The Energetics of Reptilian Activity

ALBERT F. BENNETT

School of Biological Sciences, University of California at Irvine, Irvine, California, U.S.A.

I. General Introduction

Most of the early investigations of energy utilization by reptiles involved the measurement of resting metabolic rates. These studies sought to establish the cost of living of quiet, undisturbed animals and to set a lower boundary on energy demands, that is, on the minimal amount of energy required from the environment. Because resting metabolic rates vary with temperature in these ectothermic animals, the thermal dependence of metabolism was often the organizational theme of these studies. These investigations were successful in permitting the establishment of quantitative allometric relationships at different body temperatures between body mass and minimal energy demand. These relationships have been developed and reported by several authors (Bartholomew and Tucker, 1964; Templeton, 1970; Dmi'el, 1972; Wilson, 1974a; Bennett and Dawson, 1976). Consequently, the energetic requirements of maintenance existence may now be predicted for most reptiles of known body size and temperature. In addition, these generalized relations may also serve as the basis from which to compare energetic adaptations of different species with some special feature of interest (e.g. habitat, body size, phylogenetic group). Examinations of the maintenance energy requirements of reptiles have found them to be very similar to those of amphibians, fish, and invertebrates, and an order of magnitude below those of mammals and birds (Hemmingsen, 1960).

With the delimitation of minimal requirements, interest arose in the operation of these animals during sustained and maximal exertion. Studies have attempted to measure the costs of low level, sustainable activity of the sort in which most reptiles engage on a daily basis. An examination of energy utilization during intense activity permitted an analysis of maximal energy

utilization and set an upper limit on energy demand and processing. It also led to determination of differential metabolic support for its maintenance. These two types of studies on active reptiles have revealed them to be animals of generally low stamina but capable of impressive bursts of short-term activity. The behavioral repertoire of reptiles reflects the limitations imposed by the metabolic systems used in transducing energy. These themes will be examined and expanded in this chapter. After an initial discussion of the metabolic support for activity, the degree and costs of sustainable activity will be examined. The relationships of burst activity and its consequences for energy utilization will also be discussed.

This area of research is expanding rapidly at present. Most of our knowledge has been gathered within the past decade. In another ten years we will have a substantially expanded data base, both phylogenetically and experimentally, from which to generalize. This present review will summarize the findings of the fifty-odd investigations into these problems and attempt to point to areas in need of further research. From the outset, however, it is important to keep in mind the limitations of interpreting the data available to us. There are two principal shortcomings which should inhibit our speculation and generalization, or at least lead us to proceed more cautiously. First, the phylogenetic scope of the observations available is not broad. The number of species that have been studied is small, and the species studied are not necessarily representative of their taxa. Nearly one-half of our data have been obtained, for instance, from the iguanid lizards of North America. Second, essential information about the ecology and behavior of these reptiles active in the field is almost nonexistent. It is consequently difficult to correlate performance determined in the laboratory with natural function or to known the extent to which animals are truly "active" or "sedentary." The former of these difficulties will be overcome with the accumulation of laboratory observations on a greater number of selected species. The latter requires a more quantitative approach in the construction of time and activity budgets by behaviorists and ecologists.

Some aspects of activity and activity metabolism in reptiles have been previously reviewed by the following authors. Benedict (1932) reviewed the early literature and made substantial contributions on energy utilization, particularly in large reptiles. The thermal dependence of activity metabolism was reviewed by Dawson (1967, 1975) and Templeton (1970). Various aspects of reptilian metabolism and energetics, primarily in resting reptiles, were presented by Bennett and Dawson (1976). Patterns of activity and metabolism were compared among reptiles, amphibians, and fish by Bennett (1978). The interrelations of behavior and activity physiology of reptiles are discussed by Regal (1978), Bennett and Ruben (1979), Pough (1980, in press), and Bennett (1980a, 1981).

II. Sustainable Activity and Its Aerobic Support

A. GENERAL

Useful work and locomotory activity involve the conversion of energy stored in the molecular bonds of foodstuffs into a form that is more directly available to an organism. Several such conversions are possible for reptiles and those that predominate depend upon the intensity of the activity undertaken. Resting energetic requirements are met by aerobic catabolism: the degradation of storage compounds to carbon dioxide and water (and nitrogenous excretory products in the case of proteins), the consumption of oxygen, and the simultaneous production of high-energy phosphate molecules. A continuous delivery of oxygen to metabolizing tissues is required to sustain aerobic energy production. As the level of activity increases above rest, additional amounts of oxygen are delivered to support increased energy demands. The limit of aerobic metabolic support is attained with the development of maximal levels of oxygen consumption. Further increments in activity levels must be fueled through other, anaerobic sources of energy production. Unlike steady-rate oxygen consumption, these cannot be sustained and result in the accumulation of metabolic end-products within the tissues or in the depletion of high-energy phosphate compounds. Exhaustion or diminished behavioral capacities often follow bouts of anaerobic metabolism.

Research on aerobic activity capacity in reptiles has concentrated upon determinations of maximal oxygen consumption and the level of exertion at which it is attained. The theoretical foundation for examining aerobically supported work in ectothermic organisms was established in a comparatively early paper by Fry (1947). Although this work addressed the activity energetics of fish, it has exerted a controlling influence on the development of earlier studies on reptilian activity as well. Fry emphasized the difference between maximal and resting oxygen consumption, a factor termed the *scope for activity*, as being the potential of an organism for doing work. The envelope created by these values at different temperatures establishes the work capacity of an ectotherm over its entire thermal range. Although several shortcomings of this concept were subsequently recognized (summarized in Bennett, 1978), this measurement, now termed *aerobic scope* or *aerobic metabolic scope* (Bennett, 1972), is still a widely used comparative index of aerobic ability during activity. The hypothesis that maximal aerobic scope coincides with maximal sustainable work capacity has been validated for several species of lizards (*Iguana*, Moberly, 1968a,b; *Cnemidophorus*, Bennett and Gleeson, 1979; *Amblyrhynchus*, Gleeson, 1979b, 1980b; *Varanus*, Gleeson et al., 1980; *Dipsosaurus*, John-Alder and

Bennett, 1981). To examine aerobic scope and maximal aerobic work capacity, it is necessary to summarize our knowledge of both resting and maximal rates of oxygen consumption in reptiles.

B. Resting and Maximal Aerobic Power Input

1. Maintenance Metabolic Levels

The rate of oxygen utilization in reptiles is strongly influenced by body temperature, body mass, and physical activity. The contributions of each of these factors is discussed in detail below. However, certain aspects of each of these must be considered in the specification of resting metabolic level.

Oxygen consumption of the lizard *Iguana* at rest and during intense struggling activity is shown in Fig. 1. Clearly activity results in greatly increased resting metabolic values. Undoubtedly, many of the published observations on reptiles were not obtained under truly quiescent conditions. Estimates based on summaries of these values should be recognized as being only approximations of resting metabolic rate, and not as being true standard metabolic rates. The influence of body temperature on oxygen consumption is likewise very great. Metabolic data, such as those in Fig. 1, have consequently been summarized at different body temperatures as
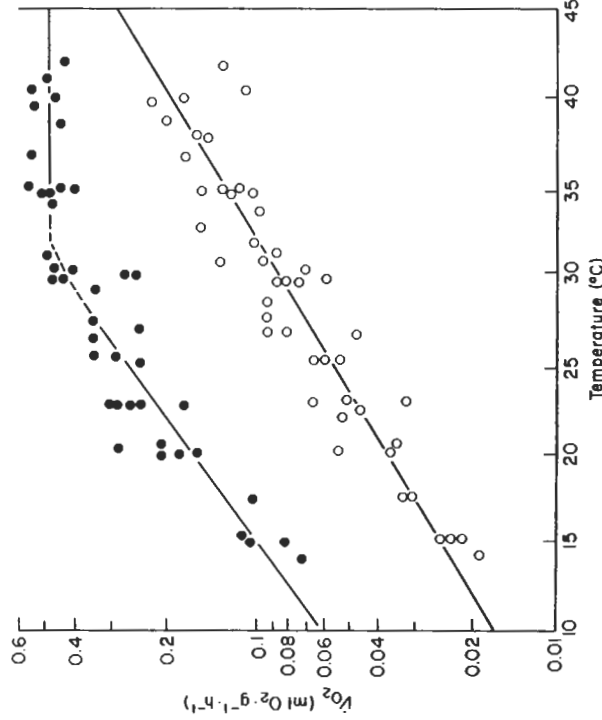

Fig. 1. *Iguana iguana*. Resting (open circles) and maximal (closed circles) oxygen consumption as a function of body temperature. Redrawn from Moberly (1968a).

functions of body mass. These equations are of the form $MR = am^b$, in which MR is metabolic rate in oxygen consumption or power input and m is body mass; a and b are empirically determined values. Weight-relative or mass-specific metabolic values (oxygen consumption or power input per unit mass) are obtained by using $(b-1)$ as the power exponent.

Equations for resting values of aerobic metabolism are summarized in Table I. These regressions conceal considerable variability in their component data, much of it due to experimental differences in data collection (Bennett and Dawson, 1976). However, a certain amount is undoubtedly due to taxonomic, morphological, and/or ecological differences among groups of reptiles. For instance, energy utilization of resting xantusiids is substantially below that of other lizards. This metabolic depression is thought to represent an adaptation for life in environments of low productivity (Mautz, 1979). In contrast, lacertid lizards of the genus *Acanthodactylus* have metabolic rates in excess of predicted levels (Duvdevani and Borut, 1974; Pough and Busack, 1978). The advantage conferred by this augmented metabolism is not known. Turtles have metabolic rates lower than anticipated for reptiles of comparable mass; the possession of an essentially metabolically inert shell is thought to account for this difference

TABLE I

The allometric relationship of resting oxygen consumption in resting reptiles.

Group	T_B °C	a $\dot{V}_{O_2}$ ml O_2/h	mW	b	r	n of species
Lizards	20	0.096	0.54	0.80	0.80	24
	30	0.240	1.34	0.83	0.86	24
	35	0.450	2.53	0.78	0.77	14
	40	0.575	3.14	0.79	0.73	13
Snakes	20	0.120	0.67	0.77	0.80	35
	30	0.280	1.57	0.76	0.91	13
Turtles	20	0.066	0.37	0.86	0.78	10
All reptiles	20	0.102	0.57	0.80	0.83	73
	30	0.278	1.55	0.77	0.91	44
	35	0.445	2.51	0.76	0.57	21
	40	0.562	3.16	0.79	0.55	16

Mass is measured in g. Data at 20 and 30°C from Bennett and Dawson, 1976; data at 35 and 40°C calculated from references listed in Table II. T_B = body temperature.

(see Bennett and Dawson, 1976). Further differentiation along ecological lines (e.g. species adapted to temperate versus tropical or mesic versus xeric environments) remains unanalyzed and would seem to be a worthwhile and rewarding effort. Likewise, most metabolic observations have been made on restricted sets of reptilian taxa, and a broader phylogenetic examination might also be valuable in turning up other energetic adaptations. In any event, the metabolic level represented by resting reptiles (Table I) is low and indistinguishable from that of other ectothermic vertebrates or invertebrates of similar size and temperature (Hemmingsen, 1960). Although this economy translates into low food demands and high efficiency of generating new biomass (Golley, 1968; Mueller, 1970; Turner et al., 1976; Pough, 1980, in press), it also may limit the maximal level of oxygen consumption and consequently aerobically sustainable behavior (Bennett and Ruben, 1979).

Many reptiles under natural conditions are inactive for long portions of the daily cycle and their rates of energy expenditure during these times are closely approximated by metabolic rates measured at rest in the laboratory. Consequently, these maintenance metabolic determinations also have utility in the estimation of energy utilization in the field. Quiescent metabolism may figure prominently in the total daily metabolic expenditure (see below).

2. Maximal Oxygen Consumption and Aerobic Scope

Maximal oxygen consumption sets the upper boundary on aerobic metabolism and consequently on sustainable levels of activity. Maximal aerobic power input consequently can provide both absolute and comparative information on the stamina and work capacity of different animals. A considerable literature has accumulated on maximal oxygen consumption and aerobic scope of reptiles since their first determination by Bartholomew and Tucker in 1963. Allometric relationships of maximal oxygen consumption were previously calculated for active reptiles at 30°C (Wilson, 1974a; Bennett and Dawson, 1976). These can now be expanded to include a broader range of body temperatures and recent measurements. Maximal rates of oxygen consumption of active reptiles at 20, 30, 35, and 40°C are reported in Table II and the exponents of the allometric equation $MR = am^b$ are given in Table III for lizards and for all reptiles. Little intergroup differentiation is evident in the limited data base of Table II. As in other groups, maximal aerobic power input scales as a fractional power of body mass that approximates 0.75 (except at 40°C, see below). Larger animals have a greater total aerobic power capacity and smaller animals have a greater mass-specific maximal oxygen consumption and oxygen delivery capacity.

The range of capacities of maximal oxygen transport are very similar in

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TABLE II

Maximal oxygen consumption of active reptiles

Species	Mass g	$\dot{V}_{O_{2max}}$ [ml O_2/(g h)]				Reference
		20°C	30°C	35°C	40°C	
Turtles						
Chelydra serpentina	3473	0.19	0.49	—	—	Gatten, 1978
Pseudemys scripta	305	0.28	0.64	0.85	1.03	Gatten, 1974
Terrapene ornata	354	0.21	0.36	0.46	0.73	Gatten, 1974
Rhynchocephalians						
Sphenodon punctatus	520	0.15	0.16	0.15	—	Wilson and Lee, 1970
Lizards						
Amblyrhynchus cristatus	489	—	0.61	0.80	0.75	Bennett et al., 1975
Amphibolurus barbatus	239	0.24	0.56	0.65	0.62	Wilson, 1974b
Cnemidophorus murinus	55.2	—	—	—	1.63	Bennett and Gleeson, 1979
Cnemidophorus tigris	18.0	0.41	0.90	1.6	2.1	Asplund, 1970
Dipsosaurus dorsalis	35.2	—	0.89	1.64	2.45	Bennett and Dawson, 1972
Egernia cunninghami	257	0.25	0.50	0.60	0.56	Wilson, 1974b
Gerrhonotus multicarinatus	24	0.30	0.55	1.13	—	Hoffmann, 1973
Iguana iguana	795	0.16	0.46	0.50	0.51	Moberly, 1968a
Lacerta spp.	10	—	1.49	—	—	Cragg, 1978
Physignathus lesueuri	549	0.23	0.46	0.45	0.45	Wilson, 1974b
Sauromalus hispidus	574	0.26	0.45	0.53	0.58	Bennett, 1972
Sceloporus occidentalis	13.1	0.52	1.32	1.78	1.80	Bennett and Gleeson, 1976
Tiliqua scincoides	493	0.14	0.24	—	0.40	Bartholomew et al., 1965
Trachydosaurus rugosus	421	0.24	0.46	0.50	0.51	Wilson, 1974b
Varanus exanthematicus	1025	—	—	1.26	—	Gleeson et al., 1980
Varanus gouldii	674	0.32	0.57	0.76	1.01	Bennett, 1972
Varanus spp.	714	0.18	0.37	—	0.75	Bartholomew and Tucker, 1964
Snakes						
Coluber constrictor, Masticophis flagellum	262	—	—	1.02	—	Ruben, 1976
Crotalus viridis	301	—	—	0.52	—	Ruben, 1976
Pituophis catenifer	548	0.27	0.47	0.52	—	Greenwald, 1971
Spalerosophis diadema	386	0.29	0.38	0.46	0.65	Dmi'el and Borut, 1972

lizards and snakes. Three of the four turtle species investigated (*Chelydra*, *Pseudemys*, and *Chelonia*—Jackson and Prange, 1979) have maximal rates of oxygen consumption exceeding predicted values. *Chelonia*, not necessarily maximally active, have aerobic metabolic rates twice those predicted by the 30°C regression equation for reptiles. However, their large size (128 kg) makes suspect such size-dependent extrapolations. The aerobic abilities of *Sphenodon* at high body temperatures are distinctly lower than those of other reptiles investigated. This low aerobic capacity may reflect adaptations for activity at very low body temperatures or it may possibly reflect a relatively sluggish activity pattern for this species, although little is known about its natural activity.

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TABLE III

The allometric relationship of maximal oxygen consumption and aerobic power input of active reptiles

Group	T_B °C	a $\dot{V}_{O_2}$ ml O₂/h	a mW	b	r	n of species
Lizards	20	0.69	3.9	0.81	0.78	12
	30	1.96	11.0	0.76	0.82	15
	35	2.92	16.3	0.76	0.76	13
	40	5.86	32.8	0.64	0.86	14
All reptiles	20	0.65	3.6	0.83	0.72	18
	30	1.78	10.0	0.77	0.71	21
	35	3.43	19.2	0.71	0.66	20
	40	5.87	32.8	0.64	0.85	17

Data are given in Table II.
Mass is in g. T_B = body temperature.

Aerobic capacity is expressed either as aerobic metabolic scope, the difference between maximal and resting oxygen consumption, or as the ratio of these two quantities, termed either the index of metabolic expansibility or the maximal factorial increment. The mass-dependent exponent of resting and maximal oxygen consumption is similar (approximately $m^{0.75}$) at 20, 30, and 35°C (Table I and III). Thus, aerobic scope scales with mass to the same degree ($m^{0.75}$). These mass-specific values are equivalent to those found for mammals (Lechner, 1978; Taylor et al., 1978) and birds (Berger et al., 1970). However, as reptilian body size increases, maximal oxygen consumption at 40°C does not increase to the same degree as does that at rest ($b = 0.64$ and 0.79 for activity and rest respectively). Consequently, aerobic scope scales to only $m^{0.6}$ and the factorial increment declines with increasing body size. At 40°C, a 10-g lizard can increase its oxygen consumption to 7.2 times resting levels, but a 1-kg lizard, can only increase it to 3.6 and maximal values are only one-half anticipated levels (Fig. 2). These relationships might suggest that large reptiles at high body temperatures might find it difficult to procure sufficient oxygen to support activity. However, many of the species of larger animals listed in Table II appear to maximize aerobic scope at their mean selected body temperatures. These are generally below 40°C. This relationship may thus be an adaptation to promote maximal aerobic work capacity at normal body temperatures and may not represent a failure of transport capacities *per se*. At any rate, at high temperatures some
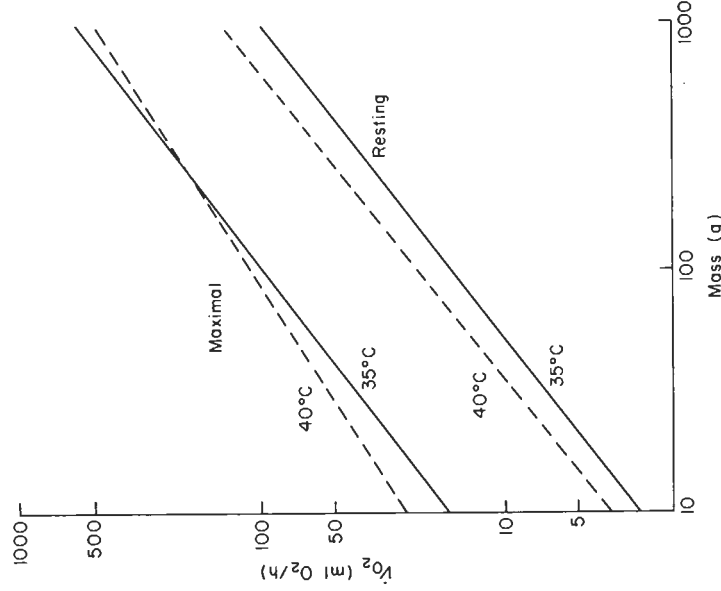
FIG. 2. Predicted relationships of resting and maximal oxygen consumption of lizards as a function of body mass and temperature. Data from Tables I and III.

larger reptiles do not increase oxygen consumption as much as they can at lower temperatures. Smaller reptiles do not seem to experience this limitation.

Allometric analyses are useful for examining the functional capacities of groups of animals or for predicting the functional level of previously uninvestigated species. However, they obscure real interspecific variation. Reptiles of similar body size may differ greatly in their capacities to support aerobic activity. For instance, maximal oxygen consumption may vary at least fourfold among different species of snakes of similar size and body temperature (Table IV). Snakes that are capable of intense and prolonged struggling, such as *Coluber* and *Masticophis*, sustain greater levels of aerobic transport than do more moderately active (*Nerodia*, *Pituophis*) or sluggish (*Lichanura*) animals (Ruben, 1976). Tucker (1967) first noted the associated of high capacities for activity and rapid flight with high aerobic scope in some species and the correlation between static defense postures, low activity capacity, and low aerobic scope in others. As examples he noted the

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TABLE IV

Maximal aerobic power input of several species of snakes

Species	Mass	T_B	Aerobic power input	Reference
	g	°C	mW/g	
Coluber constrictor,	195	35	5.70	Ruben, 1976
Masticophis flagellum				
Crotalus viridis	301	35	2.91	Ruben, 1976
Lichanura trivirgata	314	32	1.45	Ruben, 1976
Nerodia rhombifera	211	35	1.99	Gratz and Hutchison, 1977
Pituophis melanoleucus	548	35	2.91	Greenwald, 1971
Spalerosophis diadema	386	35	2.57	Dmi'el and Borut, 1972

T_B = body temperature

lizards *Varanus, Iguana, Amphibolurus,* and *Tiliqua,* which were considered to form an activity series similar to that noted previously for the species of snakes. The capacity for sustained activity among reptiles under experimental conditions appears to be well reflected in and directly correlated with aerobic scope and maximal oxygen consumption.

In addition to body temperature, mass, and phylogenetic affinity, other factors also influence maximal levels of aerotic metabolism. For instance, the state of thermal acclimation has been shown to influence maximal oxygen consumption of snapping turtles (*Chelydra serpentina;* Gatten, 1978). Turtles acclimated at 10°C do not attain levels of oxygen consumption of those acclimated at 25°C, even when both are measured at the same test temperatures. In the single study on the topic, no influence of time of day on maximal oxygen consumption was found for the snake *Nerodia rhombifera* (Gratz and Hutchison, 1977). More detailed studies on such factors are required before it is possible to make any sort of satisfactory generalization regarding the influences that affect maximal levels of aerobic metabolism in reptiles.

3. *Body Temperature and Oxygen Consumption*

Body temperature has a pronounced effect on the rate of oxygen uptake (Fig. 1; Tables I and III), as the resting metabolic rates of reptiles tend to be strongly thermally dependent (Dawson, 1967; Templeton, 1970; Bennett and Dawson, 1976). Low temperatures reduce aerobic energy utilization. The generalized relationships of maximal oxygen consumption and body

size indicate that maximal oxygen transport has a temperature coefficient (Q_{10}) of 2.0–2.5 between 20 and 35°C for lizards of all body sizes (Table V). That is, aerobic power input during activity increases two or more times when body temperature increases 10°C. Small lizards maintain this relationship at 35–40°C, but in larger animals the maximal oxygen consumption over this range is nearly independent of temperature ($Q_{10} \simeq 1.0$). The thermal dependence of maximal oxygen consumption imposes constraints on stamina and power input for animals that undergo daily thermal cycles and must start morning activity with low body temperatures. This thermal dependence has even more important consequences for animals that are normally active at low body temperatures. These consequences are discussed in Section II. C. 2.

For many lizards, maximal oxygen consumption ($Q_{10} \simeq 1.0$) becomes independent of temperature at body temperatures exceeding normally preferred or maintained levels (Wilson, 1974b). That is, maximum oxygen consumption increases with anticipated thermal dependence up to preferred body temperature and then remains constant up to damaging thermal levels (see, for example, Fig. 1). Animals in which such constant levels have been reported include *Amblyrhynchus cristatus* (Bennett *et al.*, 1975), *Amphibolurus barbatus*, *Egernia cunninghami*, *Physignathus lesueuri*, and *Trachydosaurus rugosus* (Wilson, 1974b), *Dipsosaurus dorsalis* (Bennett and Dawson, 1972), *Iguana iguana* (Moberly, 1968a), *Sauromalus hispidus* (Bennett, 1972), and *Sceloporus occidentalis* (Bennett and Gleeson, 1976). This attainment of maximal oxygen consumption at selected thermal levels results in a maximal aerobic scope (and presumably aerobic work capacity) at these temperatures. At higher temperatures, resting oxygen consumption continues to increase and the difference between these factors consequently

TABLE V

The temperature dependence of maximal aerobic power input of lizards.

Mass	Q_{10}		
g	20–30°C	30–35°C	35–40°C
10	2.52	2.23	2.32
100	2.24	2.23	1.33
1000	2.00	2.23	0.77

Data are taken from regression equations in Table III.

declines. Such coincidence of maximal functional capacity and experienced thermal level is at first glance rather pleasing, as it suggests that animals may be adapted to function best under the conditions they normally experience. This was also the thermal pattern of work capacity predicted and described for fish (Fry, 1947).

However, many other species of reptiles do not conform to this relationship; their maximal oxygen consumption continues to increase up to the highest body temperatures measured. These species include the lizards *Eumeces obsoletus* (A. F. Bennett and W. R. Dawson, unpublished), *Gerrhonotus multicarinatus* (Hoffmann, 1973), and *Tiliqua scincoides* (Bartholomew et al., 1965); the snakes *Pituophis melanoleucus* (Greenwald, 1971) and *Spalerosophis diadema cliffordi* (Dmi'el and Borut, 1972); the rhynchocephalian *Sphenodon punctatus* (Wilson and Lee, 1970); and the turtles *Pseudemys scripta* and *Terrapene ornata* (Gatten, 1974). In these species, maximal oxygen consumption continues to increase in parallel to body temperature up to lethal levels. Consequently aerobic scope and work capacity are not maximized at field-active body temperatures. Rather, these functions are optimized at body temperatures that are rarely if ever attained under natural conditions. Normally active body temperatures of *Cnemidophorus* (Asplund, 1970) and *Varanus* (Bartholomew and Tucker, 1964; Bennett, 1972) are so close to damaging thermal levels that it has not been possible to discriminate which pattern these animals follow.

An examination of the species in each category reveals an interesting phylogenetic relationship. The species which optimize aerobic function at preferred thermal levels are, with two exceptions, iguanid or agamid lizards; no iguanids or agamids examined fail to show this maximization. Among the skinks, two species (*Egernia cunninghami*, *Trachydosaurus rugosus*) reach steady maximal oxygen consumption and two do not (*Eumeces obsoletus*, *Tiliqua scincoides*). In contrast, the maximal oxygen consumption of other families of lizards and other groups of reptiles shows a strict thermal dependence. Thermal dependence is more phylogenetically widespread among reptiles and is in conformity with anticipated thermal effects on biological rate processes. It is reasonable to assume that the condition in iguanid and agamid lizards, which belong to closely related families, is a later derivation and represents a specific adaptation in their systems of oxygen transport and consumption. The advantage of maximizing aerobic work ability at body temperatures that are experienced normally are clear. The failure of other groups to do so is more puzzling. For whatever selective reasons, the present data indicate that the thermal dependence of aerobic transport in iguanid and agamid lizards is different from that of most other reptiles. Consequently, care should be taken in generalizing data from these groups to a broader reptilian context. It is somewhat unfortunate that most

data regarding activity energetics derive from these metabolically atypical forms.

Such regulation of body temperature as occurs among reptiles, is generally accomplished by behavioural rather than by metabolic means (Avery, Bartholomew and Huey, volume 12). However, under certain thermoregulatory circumstances, reptiles do increase oxygen consumption and heat production. Metabolic rates are greater in some animals experiencing a decline in body temperature than they are in the same animals when body temperature is increasing (Alligator, Smith, 1975; Amblyrhynchus, Bartholomew and Vleck, 1979; Spalerosophis, Dmi'el and Borut, 1972). The resulting heat production may delay cooling and maintain higher temperatures for longer periods of time, presumably increasing the active period under natural cooling conditions. The mechanism of this thermogenesis is presumed to be increased muscular activity. In contrast to this metabolic response to transient thermal conditions, metabolic thermogenesis maintaining a body temperature above ambient (i.e. the condition of endothermy) is apparently rare in reptiles. The only well-documented case is that of incubating female pythons (Hutchison et al., 1966; Vinegar et al., 1970). Several species of these snakes maintain body and egg temperature as much as 5–6°C above ambient temperature by spasmodic contractions of their body musculature. This thermoregulatory activity is expensive and increases oxygen consumption as much as tenfold above resting levels.

4. Effect of Training on Aerobic Ability

Certain mammals may modify their capacity for maximal aerobic performance and oxygen consumption by prior physical conditioning (Ekblom, 1969; Holloszy, 1973). The extent to which reptilian performance is influenced by similar conditioning or inactivity has been little investigated. As reptiles are often maintained in laboratories for a variable length of time before metabolic analysis, the degree to which performance is altered by this inactivity is a matter of concern. A single study (Gleeson, 1979a) found no significant effect of training on performance or oxygen transport ability in the lizard Sceloporus occidentalis. Maximal aerobic ability was unchanged by 6–8 weeks of daily physical activity or by a similar period of inactivity in comparison with that of animals recently removed from the field. These lizards were consequently characterized as "metabolically inflexible," indicating that, unlike mammals investigated, aerobic metabolic systems do not seem influenced by the degree of prior physical activity. The behavior of these lizards is characterized by short bursts of activity and little sustained exertion. Comparable studies on reptiles that engage in longer bouts of aerobically supported activity would indicate whether this metabolic inflexibility is characteristic of the entire group.

C. Locomotory Energetics

1. General

Resting and maximal levels of oxygen consumption present boundary conditions within which aerobic metabolism can be supported. As an animal becomes active and its level of activity increases, so will its oxygen consumption. The quantitative relationship between oxygen consumption and performance level characterizes the cost of locomotion, and much recent study has been devoted to the quantification of locomotory energetics over the range of sustainable levels of exertion. At some exercise level, maximal oxygen consumption is attained. Even though work output may increase further, the maximal aerobic power input remains constant and additional, non-sustainable metabolic support has to be provided. In reptiles this transition point occurs at rather low work levels; consequently these animals cannot support or sustain vigorous activity by aerobic means. The point of transition from aerobic to anaerobic metabolism provides a good indicator of physiological limitation on reptilian behavioral patterns.

2. Energetics of Walking and Running

The locomotory energetics of terrestrial reptiles have been determined in animals walking on motor-driven treadmills over a range of speeds. Rates of oxygen consumption are determined simultaneously, according to the pattern established for comparative mammalian studies (Taylor *et al.*, 1970). Numerous studies of this type show that aerobic power input during walking increases linearly with speed up to maximal levels of oxygen consumption. Such a relationship is shown in Fig. 3 for *Varanus exanthematicus* (data from Gleeson *et al.*, 1980), in which the terminology associated with locomotory energetics is also indicated. A linear extrapolation of the rate of oxygen consumption at zero speed (the *Y*-intercept, Schmidt-Nielsen, 1972) is 1.5–2.0 times resting levels and is assumed to be associated with postural adjustments associated with activity (Schmidt-Nielsen, 1972). The mass-specific aerobic power input divided by the speed of locomotion is termed the *cost of transport* (Tucker, 1970) or the *total cost of locomotion* (Schmidt-Nielsen, 1972). It is the amount of energy expended to move a unit mass over a unit distance and is measured as joules, calories, or milliliters of oxygen per (gram × kilometer). This is the actual cost incurred by a moving animal and is useful in estimating the real cost of movements, such as those associated with feeding, courtship, in time–energy budgets of animals. It has a considerable component associated with maintenance metabolism and is also speed dependent. For studies investigating locomotory energetics *per se*, the presumptive maintenance and postural components are removed by subtracting these costs (equal to
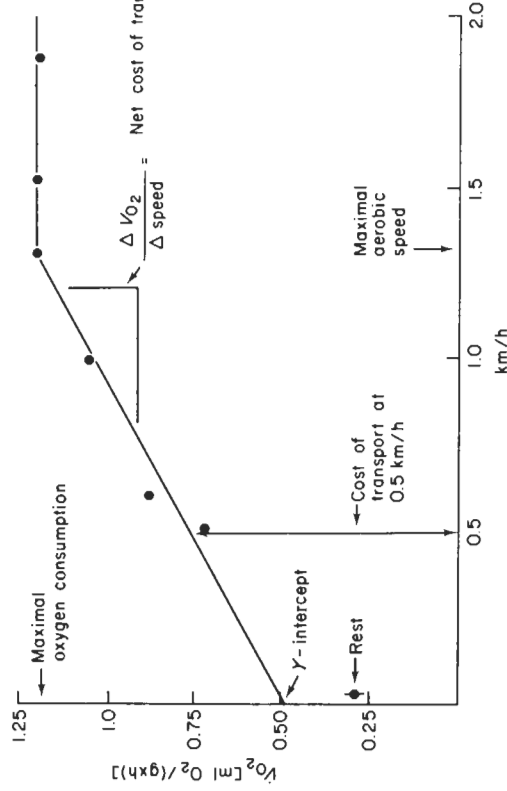
FIG. 3. *Varanus exanthematicus*. Oxygen consumption as a function of walking speed at 35°C. Data from Gleeson et al. (1980b). Locomotory terminology is illustrated on the figure.

the *Y*-intercept from the metabolic expenditure and obtaining the *net cost of transport*. This is effectively the slope of oxygen consumption as a function of speed (Schmidt-Nielsen, 1972). This number is independent of speed traveled. The aerobic power input required for movement at a given speed may be approximated by adding the product of the net cost of transport and the speed to 1.7 times the resting oxygen consumption (Taylor, 1973). Oxygen consumption continues to rise to maximal values and then remains constant as speed increases. This transition is here termed the *maximal aerobic speed*. As power requirements do not increase linearly with speed in swimming organisms, locomotory energetics are generally analyzed only as the total cost of transport or locomotion.

Lizards are the only reptilian group for which locomotory energetics have been analyzed in sufficient detail to permit partial generalization and analysis of data (Moberly, 1968b; Bakker, 1972; Dmi'el and Rappeport, 1976; Cragg, 1978; Gleeson, 1979b; Bennett and Gleeson, 1979; John-Alder and Bennett, 1981). Based on a recent analysis (Gleeson, 1979b), the net cost of transport for these animals as a function of body size is presented in Fig. 4. The cost decreases with increasing body size according to the relation

$$\text{Net cost of transport} = 3.77 \, m^{-0.25}$$

where net cost of transport is measured in ml $O_2/(g \cdot km)$ and m is mass in g ($n = 28$, $r = 0.87$). Consequently, it is less expensive for a large lizard to move a unit of its mass over a given distance than it is for a smaller lizard.

However, the total locomotory cost is greater for a larger animal, as it must move a greater mass. Similar mass-dependent relationships occur during terrestrial locomotion in mammals (Taylor et al., 1970; Schmidt-Nielsen, 1972). The data in Fig. 4 show considerable variation, not all of which may be attributable to different methodologies. For instance, the locomotory costs of Iguana (Moberly, 1968b; Gleeson et al., 1980) are consistently nearly twice those of other lizards of similar size, including the other iguanids Amblyrhynchus and Conolophus. The accumulation of more data may permit a finer analysis of interspecific differences in locomotory costs. An interesting comparative observation is the additional determination of the locomotory energetics of a garter snake (Thamnophis sirtalis; Chodrow and Taylor, 1973). The net cost of transport [0.52 ml O_2/(g·km), 24 g snakes] is only 31% that anticipated for a lizard of similar size. Limbless locomotion may thus be much more economical than quadrupedal, probably because of the elimination of anti-gravitational support and the lack of vertical displacement of the center of mass. This may be an energetic consideration involved in the frequent independent evolution of reptilian groups with greatly reduced limbs. The energetic cost of locomotion is, of course, only one factor influencing the evolution of a locomotory mode.

The influence of body temperature on reptilian locomotory costs have been measured in only three species of lizards: Iguana (Moberly, 1968b), Uromastyx (Dmi'el and Rappeport, 1976), and Dipsosaurus (John-Alder and Bennett, 1981). Different patterns of temperature influence have been observed. In Uromastyx, the cost of transport (measured as total oxygen
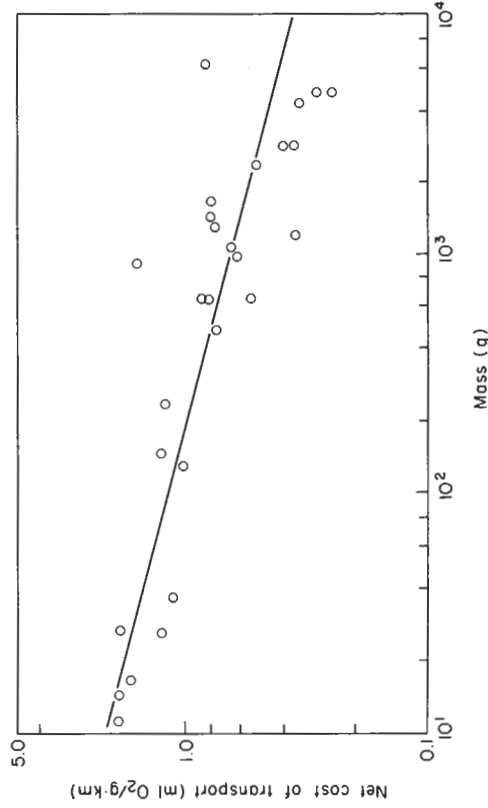

FIG. 4. Net cost of transport in walking lizards as a function of body mass. Redrawn from Gleeson (1979b).

consumption while walking at a given speed) is independent of temperature. In *Iguana* and *Dipsosaurus*, the cost of transport increases with increasing body temperature. Thus, walking at a given speed requires more energy as temperature increases. Clearly, further investigation of the thermal dependence of locomotory costs of reptiles is required. The results of these studies may be anticipated to have important energetic and ecological implications.

Body temperature has been shown in the previous section (Section II-B) to influence maximal oxygen consumption of reptiles. Low body temperatures inhibit maximal rates of oxygen utilization. It may be anticipated then that capacities for sustainable locomotion might likewise be inhibited by low body temperatures. A reptile at low temperatures might attain the limits of its aerobic scope and its maximal aerobic speed at lower levels of exertion. The basis for this prediction is shown in Fig. 5. In this figure, oxygen consumption is given as a function of speed for lizards of 10-, 100-, and 1000-g body mass. Locomotory costs were estimated by calculating the Y-intercepts as 1.7 × resting oxygen consumption at 30°C (Table I) and adding the net cost of transport (previous equation, Gleeson, 1979b). These
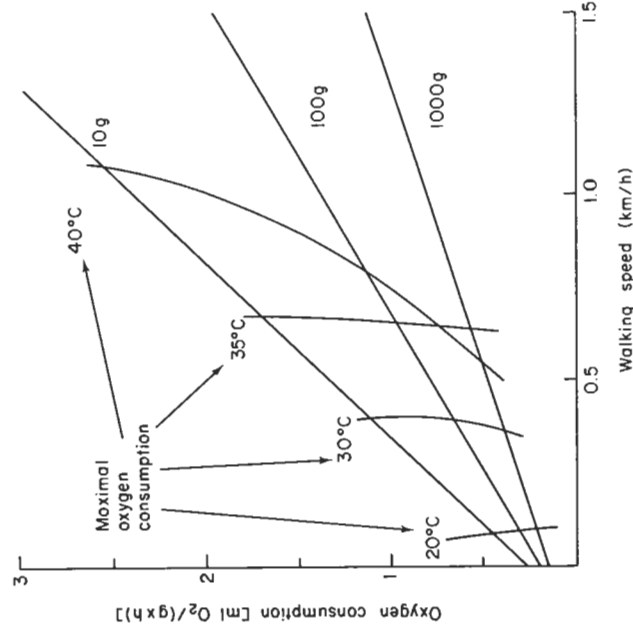

FIG. 5. Oxygen consumption as a function of walking speed in lizards of different body mass. Maximal oxygen consumption as a function of body temperature is also indicated. See text for method of calculation.

values are only generalized estimates and will actually vary somewhat with body temperature. Overlaid on these data are independent calculations of maximal oxygen consumption (Table III). The intersections of the two sets of lines indicate the predicted maximal aerobic speeds, i.e. the greatest speed which could be sustained at that temperature. Body temperature is predicted to have a pronounced influence on sustainable activity capacity. Maximal aerobic speed is predicted at only 0.1 km/h at 20°C for lizards over this entire size range. It increases to 0.4 km/h at 30°C and 0.65 km/h at 35°C. The predicted Q_{10} values over this range are 3.7–4.4 at 20–30°C and 2.8–3.0 at 30–35°C, indicating a very great temperature dependence. The size dependence of maximal oxygen consumption at 40°C (Section II-B) makes the predicted maximal aerobic speed highly size dependent, decreasing from 1.1 km/h for a 10-g lizard to 0.55 km/h for a 1000-g animal. In the latter size class, the predicted performance actually decreases between 35 and 40°C.

The predictions of this model accord fairly well with the thermal dependence of sustainable locomotory capacity observed in *Iguana* (Moberly, 1968b) and *Dipsosaurus* (John-Alder and Bennett, 1981). In *Iguana*, maximal sustained walking speeds (>10 min) are 0.17, 0.45, 0.52, and 0.45 km/h at 20, 30, 35, and 40°C respectively. Both the quantitative levels of maximal aerobic speed and the pattern of thermal dependence ($Q_{10}=2.7$ at 20–30°C, 1.3 at 30–35°C, and 0.7 at 35–40°C) are similar to predicted values of 1-kg lizards. Sustainable speed (>15 min) increases from 0.3 km/h at 25°C to 0.8 km/h at 40°C in 50-g *Dipsosaurus* ($Q_{10}=1.9$). These values are also very close to predicted performance levels. It should be emphasized that this regression model obscures real variability in the activity capacities among different species and should be used only to examine general trends. For instance, the locomotory capacities of the lizard *Cnemidophorus murinus* fall considerably short of those predicted (Bennett and Gleeson, 1979). *Varanus exanthematicus* has substantially greater aerobic scope and consequently twice the maximal aerobic speed of similarly sized *Iguana iguana* (Wood et al., 1978; Gleeson et al., 1980). However, the predicted effect of body temperature on locomotory stamina is generally supported by the available data and merits additional investigation.

The maximal aerobic speeds calculated and observed for terrestrial reptiles are very slow and the range of sustainable rates of locomotion is quite narrow, particularly so at low body temperatures. Terrestrial mammals, with their substantially greater aerobic scopes and maximal rates of oxygen consumption, are capable of sustaining much faster speeds using aerobic metabolism alone. Figure 6 compares the metabolic rates and speeds of *Iguana* and a hypothetical mammal of equal size (see Bennett and Ruben, 1979, for method of calculation of predicted mammalian aerobic factors).

The lizard reaches maximal aerobic speed at 0.5 km/h; the mammal at 4.1 km/h. The greater aerobic scope permits a much broader range of aerobically supported activities in the mammal. Energetically, mammalian locomotion *per se* is quite similar to that of lizards. The net cost of transport i.e. the slope of oxygen consumption as a function of speed, in the two groups is almost identical (Bakker, 1972; Taylor, 1973; Gleeson, 1979b). Consequently, the sprawling-type gait of lizards with limbs flexed at right angles to the body appears no more expensive than the more erect gait and columnar stance of mammals (Bakker, 1972; Taylor, 1973). However, these differences in limb suspensions are more apparent than real, since many mammals have only planar rotation of the limb and maintain the flexion about the joints (Bennett and Dalzell, 1973). In total metabolic cost, however, locomotion is considerably less expensive for the lizards, as is inactivity. The iguana can walk at its maximal aerobic speed with a metabolic rate equivalent to that of a resting mammal. At any sustainable speed, it has a considerably lower oxygen consumption than a mammal traveling at the same speed.

We may examine how different factors affect locomotory energetics by calculating how much energy is required for a reptile to move a given distance. In this case, we can calculate the energy required for a lizard to walk 1 km. Total power inputs are calculated in Table VI. The cost depends on speed and on body size, and on body temperature (in two of three species examined). The total work required decreases as speed increases, as
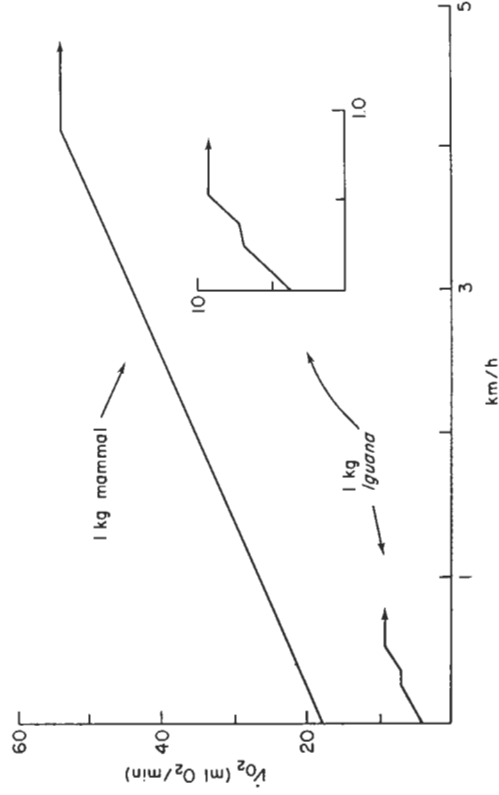

FIG. 6. Oxygen consumption as a function of speed in a 1-kg lizard (*Iguana*) and a hypothetical mammal of equal size. Redrawn from Bennett and Ruben, (1979); see reference for method of calculation.

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TABLE VI

Cost of walking 1 km

Speed	Kilojoules		
km/h	10 g	100 g	1000 g
Lizards			
0.1	0.98	6.14	38.82
0.5	0.54	3.15	18.54
1.0	0.48	2.77	16.01
Mammals			
0.1	7.46	40.82	225.18
0.5	2.03	10.33	53.63
1.0	1.35	6.51	32.18

Work input calculated at 1.0 ml $O_2 = 20.1$ J (RQ=0.8). Lizard data from Table I and Gleeson, 1979b; mammalian data from Taylor, 1973.

Moberly (1968b) pointed out, because of the longer duration of "maintenance costs," at slow speeds. Thus, only about half as much energy is required to walk the distance at 1.0 km/h as at 0.1 km/h. Thus, if traversing a given distance were the only factor of importance, energy would be most conserved by walking at the greatest possible speed within aerobically supportable limits. The aerobic scope and maximal sustainable speed set an upper limit on these rates, and both body temperature (Fig. 5) and aerobic physiology may prevent the maintenance of even moderate speeds. For instance, at 20°C, only 0.1 km/h is an accessible speed; anything greater requires supplemental anaerobic metabolism and entails exhaustion. The total cost of transport increases with body size, as the mass to be transported through the distance is greater. A tenfold increment in mass requires a sixfold increment in work input to move it. The mass-specific costs are lower for larger animals, but this is scant comfort as they must move their entire bodies when they walk. The energetic economy associated with ectothermic metabolism is underscored by comparison of these data with those for mammals. Particularly at slow speeds, the cost of moving a given distance for a reptile is only a fraction of that for a mammal of the same size at the same speed.

In summary, the costs of terrestrial locomotion are very high for reptiles in comparison with their limited aerobic scopes. They reach their aerobic limits at very low speeds and must supplement aerobiosis with other metabolic pathways. The strong thermal dependence of their oxygen

consumption, although reducing energy expenditure at low temperatures, creates additional behavioral difficulties, very greatly reducing ability to support and sustain activity at these low temperatures. These relationships place severe limitations on the behavioral potential of reptiles.

3. Cost of Swimming

Swimming, by organisms adapted to it as their primary means of locomotion, is the most economical form of transport (Tucker, 1970; Schmidt-Nielsen, 1972). Locomotory costs of a 1-kg fish, for instance, are only one-eighth those of an equal-sized terrestrial walker (Schmidt-Nielsen, 1972). The cost of swimming has been evaluated for only two reptiles: green turtles (*Chelonia mydas*) (Prange, 1976) and marine iguanas (*Amblyrhynchus cristatus*; Gleeson, 1979b; Vleck et al., 1981). These animals differ from fish, as their oxygen consumption increases linearly with increasing speed. Both reptiles while swimming achieve significant economy over terrestrial locomotion, but neither attains the low energy costs of swimming fish. The net cost of transport of green turtles is approximately twice that of marine iguanas and is about five times that of salmonid fishes (Brett, 1964; Schmidt-Nielsen, 1972). These additional costs may be due to surface swimming activity; the turtle surfaces for air and the iguana remains buoyantly swimming at the surface, both creating considerable wake formation and thus increasing total energy expenditure (Prange, 1976; Vleck et al., 1980). The costs of swimming and walking in marine iguanas are compared in Fig. 7. The (total) cost of locomotion of an iguana walking at 1.0 km/h, its maximal aerobic speed, is four times that when swimming at
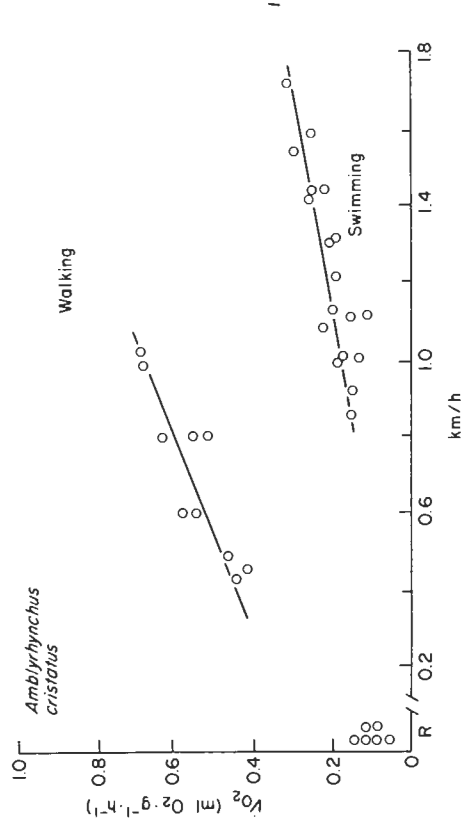

Fig. 7. *Amblyrhynchus cristatus*. Oxygen consumption of adult marine iguanas walking on a motor-driven treadmill at 35°C and swimming at 25°C. Redrawn from Gleeson (1979b).

and oxygen consumption during activity. Although these measurements are feasible, they have not yet been undertaken for reptiles.

Very short-term activity (i.e. a few seconds) may be supported by the catabolism of endogenous stores of ATP and/or creatine phosphate within the skeletal muscle. Levels of both these compounds decrease during burst behavior in the lizard *Sceloporus occidentalis* (A. F. Bennett and T. T. Gleeson, unpublished). Due to methodological difficulties, no extensive measurements of the utilization of these compounds have been made for active reptiles. It is probable that their catabolism is very significant in fueling short, intense bursts that characterize much avoidance behavior of reptiles. Their significance merits much further examination.

In alligators, turtles, lizards, and snakes, intense behavior of longer duration (i.e. 5 s to 5 min) involves the production and accumulation of large amounts of lactic acid (Coulson and Hernandez, 1964; Moberly, 1968a,b; Bennett and Licht, 1972; Bennett and Dawson, 1972; Bennett, 1973; Gatten, 1974, 1975; Bennett and Ruben, 1975; Bennett *et al.*, 1975; Bartholomew *et al.*, 1976; Ruben, 1976; Bennett and Gleeson, 1976; Gratz and Hutchison, 1977; Pough, 1977, 1978; Gleeson, 1980ab; Mitchell *et al.*, 1981). The extent and significance of reptilian anaerobic metabolism involving lactic acid formation has received considerable attention; these findings are discussed here. The accumulation of other anaerobic end-products has not been widely studied; however, preliminary evidence suggests these products have little energetic significance. In the lizards *Sceloporus occidentalis* and *Xantusia vigilis*, the total formation of pyruvic acid, succinate, and alanine account for less than 4% of the ATP formation associated with lactic acid production (A. F. Bennett and T. T. Gleeson, unpublished).

2. Advantages and Disadvantages of Anaerobic Metabolism

In comparison to aerobic energy utilization, anaerobic metabolism as a means of supporting muscular activity has conspicuous advantages and disadvantages (Bennett and Ruben, 1979; Coulson, 1979; Bennett, 1980a). Oxygen must be transported for a considerable distance to its site of utilization; however, the reactants for anaerobic metabolism are enclosed within the muscle cells. Enzymes, fuel (muscle glycogen), and storage forms of high energy phosphate compounds (ATP, creatine phosphate) are available for immediate activation and utilization without a significant time lag. In addition, the potential rate of ATP generation by anaerobic systems is much larger than that for reptilian aerobic metabolism (see below). Thus, anaerobic metabolism lacks the temporal and quantitative limitations of aerobiosis.

However, anaerobiosis creates pronounced physiological difficulties.

the same speed. Swimming animals are capable of sustaining speeds nearly twice this great. However, maximal burst speeds while running on land are much greater than burst swimming speed in the water (9.0 versus 2.7 km/h; Bartholomew et al., 1976; Gleeson, 1979b). The economy associated with sustained swimming may be partly due to decreased body temperature in the water and/or the buoyant support of the water. Swimming transport, then, is more energetically conservative and should be favored on strictly energetic grounds by an organism which may choose either. There are, however, compensatory disadvantages, such as exposure to a new set of predators, reduced maximal speed, and generally reduced body temperature, affecting many other physiological systems.

III. Non-sustainable Activity and Anaerobic Metabolism

A. General

The level of exertion that most lizards can support aerobically is very limited, as seen in the previous section. Any activity greater than these modest levels must be fueled with supplemental anaerobic metabolism. In addition, even moderate levels of activity often have an initial anaerobic component as oxygen consumption cannot be raised instantly to its final maximum value. The lag in its development must also be supplemented anaerobically. This section will review our current knowledge concerning the extent and significance of anaerobiosis during activity in reptiles and Section IV will examine the differential utilization of aerobic and anaerobic metabolism.

B. Types and Consequences of Anaerobic Metabolism

1. Anaerobic Pathways in Reptiles

Since "anaerobic metabolism" refers to any metabolic pathway that does not involve the utilization of molecular oxygen, numerous potential reaction series could yield a net amount of ATP in support of muscular activity. These series have not been characterized for any animal. Accumulation of some likely anaerobically formed end-products and depletion of potential energy stored has been measured for some reptiles. However, this ecletic approach may miss important reactions and may lead to an underestimation of the extent of anaerobic metabolism if significant and unknown pathways are not assayed. Determination of the extent of anaerobiosis requires simultaneous measurements of total heat production by direct calorimetry

and oxygen consumption during activity. Although these measurements are feasible, they have not yet been undertaken for reptiles.

Very short-term activity (i.e. a few seconds) may be supported by the catabolism of endogenous stores of ATP and/or creatine phosphate within the skeletal muscle. Levels of both these compounds decrease during burst behavior in the lizard *Sceloporus occidentalis* (A. F. Bennett and T. T. Gleeson, unpublished). Due to methodological difficulties, no extensive measurements of the utilization of these compounds have been made for active reptiles. It is probable that their catabolism is very significant in fueling short, intense bursts that characterize much avoidance behavior of reptiles. Their significance merits much further examination.

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However, anaerobiosis creates pronounced physiological difficulties.

Activation of considerable anaerobic metabolism is strongly associated with exhaustion. Reptiles with large accumulations of lactic acid have greatly diminished behavioral capacities and will not respond to further stimulation (Moberly, 1968b; Bennett and Licht, 1972; Bennett et al., 1975; Bartholomew et al., 1976; Ruben, 1976; Bennett and Gleeson, 1976; Gratz and Hutchison, 1977; Pough, 1977, 1978; Gleeson, 1980a, b). The casual relationships associated with this exhaustion are not known and would constitute an interesting area of study. Lactic acid is a moderately strong acid (pK=3.9). Its production during reptilian activity greatly elevates the concentration of hydrogen ions in both blood and muscle (Bennett, 1973; Gatten, 1975; Ruben, 1979; Mitchell et al., 1981). For instance, in the rattlesnake, Crotalus viridis, blood pH decreases from 7.38 to 6.79 after 5 min of intense activity at 35°C. This change in acid–base balance of body fluids induces considerable difficulties for hemoglobin and enzymatic function. The acidosis is also associated with major disruptions in blood calcium levels (Ruben and Bennett, 1981; Ruben, 1983).

Another disadvantage of anaerobic metabolism is its low yield of ATP to substrate catabolized. A net yield of only three ATP molecules is produced during the anaerobic breakdown of a glycogen unit to lactic acid, whereas 37–39 ATP molecules would be produced by aerobic metabolism. Hence, anaerobiosis is only 8–10% as efficient as aerobiosis on the basis of energy production per unit of fuel substrate. Consequently, the rate of substrate depletion must be 10–12 times as great to sustain an equivalent rate of ATP production. If substrate is limiting, this inefficiency may constitute an important factor curtailing activity. However, this anaerobic pathway is not inherently inefficient on a thermodynamic basis; both pathways trap approximately 40% of the potential energy released (Lehninger, 1975). The lactic acid produced may be reconverted to glycogen and reused subsequently, but such gluconeogenic resynthesis requires seven high energy phosphate molecules per glycogen unit, a net loss of four ATP equivalents for one cycle. This synthetic cost would be an additional longer-term expense associated with recovery from anaerobically supported activity. However, the fate of lactic acid during recovery from activity in reptiles is unknown. Several studies have attempted compartmental analyses of lactate removal and/or carbohydrate resynthesis during recovery (Moberly, 1968a; Bennett and Licht, 1972; Gratz and Hutchison, 1977; Coulson, 1980; Gleeson, 1980b), but the crucial studies examining the quantitative fate of exogeneously administered labeled lactate have not been undertaken. This is another area in which further research may be expected to increase our understanding of the energetic basis of reptilian activity.

In contrast to the inefficiencies of ATP generation and resynthesis, anaerobic metabolism is much more efficient at generating ATP per unit

time in reptiles than is aerobic metabolism (see below). From a behavioral viewpoint, anaerobiosis is thus more efficient than aerobiosis during very intense activity, such as rapid escape or pursuit. Metabolic modes should not be characterized as "efficient" or "inefficient" without specifying the criteria considered for efficiency.

C. MAGNITUDE OF ANAEROBIC ENERGY GENERATION DURING ACTIVITY

1. Introductory

Anaerobic activity energetics have been examined for two different aspects of energy utilization: the maximal speed of energy production and the total contribution to a bout of activity (Bennett and Licht, 1972). The former is measured as the *anaerobic scope*, the rate of lactic acid formation during the initial stages of vigorous activity, usually during the first 30 s. The *anaerobic capacity* is the amount of lactic acid formed during a longer bout of activity, usually that preceding exhaustion. The rate of lactic acid formation in reptiles is greatly decreased after the first minute of activity and 90% of the eventual accumulation has occurred at 1.5 min (Bennett and Licht, 1972; Coulson, 1980); consequently, anaerobic capacity in these animals may be estimated on the basis of lactic acid content after 2 + min of activity. Determination of such values requires analysis of whole body lactate concentrations in different groups of animals before and after the desired activity period. Blood lactate concentration may indicate the general level of anaerobic metabolism, but provides an inadequate estimate of anaerobic energetics because of the temporal and compartmental nature of lactate distribution (Bennett and Licht, 1972).

2. Anaerobic Scope

Table VII shows the maximal rates of lactic acid formation (anaerobic scopes) of several small reptiles. Each value is the highest reported over the range of body temperatures examined in the study. A greater anaerobic scope reported for *Anolis* during very short-term activity (Coulson, 1980) is in error, because the resting lactate content was not subtracted prior to calculation. Some interspecific variability is apparent; the fastest rate is twice that of the slowest. Lizards that exhibit more intense and prolonged activity responses under experimental circumstances (e.g. *Dipsosaurus*, *Sceloporus*, *Uta*) have greater anaerobic scopes than do those that are less responsive (e.g. *Anolis*, *Phrynosoma*, *Xantusia*). Such a relationship is anticipated as anaerobic metabolism provides the metabolic basis of the rapid activity. On the average, small lizards have anaerobic scopes of approximately 0.8 mg lactate/(g mass × 30 s). These data show no size dependence of anaerobic scope (Table VII; $r = 0.1$, $P > 0.5$). Presumably

TABLE VII

Maximal anaerobic scope of small reptiles and amphibians

Species	Mass g	T_B °C	Rate of lactate acid formation mg lactate/ (g mass × 30 s)	Reference
Reptiles				
Anolis carolinensis	4.5	37	0.77	Bennett and Licht, 1972
Dipsosaurus dorsalis	33.4	37	0.85	Bennett and Licht, 1972
Nerodia sipedon*	3.7	25	0.49	Pough, 1978
Phrynosoma platyrhinos	18.5	37	0.49	Bennett and Licht, 1972
Sceloporus occidentalis	12.0	35	1.07	Bennett and Ruben, 1975
Uta stansburiana	4.0	37	0.89	Bennett and Licht, 1972
Xantusia vigilis	1.2	30	0.78	Bennett and Licht, 1972
Amphibians				
Aneides flavipunctatus	1.9	20	0.27	Bennett and Licht, 1974
Aneides lugubris	4.1	20	0.21	Bennett and Licht, 1974
Batrachoseps attenuatus	0.7	20	0.65	Bennett and Licht, 1974
Bufo boreas	22.0	30	0.18	Bennett and Licht, 1974
Geotrypetes seraphinii	1.9	20	0.33	Bennett and Wake, 1974
Hyla regilla	2.6	20	0.40	Bennett and Licht, 1974
Notophthalmus viridescens	1.5	20	0.16	Bennett and Licht, 1974
Rana catesbeiana tadpoles	9.2	20	0.06	Bennett and Licht, 1974
Rana pipiens	39.7	20	0.51	Bennett and Licht, 1974

* Juvenile.

different behavioral responses overwhelm any mass-specific trends, such as those expected on the basis of differential muscularity. Few comparative data exist for other groups of vertebrates and thus it is difficult to place these scopes in a broader comparative framework. The scopes are clearly greater than those of most amphibians (Table VII), which range more widely. The greatest scopes for amphibians (*Batrachoseps, Rana*) are equivalent to the lowest ones for reptiles. These differences are probably not attributable to differential of body temperature, as anaerobic scope has a low thermal dependence in the reptiles (see below) and the amphibian temperatures are environmentally realistic. The rate of activation of the reptilian anaerobic response appears particularly high.

3. *Anaerobic Capacity*

Table VIII presents the total amount of lactic acid formed during longer-term activity as the differential between postactive and resting

TABLE VIII

Maximal anaerobic capacity in small reptiles

Species	Mass	T_B	Lactic acid formed during activity	Duration of activity	Reference
	g	°C	mg/g mass	min	
Testudines					
Pseudemys scripta	416	30	0.55	2	Gatten, 1974
Terrapene ornata	340	30	0.59	2	Gatten, 1974
Sauria					
Anolis carolinensis	4.5	37	1.19	5	Bennett and Licht, 1972
Dipsosaurus dorsalis	35.2	40	1.82	2	Bennett and Dawson, 1972
Eumeces obsoletus	30	40	1.18	2	A. F. Bennett and W. R. Dawson, unpublished
Phrynosoma platyrhinos	18.5	37	1.16	5	Bennett and Licht, 1972
Sceloporus occidentalis	13.1	30	1.76	5	Bennett and Gleeson, 1976
Scincella lateralis	1.7	20	0.94	6	Bennett and Licht, 1972
Uta stansburiana	4.0	37	1.12	3	Bennett and Licht, 1972
Xantusia vigilis	1.2	30	1.32	6	Bennett and Licht, 1972
Serpentes					
Crotalus viridis	292	35	0.97	5	Ruben, 1976
Masticophis flagellum and Coluber constrictor combined	195	35	1.75	5	Ruben, 1976
Lichanura trivirgata	314	32	0.30**	5	Ruben, 1976
Nerodia rhombifera	649	25	1.81	10	Gratz and Hutchison, 1977
Nerodia sipedon	65.1	25	1.5	40	Pough, 1978
Thamnophis sirtalis	54.3	25	1.4	22	Pough, 1977

* Measured as lactate formed during 2+ min of intense activity.
** Estimated from blood lactate.

lactate contents (anaerobic capacity). The anaerobic capacities of snakes and lizards are broadly overlapping. Species with the greatest potential activity levels during activity (*Dipsosaurus, Masticophis, Nerodia, Sceloporus*) have the highest anaerobic capacities. The two turtle species examined accumulate substantially less lactate during activity than do the other reptiles. These low concentrations contrast to the very great production of lactic acid during forced diving in turtles (Robin *et al.*, 1964; Penny, 1974). Long-term anaerobic energy generation and tolerance do not indicate capacity for aerobic activity (Bennett, 1978). The mass-specific anaerobic capacities of the species listed in Table VIII do not show a significant size dependence: $r = 0.5$ ($P > 0.4$) for lizards and $r = 0.28$ ($P > 0.5$) for all reptiles [log (mg lactate/g mass) versus log mass]. As is the case for anaerobic scope, behavioral type is a more important determinant of anaerobic capacity than is body size *per se*.

The anaerobic capacities of reptiles are generally greater than those of amphibians, but the differential is much smaller than that for anaerobic scopes. Anaerobic capacities of 18 species of amphibians (at 15–20°C, Bennett and Licht, 1972; Hutchison and Miller, 1979) range from 0.29 (*Notophthalmus*) to 1.77 (*Xenopus*) mg lactate/g mass and average 0.88 mg/g. This may be compared with an average of 1.21 mg/g for the 16 species of reptiles reported in Table VIII. Although the ranges overlap broadly and some amphibians have very high anaerobic capacities, the mean values of these groups are significantly different ($P < 0.05$, Student's *t*-test). Anaerobic capacities of the rodents *Microtus montanus* and *Dipodomys merriami* are 0.76 and 0.51 mg/g respectively (Ruben and Battalia, 1979), substantially lower than those of most snakes and lizards. Reptiles as a group have a greater potential to utilize anaerobic metabolism during activity than do the amphibians and mammals investigated thus far.

4. *Thermal Dependence of Anaerobic Metabolism*

The thermal dependence of anaerobic energy generation, of both anaerobic scope and anaerobic capacity, is substantially less than that of aerobic metabolism and is less than that anticipated for biological reaction rates in general. Figure 8 shows anaerobic scope as a function of body temperature of three lizards. At temperatures above 20°C, Q_{10} values for the maximal rate of lactic acid production range between 1.1 and 1.3 for these species, considerably less than those of 2–3 normally anticipated. At lower temperatures, anaerobic scope and burst activity capacity decline. Anaerobic capacity has a similarly low thermal dependence (Table IX) with Q_{10} values ranging from 0.76 to 1.39. The thermal dependence of peak blood lactic acid levels following activity is also low in the lizards *Iguana iguana* (Moberly, 1968a) and *Amblyrhynchus cristatus* (Bennett *et al.*, 1975),
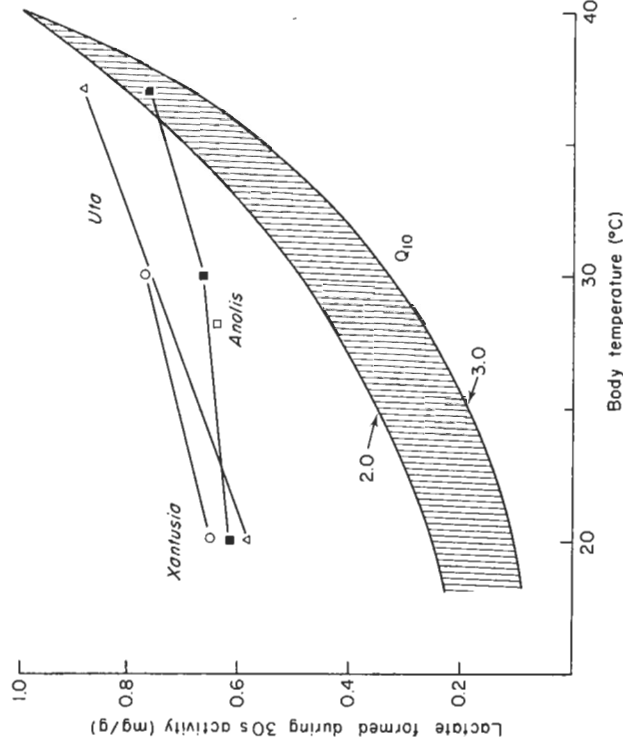
FIG. 8. Anaerobic scope as a function of temperature in three lizards (*Anolis carolinensis*, *Uta stansburiana*, *Xantusia vigilis*). The shaded region indicates values anticipated on the basis of Q_{10} values of 2 (upper bound) and 3 (lower bound) of an anaerobic scope of 1.0 mg lactate/(g × 30 s) at 40°C. Data from Bennett and Licht (1972), and Coulson (1979) for *Anolis* at 28°C (open square).

indicating temperature-independent anaerobic capacities in these lizards as well. This thermally independent metabolism permits these animals to perform over a broad range of body temperatures. Rapid activity and escape behavior are possible by means of anaerobic metabolism even at temperatures 15–20°C below selected thermal levels.

The influence of temperature on reptilian behavioral performance has been examined in only a few instances. In general, the thermal dependence of this performance is similar to that of anaerobic metabolism and is lower than normally anticipated ($Q_{10}=2$–3). The maximal striking speed of gopher snakes (*Pituophis melanoleucus*) has a Q_{10} of 1.4 over the range of 18–27°C (Greenwald, 1974). The number of limb movements possible before exhaustion is temperature independent from 25 to 40°C in marine iguanas (*Amblyrhynchus cristatus*; Bennett *et al.*, 1975). Burst speeds and distance running capacities are essentially temperature independent ($Q_{10}=0.7$–1.5) between 30 and 40°C in six species of lizards (*Cnemidophorus murinus*, *Dipsosaurus dorsalis*, *Eumeces obsoletus*, *Gerrhonotus multicarinatus*, *Sceloporus occidentalis*, *Uma notata*; Bennett, 1980). In the latter four species, these activities have Q_{10} values of only 1.4–1.9 between 20 and 30°C.

TABLE IX

Thermal dependence of anaerobic capacity of reptiles

Species	Temperature range °C	Q_{10}	Reference
Terrapene ornata	30–40	0.76	Gatten, 1974
Anolis carolinensis	20–37	1.09	Bennett and Licht, 1972
Dipsosaurus dorsalis	25–40	1.39	Bennett and Dawson, 1972
Eumeces obsoletus	20–40	1.36	Bennett and Dawson, unpub. data
Scincella lateralis	12–30	0.87	Bennett and Licht, 1972
Sceloporus occidentalis	20–35	1.26	Bennett and Gleeson, 1976
Uta stansburiana	20–37	1.00	Bennett and Licht, 1972
Xantusia vigilis	12–30	1.08	Bennett and Licht, 1972
Nerodia rhombifera	15–35	1.34	Gratz and Hutchison, 1977

Whether lactic acid production is the basis for all these performance characteristics is not known, but its involvement is likely. The low thermal dependence of these behaviors is certainly of considerable ecological significance.

5. *Other Factors Affecting Anaerobic Metabolism*

Undoubtedly several additional factors besides behavioral type and body temperature influence the capacity and scope of anaerobic metabolism. As stated previously, anaerobic scope and capacity are apparently independent of body size in small reptiles (Coulson, 1979), at least judging on the basis of the very few data available. However, a much larger size range is required before we may have confidence in this conclusion. Such variables as time of day, stage of development, acclimatory and seasonal states, and sex affect the aerobic metabolic levels of reptiles (Bennett and Dawson, 1976), but we do not know the influence of these variables on anaerobic metabolism. Diel cycles have been demonstrated to influence the anaerobic capacity of the snake *Nerodia rhombifera*, with a 40% decrement occurring at night (Gratz and Hutchison, 1977), but no other species has been examined. Both anaerobic capacity and duration of activity increase during ontogeny in the snakes *Thamnophis sirtalis* and *Nerodia sipedon* (Pough, 1977, 1978). Such major changes during maturation as a 50% increase in anaerobic capacity and a four- to sevenfold increment in time to exhaustion must have profound ecological and behavioral consequences for these species. Anaerobic scope and capacity are unaffected by the altitude of the test site or prior residence in the lizard *Sceloporus occidentalis*, the geographical range of which extends over a broad altitudinal gradient (Bennett and Ruben, 1975).

The influence of these and other factors requires much further examination and should constitute a rewarding field of research in the future.

IV. Total Metabolic Power Input: The Capacities of Aerobic and Anaerobic Energetics

The relative contribution of aerobic and anaerobic metabolism to activity energetics may be estimated by calculating the net yield of high energy phosphate compounds formed during a behavioral sequence. Simultaneous measurements of oxygen consumption and lactic acid formation during activity permit an evaluation of their relative importance in energy utilization. These relationships are usually estimated with the following formulas

$$1.0 \text{ ml } O_2 \text{ (STPD) consumed} = 290 \ \mu\text{moles ATP}$$
$$1.0 \text{ mg lactic acid formed} = 16.7 \ \mu\text{moles ATP}$$

(Bennett and Licht, 1972). These equations assume net yields of 39 and 3 ATP molecules per glycogen unit via aerobic and anaerobic metabolism respectively. The former value may overestimate aerobic ATP production by 5% due to uncertainties in the ATP yield of carbohydrate catabolism. The fuel is assumed to be glycogen, as the depletion of muscle glycogen is more than adequate to account for the formation of all muscle lactic acid in *Iguana iguana* (Moberly, 1968a) and *Nerodia rhombifera* (Gratz and Hutchison, 1977).

Maximal rates of ATP formation in each metabolic mode can be calculated by comparing maximal aerobic and anaerobic scopes. Average values of these factors for small lizards are estimated as 2.2 ml $O_2/(g \times h)$ at 40°C for a 10-g lizard (Tables I and III) and 0.8 mg lactate/$(g \times 30 \text{ s})$ (Table VII). The aerobic and anaerobic scopes are equal to 10.7 and 26.7 μmoles ATP/min respectively. For individual species in which both factors have been measured, aerobic and anaerobic scopes are 10.9 and 28.4 μmoles ATP/min in *Dipsosaurus dorsalis* and 6.4 and 35.7 μmoles ATP/min in *Sceloporus occidentalis* respectively (Bennett and Licht, 1972; Bennett and Dawson, 1972; Bennett and Ruben, 1975; Bennett and Gleeson, 1976). These scopes are not necessarily attained under the same conditions or at the same body temperature. However, they indicate clearly that the catabolic and ATP-generating abilities of anaerobic systems can exceed those of aerobic systems by a factor of 2–5 on a rate basis. These comparisons indicate that anaerobic metabolism in reptiles can be more efficient at ATP production per unit time than can aerobic metabolism. Because of the inefficiency of anaerobiosis on an ATP-per-substrate basis, the differential in carbohydrate utilization by these pathways is much greater; approxi-

mately 95% of the carbohydrate is catabolized anaerobically (Bennett *et al.*, 1975). Thus, in terms of fuel utilization during intense activity in reptiles, anaerobiosis is far more significant than aerobiosis.

The actual contribution of aerobic and anaerobic energetics to an activity sequence will depend upon the intensity and duration of the behavior. Low level activity will be supported aerobically, after an initial period of anaerobiosis reflecting a lag in the development of active oxygen consumption. If the activity is sustainable aerobically, the longer the duration of the activity, the smaller is the relative contribution of the initial anaerobic component. As intensity of activity increases, its duration before exhaustion decreases, and both these factors will increase the relative anaerobic contribution to the activity. The contribution of aerobic and anaerobic metabolism to the support of intense escape activity of 2–10 min duration have been estimated for several species of reptiles (Table X). Anaerobic metabolism accounts for 50–75% of the total ATP production during this intense activity. The time periods considered in the activity summarized in Table X represent rather long behavioral performance and often result in exhaustion. Intense activity of shorter duration has an even greater anaerobic reliance, as the rate of lactic acid production is highest during the initial stages of activity and active oxygen consumption requires time for full development. Anaerobic metabolism is estimated to provide at least 80–90% of the total ATP produced during the first 30 s of activity in small lizards (Bennett and Licht, 1972).

Body temperature exerts a strong influence on the total metabolic power input to activity and on the relative importance of aerobic and anaerobic support of that activity. Most of the measurements reported in Table X were made at high temperatures, at which the aerobic contribution is maximal. As temperature declines, total metabolic power input decreases. However, the aerobic contribution decreases more rapidly than does the anaerobic; the Q_{10} ranges are 2–3 and 1–1.5 respectively. Consequently, anaerobiosis provides an even greater share of the energetic support for intense activity at low body temperatures. The thermal dependence of these aspects of energy support to vigorous activity in the lizard *Dipsosaurus dorsalis* is shown in Fig. 9. Metabolic power input is maximal at 40°C, the field activity temperature of this animal, at which anaerobiosis provides 58% of ATP formation. The relative contribution of this component increases with decreasing temperature and is 83% at 25°C.

Body size may also be expected to influence the relative contributions of aerobic and anaerobic metabolism to activity. Mass-specific aerobic factors (resting and maximal oxygen consumption and aerobic scope) decline as body mass increases, approximately proportionally to $m^{-0.25}$. If anaerobic factors are independent of body mass, anaerobic factors

TABLE X

The contribution of aerobic and anaerobic energetics to intense activity in reptiles*

Species	T_B °C	Aerobic μmoles ATP/g	Anaerobic μmoles ATP/g	Total μmoles ATP/g	Percentage anaerobic contribution	Duration of Activity min	Reference
Terrapene ornata	40	6.2	7.5	13.7	55	2	Gatten, 1974
Amblyrhynchus cristatus	40	6.3	22.1**	28.4	78	2	Bennett et al., 1975
Dipsosaurus dorsalis	40	21.9	30.3	52.2	58	2	Bennett and Dawson, 1972
Eumeces obsoletus	40	20.2	19.7	39.9	49	2	Bennett and Dawson, unpublished
Iguana iguana	35	9.1	16.2	25.3	64	5	Moberly, 1968a; Bennett and Licht, 1972
Pseudemys scripta	30	5.9	9.2	15.1	61	2	Gatten, 1974
Sceloporus occidentalis	30	10.8	28.8	39.6	73	2	Bennett and Gleeson, 1976
Crotalus viridis	35	10.6	16.2	26.8	60	5	Ruben, 1976
Lichanura trivirgata	32	4.6	5.0**	9.6	52	5	Ruben, 1976
Masticophis flagellum, *Coluber constrictor*	35	23.0	29.1	52.1	56	5	Ruben, 1976
Nerodia rhombifera	25	9.1	30.2	39.3	77	10	Gratz and Hutchison, 1977

* Measured at the body temperature at which the greatest total metabolic power input occurs.
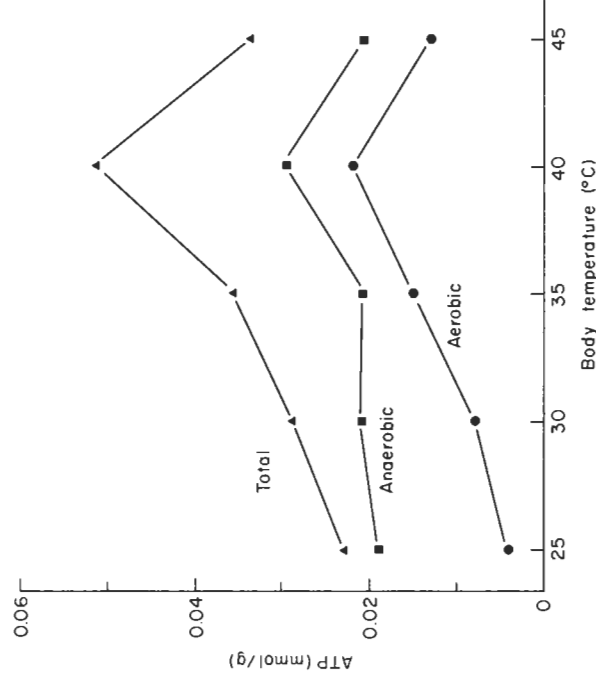** Estimated from blood lactate concentration.

Fig. 9. *Diposaurus dorsalis*. Metabolic power input (aerobic, anaerobic, and total) during 2 min of burst activity as a function of body temperature. Redrawn from Bennett and Dawson (1972).

should assume a greater significance in supporting burst activity in larger animals (Coulson, 1979). Conversely, aerobic factors would assume a greater significance in smaller animals. However, the assumptions behind mass-independence of anaerobic metabolic abilities have not been tested over a large mass range, and these speculations are only presumptive until such measurements are made.

Total metabolic power input, the sum of the aerobic and anaerobic components, is generally correlated with activity capacity among different groups of reptiles (Table X). Small lizards and diurnally active snakes (e.g. *Diposaurus, Eumeces, Masticophis, Nerodia, Sceloporus*) have the greatest levels of total power input. Turtles and boid snakes (*Lichanura, Pseudemys, Terrapene*) have correspondingly low metabolic capacities.

Little comparative information is available for maximal metabolic support of intense, short-term activity in other vertebrate groups. Total metabolic input during 2–3 min of activity in four species of amphibians at 20–25°C ranges from 14 to 31 μmoles ATP/g mass (Bennett and Licht, 1973; Hillman *et al.*, 1979). The highest values do not equal those of the most active reptiles, but few species have been examined. Similar measurements on the energetics of burst activity of mammals and birds would be of considerable interest, as these animals have such greatly

expanded aerobic capacities. Measurements based on maximal oxygen consumption are inapplicable to this comparison, because these levels cannot be instantaneously attained. The only observations available are those for the rodents *Dipodomys merriami* and *Microtus montanus*, which produce 107 and 53 μmoles ATP/g respectively during 5 min of maximal activity (Ruben and Battalia, 1979). Anaerobic metabolism accounts for 8 and 25% respectively of the total production. Although these total values for maximal activity exceed those of most reptiles, they are not an order of magnitude in excess as are their aerobic capabilities. During shorter time periods, when aerobiosis is less significant, metabolic power input to activity in reptiles may equal or exceed that of small mammals. The development of high aerobic capacities in mammals has not resulted in increased capacities for burst activity, but rather in the expansion of capacities for routine and sustainable activity (Ruben and Battalia, 1979; Bennett and Ruben, 1979).

V. Metabolic Rate under Natural Circumstances

A. GENERAL

Anaerobic metabolism significantly extends the behavioral scope of reptiles, as aerobic limits are low in these animals. However, its use is correlated with diminished behavioral capacity and exhaustion, and it is anticipated that reptiles would avoid anaerobiosis if possible. It is anticipated that reptiles will be sedentary and move slowly most of the time, perhaps patrolling at low velocity. These activities are within their meager aerobic support capabilities. The degree to which reptiles elevate their metabolism and the closeness of their approach to aerobic limits are of considerable interest in relating laboratory metabolic observations to reptilian ecological energetics. Likewise of interest is the extent of anaerobic metabolism under natural field conditions. Intense activity can be supported only anaerobically and is required in precisely those instances which are of the greatest significance to survival and reproduction (e.g. escape, pursuit, courtship, territorial defense). If the full anaerobic capacity is used only once a week or even once a year, it is likely to be used under critical circumstances. Therefore, even though it may not have a large quantitative significance in the time or energy budget of a reptile, the use of anaerobic metabolism may be crucial to survival. Unfortunately, there is very little information available about the extent of utilization of either aerobic or anaerobic metabolism in reptiles naturally active under field conditions. This will doubtlessly be one of the most exciting and productive areas of future research in reptilian metabolism.

B. Aerobic Metabolic Level

Determination of aerobic metabolic expenditure of reptiles in natural circumstances is highly desirable but very difficult technically. Direct measurement of gas exchange in field-active animals is generally impossible. However, a novel study (Jackson and Prange, 1979) determined oxygen consumption during egg laying by sea turtles (*Chelonia mydas*). Aerobic metabolism increased tenfold over resting levels, indicating both considerable exertion and energy expense. A similar metabolic increment was measured in incubating female pythons under captive conditions (Hutchison et al., 1966). The time-and-estimated-energy budget approach (e.g. Alexander and Whitford, 1968; Wilson and Lee, 1974; Bennett and Gorman, 1979) is useful only as a rough estimate of individual or population energy flow. Whereas these measurements are probably accurate for the purposes intended, they cannot be used to indicate the level of aerobic metabolism in the field as its estimate involves original assumptions and estimates concerning those costs.

Independent measurements of field metabolism are necessary to validate the approach of time-and-estimated-energy budgets and to provide an accurate assessment of the costs of natural behavior. Such measurements are feasible utilizing doubly-labeled water (Nagy, 1975, volume 12). This technique has been utilized to study the metabolic rates of two species of sceloporine lizards naturally active in the field (*Sceloporus occidentalis*, Bennett and Nagy, 1977; *S. jarrovi*, Congdon et al., 1979). During periods of the year when the lizards are active and out of their burrows during the day, the total metabolic energy expended is 2–2.5 times the integrated level of resting metabolism measured on a normal thermal cycle. That is, field aerobic expenditure is only twice that measured for an inactive animal exposed to the same thermal regime. If the animals are assumed to be inactive at night, the increment associated with activity during the diurnal period can be calculated (Bennett and Nagy, 1977). Diurnal metabolic rate in the field is 2.5–3 times resting level, or about one-half of the maximum level sustainable aerobically (maximal oxygen consumption). The average level of field metabolism of *Sceloporus* is thus well within its aerobic scope and well above resting metabolic levels. However, these measurements integrate metabolism for periods of days or weeks and cannot provide information on the variation in metabolic rate, that is, how often it approaches maximal or minimal aerobic limits.

Field energetics may also be estimated by recording behavior in the field and duplicating it while measuring metabolic rate in the laboratory. This approach was undertaken to evaluate foraging energetics of the lizard *Cnemidophorus murinus* (Bennett and Gleeson, 1979; Bennett and Gorman,

1979). This herbivorous lizard spends most of its day foraging at about 0.13 km/h, and this activity can be undertaken on a motor-driven treadmill. Metabolic rate at various speeds is shown in Fig. 10. Oxygen consumption at normal foraging speed, 0.9 ml $O_2/(g \times h)$, is four times resting levels and is one-half maximal levels. Thus, normal foraging is maintained within aerobically supportable boundaries and avoids anaerobic metabolism. However, maximal sustainable speed is only 0.3 km/h and exhaustion occurs rapidly at 0.5 km/h, so that the range of potential speeds is narrow. An indication of the significance of anaerobic metabolism to activity in this animal is given by its burst speed, which averages 8.2 km/h (Bennett, 1980b). Thus, anaerobiosis expands the activity capacity of this lizard by nearly 30-fold.

C. ANAEROBIC METABOLISM

There are very few studies of the extent of anaerobic metabolism during activity under field conditions. A recent laboratory study found significant lactic acid accumulation in garter snakes (*Thamnophis elegans*) during attack and capture of salamander prey (0.87 mg lactate/g mass versus 0.31 and 1.40 mg/g for resting and manually stimulated snakes respectively; Feder and Arnold, in press). Thus, anaerobiosis may also be used for prey capture by this snake in the wild.

Animals can be surveyed in field conditions for elevated body or blood
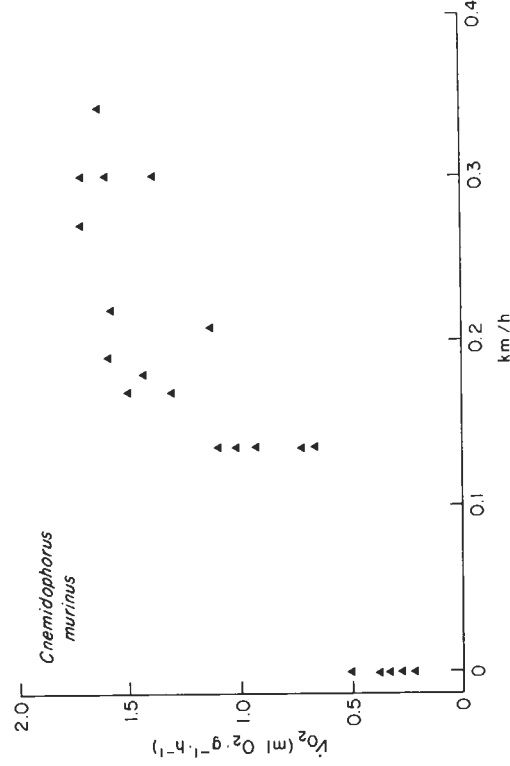

FIG. 10. *Cnemidophorus murinus*. Oxygen consumption as a function of speed at 40 C while walking on a motor-driven treadmill. Redrawn from Bennett and Gleeson (1979).

lactate concentrations. Elevated levels would indicate recent anaerobic activity. Blood lactate levels in a group of basking and beaching marine iguanas (*Amblyrhynchus cristatus*) were indistinguishable from those of animals resting quietly in the laboratory. Consequently, routine activity in this lizard, even during diving, does not appear to utilize anaerobiosis. However, both burst swimming and running behavior result in extensive anaerobic metabolism (Bartholomew *et al.*, 1976; Gleeson, 1980a). Blood lactate levels increase significantly during egg-laying behavior by the sea turtle, *Chelonia mydas* (Jackson and Prange, 1979). Whole body lactate concentrations were measured in a series of *Anolis bonairensis*, resting in the laboratory and sampled from the field throughout the day (Bennett *et al.*, 1981). Mean levels of lactate in field active lizards generally exceed resting levels and some individual animals had lactate concentrations exceeding 1.0 mg/g. Male lizards provoked into territorial defense by the introduction of another male have elevated lactate levels in proportion to the magnitude of their behavioral response.

Anaerobiosis appears to be rarely used when reptiles dive freely. Anaerobic capacities are well developed and lactic acid production is great during forced dives (*Alligator*, Andersen, 1961; *Amblyrhynchus*, Bartholomew *et al.*, 1976; *Chelonia*, Berkson, 1966; Hochachka *et al.*, 1975; *Lapemis*, Seymour and Webster, 1975; *Nerodia*, Murdaugh and Jackson, 1962; *Pseudemys*, Robin *et al.*, 1964; Altman and Robin, 1969, Penny, 1974). However, only exceptionally do freely diving animals show elevated lactate levels (Heatwole, 1978; *Amblyrhynchus*, Gleeson, 1980a; *Lapemis*, Seymour and Webster, 1975; *Laticauda*, Seymour, 1979; this volume; *Varanus*, Wood and Johansen, 1974). The pronounced anaerobic response seen in forced dives may be due to activity, stress, and/or psychological factors. Anaerobic metabolism in diving reptiles appears to be reserved for exceptional circumstances, as when prolonged dives or rapid escape behavior underwater are required.

VI. Conclusions and Future Directions

The data summarized in this chapter permit us to infer some broad, if tentative, generalizations concerning patterns of reptilian activity energetics. Maximal levels of oxygen consumption are approximately 6–10 times resting levels. Both maximal and resting rates are fairly typical of those of other ectothermic vertebrates and are low in comparison to those of birds and mammals. They are absolutely low in the level of exertion which they permit. Capacities of reptiles to support behavior aerobically are limited and their maximal aerobic speeds are only about 1.0 km/h at best. The thermal

dependence of oxygen utilization greatly decreases this already limited aerobic ability at low body temperature.

Supplementation of aerobic with anaerobic metabolism greatly expands the metabolic power which reptiles may use for activity. Anaerobic energetics are of high intensity with a greater time-dependent energy generation capacity than those of aerobiosis. The relative insensitivity of anaerobiosis to changes in body temperature allows burst activity over a broad thermal range. However, extensive anaerobic metabolism entails exhaustion and disruption of normal physiological function and is effective over a very short time.

The contrast between the aerobic and anaerobic abilities of reptiles improves our understanding of patterns of reptilian behavior. The detrimental effects of anaerobiosis make low-intensity activity advantageous. It is our impression that reptiles spend much of their time, even when "active" in the field, remaining quiescent for long periods or making only slow and deliberate movements. These are supportable through aerobic metabolism. This relative inactivity is punctuated by rapid and explosive bursts, fueled by anaerobic metabolism. The contrast between sedentary, sometimes immobile behavior and intense and rapid activity, which makes reptiles such fascinating animals to watch, finds its basis in differential metabolic support for these behavioral modes.

Our understanding of the limits and consequences of reptilian activity has moved far within the past decade. A further expansion of our knowledge is to be anticipated in the near future. Only general limits of aerobic metabolism (measurements of resting and maximal oxygen consumption) now have a satisfactory data base. However, even for these we need a much greater taxonomic breadth of observation to permit correlation of metabolic level with behavioral type or ecological circumstance. Our knowledge is incomplete in nearly all other areas of physiology, behavior, and ecology relating to reptilian activity. In numerous places throughout the chapter, I have indicated specific areas for which data are particularly scanty or extensions of new information are required. It would be useful to have more detailed information on nearly any of these areas.

Although it is somewhat risky to suggest desired directions for research, the following are probable themes which will carry this area of research forward in the future. A persistent theme in reptilian biology has been the influence of body temperature. Presumably, this will continue to be a topic of considerable interest and theoretical importance. Although the thermal dependence of aerobic capacities are fairly well determined, data are only fragmentary for many of the variables discussed here, including anaerobic scope, total metabolic input to activity, cost of locomotion and maximal aerobic speed, and behavioral capacities. All these areas require further

examination of the influence of body temperature before we can generalize effectively concerning reptilian capabilities. In another vein, the physiological bases of these performance characteristics are still largely uninvestigated. We lack mechanistic explanations for such phenomena as the thermal independence of anaerobiosis and the low level of oxygen-processing ability of reptiles. These are areas in which comparative physiologists specializing in respiratory, circulatory, and muscular physiology could make substantial contributions. Another area of interest is the significance to reptilian activity of other anaerobically formed end-products besides lactic acid, especially the contribution of ATP and creatine phosphate depletion. Studies of locomotion, in addition to examining aerobic limits and thermal dependence, should also concentrate on the energetic implications of various locomotory modifications and modes, including swimming, limblessness, and bipedality. At present, we know very little about the physiology and behavioral consequences of recovery after activity in reptiles. This is an area in which substantial work could proceed rapidly. Most significantly, we need further measurements of energetics under natural or semi-natural conditions. These should let us determine the extent to which reptilian behavior normally approaches its metabolic limits and the extent of anaerobic metabolism under field conditions.

There is still much information needed, although our understanding has increased substantially in a very short time. It is somewhat discouraging to realize that for many of the variables considered, reptiles are the best-studied group of animals. We require much more comparative data for other vertebrate groups before we can successfully understand the opportunities of and limitations on behavior and activity provided by the vertebrate plan of organization.

Acknowledgments

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