumption is then maintained as speed increases further. Power input requirements, of course, continue to increase and must be met with other, anaerobic sources of energy provision. Behavior and exertion in excess of maximal aerobic speed are not sustainable, and fatigue begins to limit performance. This transition velocity between sustainable and nonsustainable locomotion is surprisingly low in lizards. Maximal aerobic speeds for a variety of lizards are given in Table 1.2. With the exception of *Varanus*, all these are less than 1 km/h. These represent very slow velocities, an order of magnitude below those of which these same lizards are capable during burst activity.

An additional factor influencing oxygen consumption and aerobic power input is the effect of body temperature. Most aerobic processes in lizards, including maximal aerobic power input, are strongly temperature dependent. Maximal oxygen consumption generally has a temperature coefficient ( $Q_{10}$ ) of 2 to 3, that is, aerobic capacity is reduced by one-half to two-thirds by every 10° C decrement in body temperature. In view of the limiting relationship of oxygen consumption and speed, we might anticipate that low temperature would similarly curtail sustainable activity capacity and behavior. The limited data available suggest that this is so. Walking ability in *Iguana iguana* is strongly influenced by temperature (Moberly, 1968). The greatest walking speeds sustainable for 10 to 20 minutes by *Iguana* have the following thermal dependence: 20° C, 0.17 km/h; 25° C, 0.23 km/h; 30° C, 0.45 km/h; 35° C, 0.52 km/h; 40° C, 0.45 km/h. Low body temperature strongly curtails stamina; note again how low these velocities are. A similar temperature-dependent decrement in performance is found in the desert iguana, *Dipsosaurus dorsalis* (Fig. 1.1) (John-Alder and Bennett, 1981). Maximal aerobic speed declines from 0.8 km/h at 40° C to 0.3 km/h at 25° C. Body temperature obviously exerts an important influence on activity and stamina, and low or even moderate temperatures may greatly restrict behavioral capacity. It should be remembered that there are definite energetic benefits to be gained from the overall metabolic depression associated with low body temperatures. The energetic saving accrued is considered to be one of the major advantages of the poikilothermic condition (Pough, 1980).

Body temperature may also influence locomotor costs directly, beyond placing limitations on maximal aerobic speed. At present, data are too few to permit confident generalizations. In *Iguana* (Moberly, 1968)

Table 1.2 Maximal aerobic speeds and burst speeds in lizards.

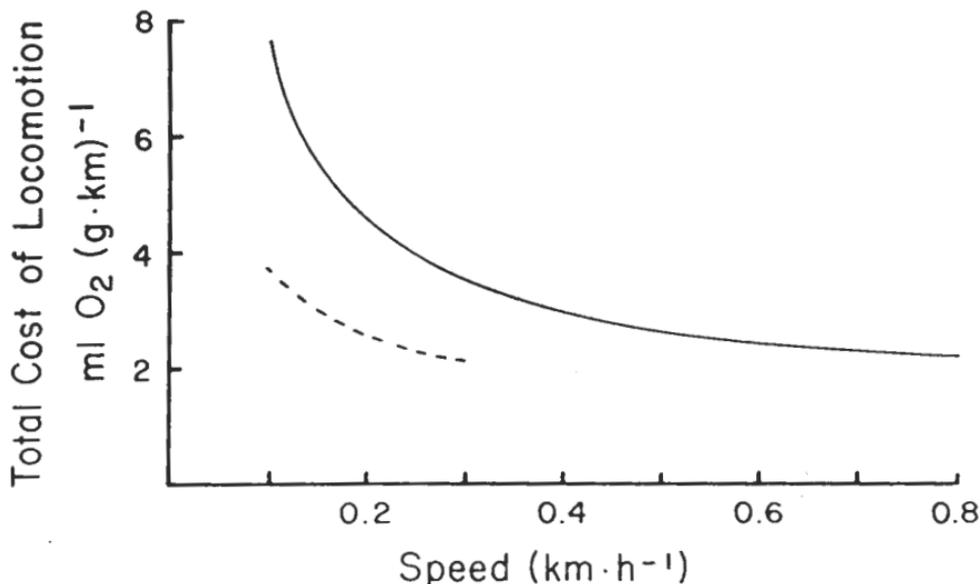
Species	Maximal aerobic speed (km/h)	Burst speed	$T_B$	Reference
<i>Amblyrhynchus cristatus</i>	1.0	9.0	35	Gleeson, 1979
<i>Cnemidophorus murinus</i>	0.3	8.8	40	Bennett and Gleeson, 1979; Bennett, 1980
<i>Dipsosaurus dorsalis</i>	0.8	7.8	40	John-Alder and Bennett, 1981; Bennett, 1980
<i>Gerrhonotus multicarinatus</i>	0.3	3.9	35	John-Alder, unpublished observations; Bennett, 1980
<i>Iguana iguana</i>	0.5	16.4	35	Gleeson, Mitchell, and Bennett, 1980; unpublished observations
<i>Tupinambis nigropunctatus</i>	0.6	14.2	35	Unpublished observations
<i>Varanus exanthematicus</i>	1.2	12.5	35	Gleeson, Mitchell; and Bennett, 1980; unpublished observations



**Figure 1.1** Endurance as a function of speed and temperature in the lizard *Dipsosaurus dorsalis*. Lines indicate the average duration of sustained walking behavior at each speed. The broken line indicates a body temperature of 25°C; the solid line, 40°C. Experiments were terminated after 15 min at both temperatures. (After John-Alder and Bennett, 1981.)

and *Dipsosaurus* (John-Alder and Bennett, 1981) increasing body temperature increases the metabolic rate of a lizard walking at a given sustainable speed but does not alter the net cost of transport, that is, the intercept but not the slope of the speed-metabolism curve is increased. Thus, walking at 35°C is more expensive than walking at 25°C, but a further increase in speed results in equal metabolic increments at both temperatures. Locomotion is consequently more expensive at higher temperatures in these lizards. This is reported not to be the case for the agamid *Uromastix aegyptius* (Dmi'el and Rapoport, 1976), in which metabolic rate while walking at a given speed is independent of temperature. Only further observations will make clear which of these patterns, if either, predominates.

It is now easier to appreciate the conflicting pressures of temperature on locomotor ability in lizards. On the one hand, low body temperatures reduce metabolic and locomotor costs but result in very low stamina. On the other hand, high temperatures greatly expand the range of sustainable behaviors but increase energy demand. The cost of activity at high temperatures may be balanced somewhat by increasing speed, since the total cost of locomotion decreases because maintenance costs form a smaller proportion of total metabolic expenditure. These relationships are given in Figure 1.2 for *D. dorsalis*. At any speed sustainable at both



**Figure 1.2** The total cost of locomotion at different speeds and temperatures in the lizard *Dipsosaurus dorsalis*. The broken line indicates a body temperature of 25°C; the solid line, 40°C. (After John-Alder and Bennett, 1981.)

body temperatures, energy expenditure is less at the lower temperature. However, the total cost of locomotion decreases as speed increases, and these values are nearly equal at maximal aerobic speeds at each temperature. That is, the cost differential associated with the difference in body temperature can be offset by walking faster at the higher temperature. The greater scope for activity and stamina at high temperatures permits behavior which may ameliorate the increased costs incurred.

These low aerobically supportable velocities set limits on the behavioral capacities of lizards. A variety of behavioral and ecological roles are not available to animals with this limited aerobic metabolic scope. For instance, certain lizards may be specialized for gliding, but the power requirements for flapping flight are far beyond the capacities of modern reptiles. The expenses cannot be met regardless of body design. Likewise, we do not anticipate herds of herbivorous lizards grazing in open fields, galloping off and outdistancing mammalian predators such as dogs. Nor do we have dog-like lizard predators, chasing down their prey. Short, intense bursts of exertion, similar to those of cats, are of course possible by carnivorous lizards, but these can last for only 1 to 2 minutes. The capacity for terrestrial migrations of any distance are also greatly limited, since they would have to be undertaken at such slow speeds that they would result in long periods of exposure to predators. Nocturnal behavior is also restricted by aerobic power input, since body temperatures are necessarily low and maximal oxygen consumption is restricted by thermal effects.

The relations between oxygen consumption, locomotion capacity, and behavior may be better understood with reference to a specific example. Locomotor and field energetics have been examined in *Cnemidophorus murinus*, a medium-sized teiid lizard found on a few Caribbean islands (Bennett and Gleeson, 1979; Bennett and Gorman, 1979). *C. murinus* is a relatively active lizard, similar to its congeners in North America or lacertids in Europe. It is a highly alert, curious, and voracious lizard. It spends about 75 percent of its emergent time in active foraging, walking more or less continuously at approximately 0.13 km/h, searching for plant or insect material. Even when moving so slowly, its oxygen consumption is four times resting values. This activity makes a substantial impact on the energy budget of this lizard, representing nearly 70 percent of the total daily energy expenditure. *C. murinus* may be unusual in devoting so much time and energy to foraging; foraging has been estimated to represent only about 10 percent of daily energy budgets of *Egernia cunninghami* (Wilson and Lee, 1974) and *Amblyrhynchus cristatus* (Gleeson, 1979). *Cnemidophorus* forages well within its aerobic capacity at about half maximal aerobically sustainable speed. The latter is attained at only 0.3 km/h, and exhaustion occurs in less than 5 minutes at 0.5 km/h. There is considerable reserve burst capacity, however, and *C. murinus* can run at speeds of about 9 km/h for short distances (Bennett, 1980). Thus, aerobically supportable behavior is only a small fraction of the performance capabilities of this lizard, even though it is apparently so active and invests so much energy in foraging activity. Normally, foraging is restricted within these aerobic limits, but additional capacity for escape or pursuit is maintained.

Estimates of locomotor costs for use in the calculation of energy budgets may be obtained from summaries of similarly derived data for lizards exercised on treadmills. The net cost of transport has been calculated to be

$$y = 75.8 m^{-0.25}, \quad (1.4)$$

where  $y$  is net cost of transport in J/(g · km) and  $m$  is mass in g (Gleeson, 1979). As is clear from the equation, it is relatively less expensive for a large lizard to move a unit mass than for a small lizard, or, stated another way, total locomotor costs increase as size increases, but they do not grow in direct proportion to body mass. For example, it costs a 1-kg lizard only one-third as much to move a unit of its weight as it costs a 0.01-kg lizard. The underlying reasons for this mass-dependent relationship are unknown. They may partially reflect the mass dependence of resting metabolic rate ( $b = 0.80$ ), the basis of which also has not been satisfactorily explained. The utility of these allometric relationships to ecologists is that they permit the estimation of foraging costs to a lizard if

body size, temperature, speed, and duration of locomotion are known. As a rough approximation, the intercept value of the speed-metabolism curve can be estimated as 1.7 times resting metabolic rate (observed values often range between 1.5 and 2.0). To this is added the product of speed and the net cost of transport. Such an equation might take the following form for a lizard at 35 °C:

$$y = 1.7(2.51 m^{0.78}) + s(21.2 m^{0.75}), \quad (1.5)$$

where  $y$  equals metabolic rate in mW,  $m$  is mass in g, and  $s$  is speed in km/h. Thus, a 100-g lizard travelling at 1.0 km/h would have a power input of approximately 820 mW. These relationships permit very general estimates of foraging costs in regard to total energy budget or in regard to a cost-benefit analysis of return gained for energy expended. Such estimates would also fit comfortably with a time-energy budget and provide more realistic estimates of activity costs than are currently available.

The components of Eq. 1.5 contain considerable variability: the net cost of transport, for example, may in fact be double or only half that predicted by Eq. 1.4. If greater precision is required, one should make direct observations on the lizard in question. Moreover, these values represent steady-state determinations which are achieved only after 5 to 10 minutes of constant-level activity. Initial oxygen consumption during the first 1 to 2 minutes of activity is considerably less than the level anticipated by Eq. 1.5, and there is often an overshoot during the next several minutes of activity. The predictive value of these relations in estimating the cost of short-term activity, such as walking between two bushes, is less than certain.

The previous discussions have treated lizards as interchangeable animals in a relatively undifferentiated group. The submergence of interspecific differences is in many ways the desired function of these analyses. However, given the very different phylogenetic histories of modern lizards and their great diversity of body form, behavioral type, and ecological role, we certainly would anticipate a degree of diversity in aerobic capacity, behavioral performance capacity, and stamina. The one group of lizards which is clearly exceptional in these regards is the varanids. They possess substantially greater aerobic capacities than do other lizards investigated so far. Maximal levels of oxygen consumption (Bartholomew and Tucker, 1964; Bennett, 1972; Wood et al., 1978; Gleeson, Mitchell, and Bennett, 1980) and maximal aerobic speeds (Bakker, 1972; Gleeson, Mitchell, and Bennett, 1980) are nearly double those of iguanid lizards of similar size. There are obvious correlates with the predatory ability and aggressive nature of these carnivorous lizards. Apart from the varanids, however, it is much more difficult to differenti-

ate among saurian groups on the basis of aerobic ability. Maximal oxygen consumption is very similar in iguanids, agamids, skinks, and teiids, the only saurian families examined in any detail. The teiids are particularly surprising in this regard since they are considered highly active and comparatively intelligent animals (Regal, 1978), fleet, and able to subdue large prey. However, aerobic capacity of *Cnemidophorus* (Asplund, 1970; Bennett and Gleeson, 1979) is no greater than that of the similarly-sized iguanid *D. dorsalis*, and the latter has a substantially greater maximal aerobic speed (Bennett and Gleeson, 1979; John-Alder and Bennett, 1981). The aerobic ability of the large teiid *Tupinambis nigropunctatus* is very similar to that of *Iguana iguana* and maximal aerobic speeds are almost identical (Bennett, unpublished observations). Consequently, we may not be able to draw easy generalizations between apparent activity level and oxygen consumption on an interfamilial or interspecific basis. With the exception of the varanids, there appears to be little differentiation between the saurian groups in maximal oxygen consumption. Aerobic support in lizards may be sufficient for and permit a variety of different types of low-level behavior, ranging from sit-and-wait predation to herbivorous foraging or low-velocity patrol.

### Supplemental Anaerobic Energy Metabolism

When the demand for energy utilization exceeds the supply capacity of aerobic metabolism, other sources of energy generation are activated. These are termed anaerobic, a catchall term signifying that their only common element is the lack of oxygen in their function. Anaerobic metabolism may take place in lizards under some anoxic circumstances such as breath holding or diving. However, a more common circumstance when anaerobic metabolism takes place is during *physical activity*. Anaerobiosis plays a significant role under two circumstances: during the initial stages of activity and during intense exercise. In the former case, oxygen consumption cannot be increased instantaneously, as can muscular movements during pursuit or escape. Until aerobic supply can catch up with demand, anaerobiosis provides supplemental energy. Sustained exercise may also create demands for energy utilization that are beyond the maximal levels which oxygen consumption can support. These exercise levels are fairly low in lizards. The more intense the activity, the greater the level of anaerobic metabolism.

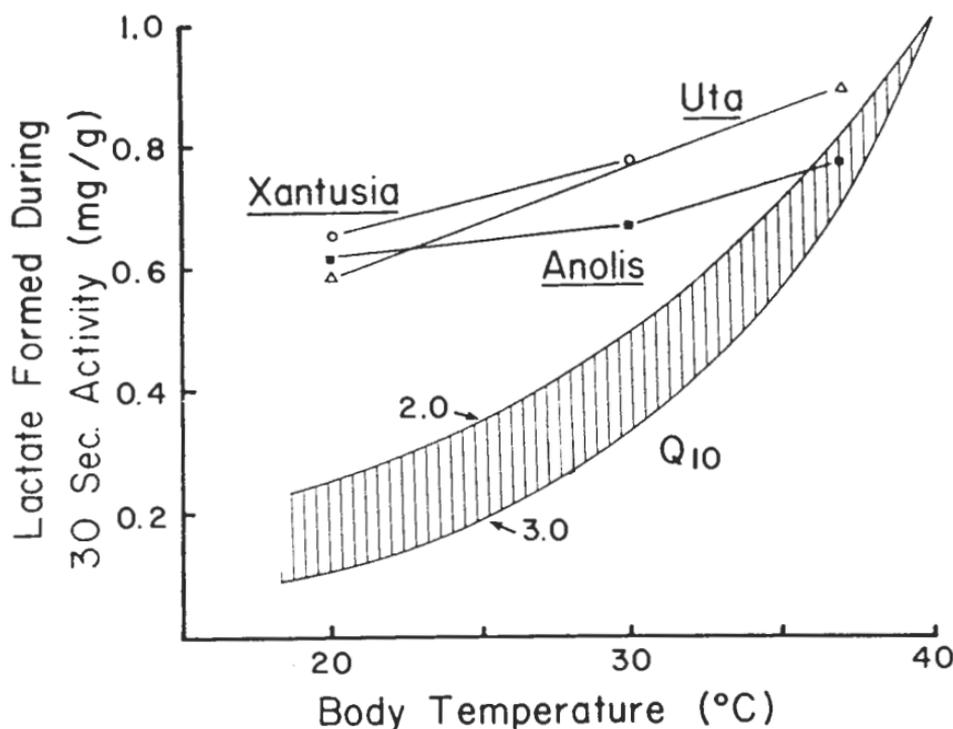
The principal anaerobic pathway during activity in lizards is the breakdown of glycogen within the skeletal muscles to lactic acid via glycolysis. Endogenous stores of adenosine triphosphate (ATP) and creatine phosphate stored in the muscle can be catabolized for fueling some muscle contraction. These compounds are used relatively early during activity over a period of a few seconds, whereas lactic acid gen-

eration provides energy for 1 to 2 minutes of maximal levels of activity in small lizards. After this time, lizards are visibly fatigued and can be driven to exhaustion shortly thereafter. The proximate causes of this fatigue after intense exercise are unknown, even in mammals.

The rate of anaerobic energy generation in lizards can be high in comparison to aerobic energy generation: maximal anaerobic power input rates range from 20 to 36 mW/g for small lizards during 30 seconds of activity (see Table 1.1) (Bennett and Licht, 1972). Rates of ATP formation via anaerobic metabolism may over short time periods greatly exceed those of aerobic metabolism: 60 to 80 percent of ATP production during 2 minutes of burst activity is produced by lactic acid formation in *D. dorsalis* and *Sceloporus occidentalis* (Bennett and Dawson, 1972; Bennett and Gleeson, 1976). The anaerobic contribution is even greater when shorter time periods are considered. This differential is still more impressive since anaerobic glycolysis is only 10 percent as efficient as aerobic metabolism at producing energy equivalents (ATP) from equal amounts of carbohydrate fuel. Consequently, the flow of carbohydrate into the anaerobic pathway is necessarily very much greater than that entering aerobic metabolic pathways. This great capacity for anaerobic energy production is responsible for the impressive capabilities for burst activity possessed by most lizards, far beyond those which aerobic systems can support. Performance capabilities are nearly tenfold greater than can be accounted for by aerobic metabolism alone (Table 1.2). Clearly anaerobiosis can provide a very significant component to the behavioral repertoire of lizards.

Another important feature of anaerobic metabolism in lizards besides its absolute magnitude is its very limited dependence on body temperature. The capacity of a variety of lizards to form lactic acid during activity is nearly as great at body temperatures of 20° C as at 40° C (Bennett and Licht, 1972) (Fig. 1.3). Temperature coefficients of anaerobic metabolism over this range are typically 1.1 to 1.3, in comparison with  $Q_{10}$ 's of 2 to 3 for aerobic metabolism. Energy mobilization for rapid activity is thus possible over a broad range of temperatures, a very important feature for rapid escape by a lizard even when it is far from its thermal preferendum. This anaerobic independence is particularly significant in view of the strong thermal dependence of aerobic metabolism. Low body temperature retards not only maximal levels of aerobically supported exertion but also the rate of development of maximal levels. Evasive behavior must be fueled almost totally anaerobically in lizards with low body temperatures. Burst speeds of lizards, as anticipated, have a fairly low thermal dependence over significant spans of body temperature (Bennett, 1980).

Although anaerobiosis provides a greatly expanded behavioral repertoire for lizards, its prolonged use may be very debilitating. One or two



**Figure 1.3** Lactate formation [mg lactate/(g body mass · 30 s)] in the lizards *Anolis carolinensis*, *Uta stansburiana*, and *Xantusia vigilis*. The hatched area indicates the anticipated thermal dependence of a biochemical reaction rate of a process with a rate of 1.0 mg lactate/(g · 30 s) at 40 °C. (Based on data from Bennett and Licht, 1972.)

minutes of intense activity can leave a lizard exhausted, even to the point of abolishing its righting reflex, and the consequent physiological disruptions may persist for hours. Consequently, we might expect an avoidance of prolonged anaerobically supported activity and its use only under infrequent conditions that demand high levels of power output. An additional factor that argues against frequent, extensive anaerobic metabolism is its inefficiency: compared to aerobic activity, 10 times as much foodstuff is required for comparable levels of exertion during anaerobic activity. Although the lactic acid formed may later be catabolized further or reconverted to glycogen, the immediate demand for ATP during activity and this inefficiency of anaerobic metabolism may severely deplete fuel reserves in muscle. If anaerobiosis occurs only infrequently, these inefficiencies would have relatively little impact on the ecological energetics of lizards and the behavioral consequences would undoubtedly be more severe than the energetic ones. The extent of utilization of anaerobic metabolism under field conditions has not received much examination, primarily because of technical difficulties in securing measurements. Some field-caught specimens of the lizard *Anolis bon-*

*airensis* possess high lactate contents (Bennett, Gleeson, and Gorman, 1981). The intensity of territorial defense also parallels lactate accumulation in these lizards. In contrast, little evidence of anaerobiosis during either basking behavior or diving was found in the marine iguanas *Amblyrhynchus cristatus*, even though anaerobic capabilities are well developed in this lizard (Gleeson, 1980). We may certainly anticipate further research into the extent of utilization of anaerobic metabolism in free-living lizards, including the circumstances of its activation and the extent of its use.

We have come to understand lizards as low-energy machines, with low maintenance costs and low capacities for sustained power output. Much of their behavior takes place within the constraints imposed by oxygen transport capacities. Anaerobic metabolism provides additional power output for emergency situations. It can greatly extend the performance capacities of lizards but has detrimental effects on subsequent behavioral capacity. Escape capabilities (burst performance) are retained over a broad thermal span, although low body temperature tends to retard sustainable behavior. This appears to be a particularly useful behavioral system, operating at low cost yet retaining high capacities for short-term performance, even under environmentally unfavorable circumstances.

All of this information, with its implications and interpretations, has been gathered in the relatively recent past. Not all the directions of future research are clear, but we can make some educated guesses as to the ways in which this area will continue to develop. First and foremost, we anticipate and require data on metabolic expenditure, both aerobic and anaerobic, under field conditions. Laboratory approaches to these problems have been very fruitful, but their interpretation and ecological significance rest ultimately upon behavior under natural circumstances. We may also anticipate on the one hand a broadening and on the other a narrowing of the phylogenetic scope of these sorts of investigations. Only two or three species have received a truly adequate examination of both their metabolic and locomotor capacities. Data are scattered for other species, and whole groups remain uninvestigated. In contrast, other studies may attempt to focus more finely on interspecific differences between closely related lizards to determine the latitude in behavioral performance which common history and similar structure and function can provide. Finally, we may expect a continuing interest in locomotor energetics per se. Interspecific differences, mass-dependent phenomena, and the cost of other types of locomotor patterns (swimming, crawling, climbing) will all undoubtedly receive attention. Lizards have in the past served as excellent models for exploring the interrelations of physiology, behavior, and ecology. We can anticipate that they still have much to provide us in the future.

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