Exercise Performance of Reptiles

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I. Introduction

The first quantitative measurements on reptilian exercise physiology were undertaken only three decades ago. This study (Bartholomew and Tucker, 1963) described the effect of body temperature on maximal oxygen consumption and aerobic scope in an agamid lizard, *Amphibolurus barbatus*. Since that time, reptiles have proved to be highly versatile and useful animals in which to examine activity and activity energetics, and hundreds of papers have subsequently appeared on these topics. In many areas of comparative exercise physiology (e.g., anaerobic energetics, burst speed performance, measurement of natural selection on performance), reptiles are the group in which new techniques were pioneered and remain today the best understood and most widely examined taxon. What accounts for the great popularity of reptiles for these types of studies? The group offers a unique combination of factors, some historical, some practical, including:

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1. Position in the evolutionary development of the vertebrates;
2. Availability of well-understood phylogenetic relationships;
3. Diversity of locomotor morphology;
4. Diversity of ecology, especially in regard to locomotion;
5. Accessibility of natural populations.

Similar factors have also been significant in the prominence of one group of reptiles, lizards, in a wide variety of ecological studies (e.g., Milstead, 1967; Huey *et al.*, 1983).

Crucial factors in the popularity of reptiles have been both their position in the evolutionary development of the vertebrates and our extensive knowledge of the taxonomy and phylogeny of the group. ["Reptiles" in this article is used in the common, not cladistic (e.g., see Gauthier *et al.*, 1988b), sense and refers to squamates, turtles, sphenodons, crocodilians, and various extinct groups of dinosaurs and their allies.] Reptiles were the first fully terrestrial vertebrate group, the first to meet all the challenges of land existence head on, including its very different characteristics for locomotor performance. Further and most significantly, the group gave rise independently to two major phylogenetic radiations of endotherms, the mammals and the birds (Fig. 1). These animals are very different in their metabolic and exercise capacities than were their reptilian progenitors, and the evolution of their endothermic condition has been a topic of sustained interest and speculation (reviewed in Bennett, 1991). In these deliberations, the metabolic and exercise status of extant reptiles have figured prominently. Surviving reptilian groups are diversified phylogenetically, and it has been argued (Bennett and Ruben, 1979) on the principle of parsimony that traits that are widely shared among extant reptilian taxa are representative of the ancestral physiological condition from which mammalian and avian endothermy evolved. For example, low resting metabolic rates are characteristic of all extant amphibian and reptilian taxa. These are in contrast to those of birds and mammals, which are 6- to 10-fold greater, even at the same body size and temperature (Benedict, 1932; Dawson and Bartholomew, 1956; Bennett and Dawson, 1976). This greater metabolic rate, coupled with greater insulation, is the physiological basis for endothermy in these groups. Although it has been proposed (Gardiner, 1982) that birds and mammals shared a common endothermic ancestor, the distribution of relevant physiological traits among extant reptiles makes this proposition exceedingly unlikely (Fig. 1). If this were the case, low levels of metabolism would have to have re-evolved at least three times among extant reptilian lineages. More probable is the independent development of
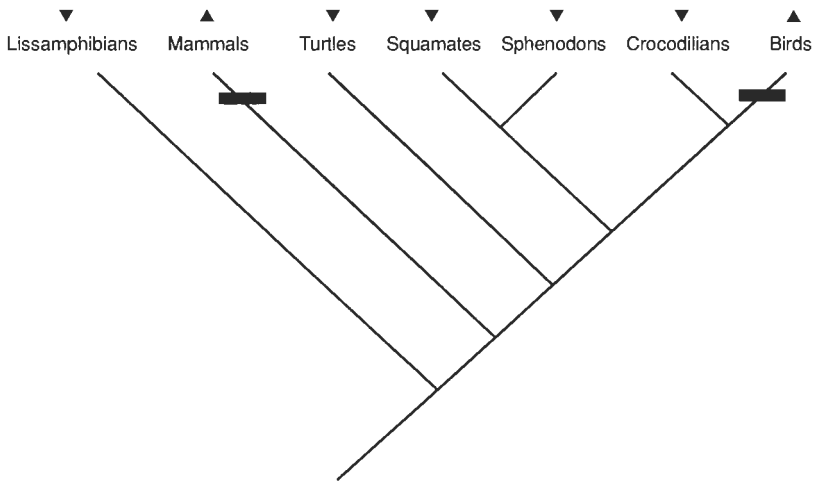
FIG. 1. A classification of extant tetrapod groups (from Gauthier *et al.*, 1988a,b). Low resting metabolic rate is indicated by a downward-pointing triangle; a high metabolic rate by an upward-pointing triangle. Solid bars indicate the probable independent acquisition of high metabolic rate and endothermy. If high metabolic rate was a shared primitive character of mammals and birds, low metabolic rate would have had to have repeatedly re-evolved in the extant reptilian groups.

endothermy in mammals and birds. Such discussions of the macroevolution of physiological characters of mammals and birds, as well as dinosaurs (Bakker, 1971, 1986) and mammallike reptiles (Bennett and Ruben, 1986), have consistently taken those of extant reptiles into account.

Phylogenetic history is increasingly recognized as an important influence on the structure and function of extant organisms (e.g., Lauder, 1981; Felsenstein, 1985; Huey, 1987; Harvey and Pagel, 1991). Comparative studies have begun to incorporate phylogenetic information into the analysis of morphological and physiological characters, attempting to determine ancestral and derived condition, directionality of evolution, and adaptive nature of the character. Analyses of reptilian activity (e.g., Huey and Bennett, 1987; Losos, 1990a,b) were among the first functional studies to incorporate and take advantage of this historical perspective. The availability of excellent phylogenies for many reptilian groups greatly facilitates this approach and ensures the continued use of reptiles in future studies of this type.

A further feature of reptiles that has prompted interest in their activity capacities is the diversity of their locomotor structures. Crocodilians and many lizards have a generalized tetrapodal limb structure

that has served as a model for that primitive condition. In addition, the diversity within the group has provided an opportunity to study the consequences of specialization for locomotor performance and energetics. Limb reduction or elimination, for instance, has occurred several times in the group. Snakes in particular have been proved popular study animals for examining the locomotor consequences of limblessness (e.g., Jayne, 1986). Other specialized features influencing locomotor ability include the boxlike shell of turtles, the zygomorphic limb structure of chameleons, and toe-pad specializations of geckos. These all invite investigation of their performance and energetic consequences for locomotion.

In addition to the diversity of their locomotor morphology, reptiles are also ecologically diverse in their habits and habitats, exhibiting a variety of different types and levels of activity under natural circumstances. Some species remain immobile for long periods and have punctuated episodes of very intense activity ("sit-and-wait foragers"), and some are continuously active for long periods ("wide foragers"). Some are active at low and some at high temperatures. Some are terrestrial, some are arboreal, some are aquatic, and some are naturally active in more than one of these habitats. In addition, many reptiles are diurnally active and highly visible and occur locally in great numbers, facilitating observations on their natural behavior and population biology. The wealth of information on reptilian ecology and their popularity in ecological studies make it much easier to place laboratory-based observations in an appropriate natural context.

There are thus many reasons that biologists have used reptiles in studies of locomotor performance and activity, reflected in the literature in a wide variety of observations, motivations, and interpretive contexts. This will not be an extensive and detailed review of all such studies. Rather it will attempt to examine the breadth of topics that physiologists have examined regarding active reptiles and the major contributions of these studies to the field of exercise physiology. Previous reviews are available on reptilian energetics (Bennett and Dawson, 1976; Waldschmidt *et al.*, 1987) and activity physiology (Bennett, 1982, 1983; Gatten, 1985; Gleeson and Bennett, 1985; Hertz *et al.*, 1988; Gleeson, 1991).

II. Endurance Activity

The first comprehensive comparative studies on active animals were done on fish by Fry, Brett, and their co-workers (e.g., Fry, 1947; Brett,

1964). This research involved the measurement of oxygen consumption over a range of sustainable swimming speeds, as well as determination of the maximum sustainable speed ("critical swimming speed"). The influence of such factors as body size and temperature on cost and limits of performance figured prominently in this research. Comparative mammalian studies that followed (e.g., Taylor *et al.*, 1970) continued to emphasize energy expenditure as a function of speed, with concomitant analysis of the influence of body size. Early work on the physiology of active reptiles was much influenced by these studies, and reptilian research therefore initially followed similar themes.

The first studies on reptilian activity involved the measurement of aerobic scope, the difference between standard and maximal oxygen consumption. Fry (1947) proposed this as an index of the sustainable work capacity of an organism, and subsequent comparative studies have generally supported this association. Reptilian studies concentrated on species differences in aerobic scope and found a positive correlation between activity level of the species and aerobic scope (e.g., Tucker, 1967; Ruben, 1976; John-Alder *et al.*, 1986) (e.g., Fig. 2). Maximal aerobic scope generally, although not invariably, was found to correlate with preferred body temperatures, so that work capacity is generally maximized under conditions experienced during field ac-
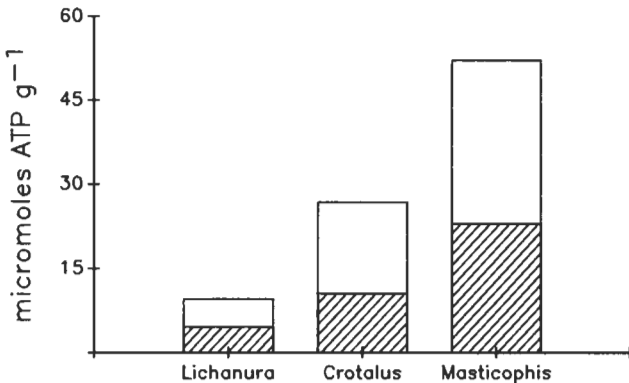

FIG. 2. ATP formed during 5 min of vigorous activity by the snakes *Lichanura rose-ofusca* (rosy boa), *Crotalus viridis* (western rattlesnake), and *Masticophis flagellum* (coachwhip) (body temperatures = 32–35°C). The boa is very slow and sluggish, the rattlesnake undertakes intense bursts of striking activity, and the coachwhip is an actively foraging predator. The aerobic contribution is measured by oxygen consumption (hatched bar) and the anaerobic (open bar) by lactic acid formation. Data from Ruben (1976).

tivity. Studies of scope, which frequently elicited maximal oxygen consumption through handling or electric shock, gave way to more detailed examinations of locomotor energetics involving treadmill exercise (e.g., Moberly, 1968b; Bakker, 1972). This latter work has been a crucial contribution to our understanding of the energetics of locomotion of animals in general.

A. Cost of Locomotor Activity

Energy expenditure of animals walking or running over a range of sustainable speeds can be adequately described with a linear regression (Fig. 3A). The slope of this function is termed the net cost of transport (Taylor *et al.*, 1970; Schmidt-Nielsen, 1972) and is expressed as energy utilized to move a unit body mass a unit distance. Bakker (1972) first demonstrated and subsequent studies (e.g., John-Alder *et al.*, 1986) have confirmed that this net cost of transport is indistinguishable in mammals and reptiles. It had previously been assumed that the sprawling-limbed posture of ectothermic vertebrates was energetically inefficient, a condition that would have been reflected in a greater net cost of transport. Bakker's data made it clear that this aspect of locomotor energetics is independent of posture. Net cost of transport was not modified during, and thus could not have been a selective factor in, the evolution of endothermy in mammals. Later comparative studies involving other vertebrates and invertebrates (summarized in Full *et al.*, 1990) found that the net cost of transport for terrestrial locomotion may be generally described by a single allometric relation (body mass exponent, b, $= -0.3$), regardless of body plan, limb number, or phylogenetic affinity. [It should be born in mind, however, that the description of terrestrial locomotor costs by a common allometric equation is not a functional explanation of those costs. Biomechanical and physiological factors that underlie this relationship (e.g., Kram and Taylor, 1990) still need to be elucidated.]

Several studies concerning locomotor costs of reptiles, in addition to those cited here, have been influential in our more general understanding of locomotor energetics. Of particular interest in this regard has been the energetic effects of the evolutionary reduction or elimination of limbs. An early report measuring the cost of crawling in snakes (Chowdrow and Taylor, 1973) suggested a lower than anticipated net cost of transport. Because limb reduction has developed repeatedly in different groups of tetrapods, these data suggested that one explanation for its evolution might have been reduction of locomotor costs and consequent energetic economy. A subsequent study, however, found net
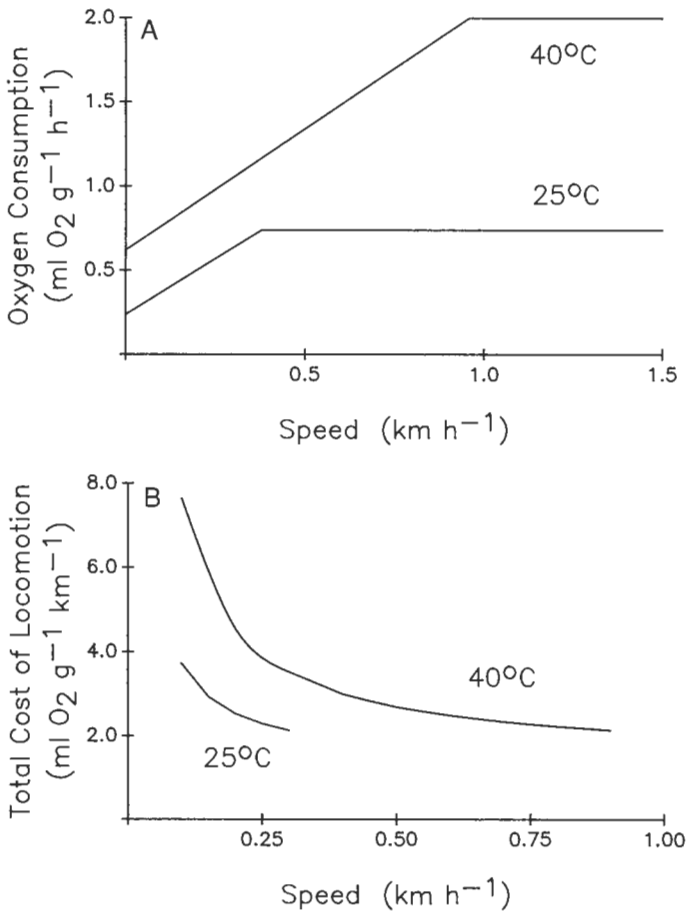
FIG. 3. Oxygen consumption by the lizard *Dipsosaurus dorsalis* walking at different speeds with body temperatures of 25° and 40°C. (A) Oxygen consumption increases up to maximal aerobic speed (0.38 km h⁻¹ at 25°C; 0.96 km h⁻¹ at 40°C). Net cost of transport (slope of the line) is temperature independent and equals 1.4 ml O₂ g⁻¹ h⁻¹. (B) Total cost of locomotion (energy used to walk 1 km) decreases with increasing speed. It is greater at 40° than at 25°C at any common sustainable speed, and is temperature independent (= 2.1 ml O₂ g⁻¹ km⁻¹) at maximal aerobic speed. Data from John-Alder and Bennett (1981).

costs of lateral undulation and concertina locomotion to be equal to or greater than those of limbed locomotion (Walton *et al.*, 1990), and hence no particular energetic advantage apparently accrued during the evolution of limblessness (Fig. 4). Sidewinding, a relatively uncommon locomotor mode even among snakes, apparently does have a lower
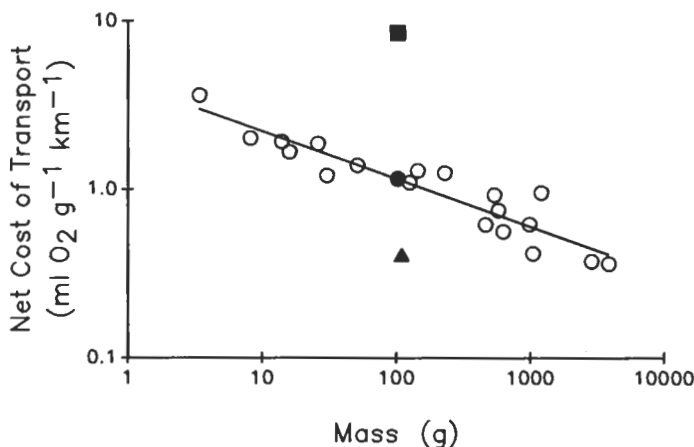
FIG. 4. Net cost of transport (slope of oxygen consumption as a function of speed) of lizards and snakes of different size. Open circles = 15 different lizard species (summarized in John-Alder *et al.*, 1986); solid circle and square = lateral undulation and concertina locomotion (respectively) by the snake *Coluber constrictor* (Walton *et al.*, 1990); solid triangle = sidewinding by *Crotalus cerastes* (Secor *et al.*, 1992). Regression line is for lizard species only (John-Alder *et al.*, 1986).

than anticipated net cost of transport, but substantially higher total costs at low speeds (Secor *et al.*, 1992).

Another topic of interest to comparative exercise physiologists is the profound difference in transport cost evident in locomotion in different media. Net costs of transport of flying animals are only about 30% and those of swimmers are only about 10% those of terrestrial walkers or runners (Schmidt-Nielsen, 1972). These comparisons, however, are made among animals of extremely different body form and phylogenetic history, such as birds, fish, and mammals, and it is difficult to disengage other morphological and phylogenetic effects on this relationship from those associated with locomotor costs alone. Marine iguanas are lizards that naturally engage in both walking and swimming behavior, so it was possible (Gleeson, 1979, 1980; Vleck *et al.*, 1981) to measure differential locomotor costs within a single species and thus reduce extraneous effects arising from intergroup comparisons (Fig. 5). Terrestrial locomotion for these lizards proved to be as expensive as in other terrestrial walkers. Swimming is in fact substantially less costly than walking for these animals, although it is not as inexpensive as it is in fish, presumably because of the energy involved in surface wake formation. Differences in the cost of transport among media are not, therefore, simply due to differences in body form in
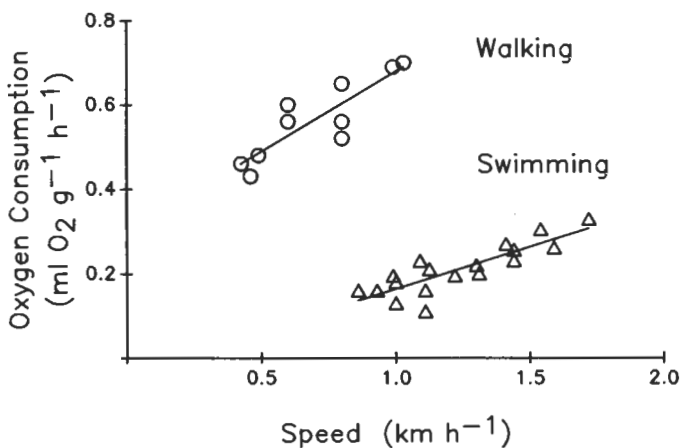
FIG. 5. Oxygen consumption during walking (body temperature = 35°C) and swimming (body temperature = 25°C) in adult marine iguanas. Locomotor costs are reduced (net cost of transport = 0.185 versus 0.373 ml O_2 g^{-1} km^{-1}) and endurance is increased by swimming in comparison to walking. Data from Gleeson (1979).

different taxa or factors such as differential amount of locomotor musculature. Rather they appear to involve more fundamental factors inherent in the media themselves, such as differential buoyancy and resistance. These studies demonstrate the past utility of reptiles in studies of locomotor energetics, and we may anticipate that reptiles will continue to play an important role in the future development and testing of bioenergetic models.

Locomotor costs are not completely accounted for by measurement of net cost of transport alone. Total metabolic rates also include those costs estimated by the extrapolation of energy use to zero speed and are variously assumed to include maintenance and postural factors (Fig. 3A) (Taylor *et al.*, 1970). These may make a substantial difference in comparisons of locomotor energetics. For instance, although net costs of transport are equal in reptiles and mammals, total metabolic rates of similar-sized animals walking at similar speeds are approximately 6- to 10-fold greater in mammals (Bennett and Ruben, 1979). Likewise, although net costs of transport are temperature independent in reptiles, maintenance costs are not, and it is more expensive for an animal to walk at a given speed with a higher body temperature (Fig. 3B). Total locomotor costs are the ones that actually must be met from the energy budget of an animal, and hence are the factors to be considered is estimating locomotor costs in natural environments.

B. Endurance and Maximal Oxygen Consumption

Walking or running is not indefinitely sustainable at all speeds at which an animal is capable of moving. As speed increases, a limit is reached, above which exhaustion ensues rapidly. This limit is termed the maximal aerobic speed and coincides with the attainment of maximal oxygen consumption during exercise (Fig. 3A) (Bennett and John-Alder, 1984). Maximal aerobic speed is correlated with maximal oxygen consumption across body temperatures within a species and these factors are positively associated among species (Bennett, 1982; Bennett and John-Alder, 1984). Speeds above maximal aerobic require sources of energy in addition to those provided by aerobic metabolism, involving in reptiles the catabolism of high-energy phosphate compounds and/or the glycolytic formation of lactic acid (Bennett, 1978, 1989). Both resting and maximal levels of oxygen consumption of reptiles are low in comparison to the costs of terrestrial locomotion, and hence maximal aerobic speeds are relatively modest, typically approximating only 1 km h^{-1} (Garland, 1982). Maximal speeds during rapid bursts of activity may exceed this value by 10- to 20-fold (Bennett, 1980, 1982), and hence only a fraction of the potential locomotor repertoire of reptiles can be accessed and sustained aerobically. Low body temperatures exacerbate this condition by decreasing maximal levels of oxygen consumption and hence decreasing maximal aerobic speeds (Bennett and John-Alder, 1984). Reptiles consequently have a much lower capacity for sustainable activity than do birds or mammals, and this has been hypothesized as one of the factors associated with the evolutionary development of endothermy in these groups (Regal, 1978; Bennett and Ruben, 1979). Reptiles are confined by their physiological capacities to undertake rather slow activities that can be met with their modest aerobic powers or to engage in bursts of rapid movement that quickly result in exhaustion.

If maximal oxygen consumption constrains sustainable activity levels, what limits maximal oxygen consumption? There have been no systematic examinations of this limitation in reptiles, in contrast to extensive investigations undertaken in mammals (Taylor and Weibel, 1981; Weibel *et al.*, 1991). This latter work has been done in the investigation of the concept of symmorphosis, the hypothesis that no single morphological or physiological system limits a complex function, such as maximal oxygen consumption. Rather design limits are hypothesized to be met in all components of the system simultaneously. This hypothesis and interpretation of data supporting it have been controversial (Lindstedt and Jones, 1987; Dudley and Gans, 1991), and it would seem well worthwhile to undertake a similar investigation in

another group of animals to test the hypothesis further. Reptiles would be a very logical choice for such an examination, because of the relative ease of investigating their physiology during sustained locomotion.

Studies on maximal oxygen consumption in reptiles have focused on the role of particular systems in providing oxygen delivery during activity. It has been proposed (Carrier, 1987, 1989, 1990) that ventilation of the lungs in lizards is incompatible with locomotion because of competing functional demands on the axial musculature during locomotion and ventilation. Hence ventilation must be restricted while animals are walking or running, forming a limitation on oxygen uptake during activity, particularly at high speeds. Other measurements on active lizards (Gleeson *et al.*, 1980; Mitchell *et al.*, 1981a,b), however, have found that breathing is sustained during lower-speed locomotion, even at velocities greater than maximal aerobic speed, at which maximal oxygen consumption is attained. Both alveolar and arterial oxygen partial pressures remain high at speeds above maximal aerobic (Fig. 6), indicating that ventilation is quite adequate for oxygen supply over this entire speed range. These observations indicate that ventilation is not necessarily compromised during locomotion and is not a limiting factor in oxygen transport at or above maximal aerobic speed in these animals. If lizards do not ventilate while running at high speeds, it may be because other portions of the oxygen transport systems are already operating at maximal capacity (Fig. 7) and continued ventilation would not increase oxygen uptake. Human sprinters, for instance, frequently avoid breathing during their runs.

In contrast to ventilation, cardiac function may be a factor limiting maximal oxygen in consumption. Limits of cardiovascular transport capacities appear to be attained at maximal aerobic speed, that is, maximal heart rate, stroke volume, and oxygen extraction are reached (Fig. 7) (Gleeson *et al.*, 1980). Several interindividual studies of reptilian populations have shown significant relationships between cardiovascular factors (e.g., ventricular mass, blood hemoglobin concentration) and maximal oxygen consumption (Schall *et al.*, 1982; Garland, 1984; Garland and Else, 1987; Garland and Bennett, 1990). The latter study also found a significant genetic, as well as phenotypic, correlation between ventricular mass and maximal oxygen consumption in garter snakes. Potentially, therefore, cardiovascular function may be a limiting factor in oxygen transport and endurance capacity in reptiles. The physiological limitations on maximal oxygen consumption in this group are certain to remain a topic of interest and scrutiny, as more comprehensive investigations and techniques are directed to the problem.
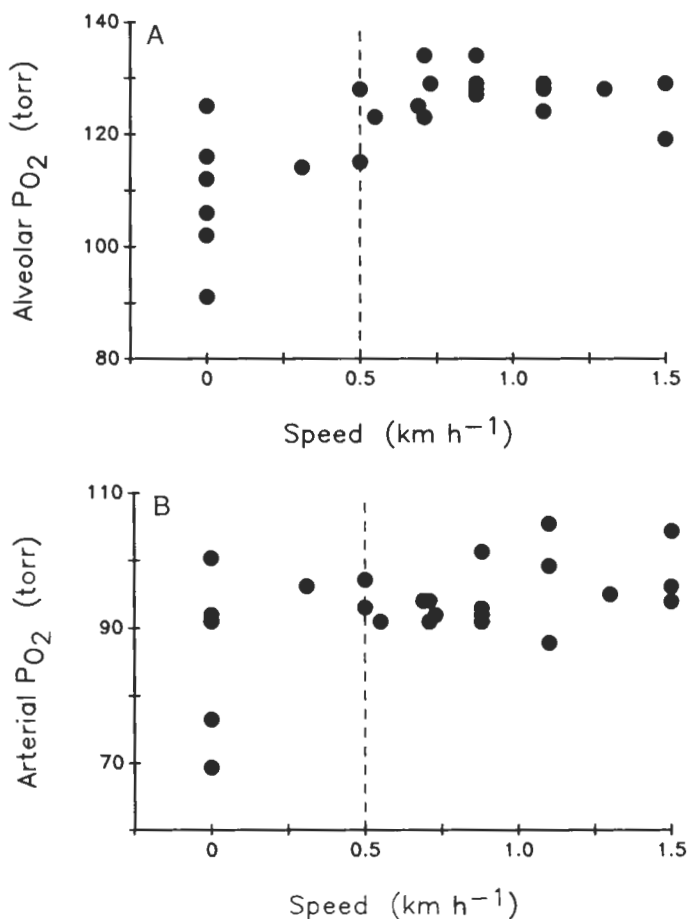
Fig. 6. Alveolar (a) and arterial (b) oxygen partial pressure in the lizard *Iguana iguana* walking at different speeds (body temperature = 35°C). Maximal aerobic speed (vertical dashed line) is 0.5 km h^{-1}. Alveolar and arterial oxygen partial pressures remain high even at 1.5 km h^{-1}, indicating that ventilation is adequate to oxygenate the blood. Ventilation therefore does not limit oxygen uptake. Recalculated from data of Mitchell *et al.* (1981a,b).

C. Ecological and Evolutionary Implications of Endurance

Do reptiles commonly utilize high levels of aerobically supported activity under natural conditions? Most reptiles probably do not engage daily in sustained levels of endurance activity (Hertz *et al.*, 1988). However, in some specific circumstances, such as egg laying in sea
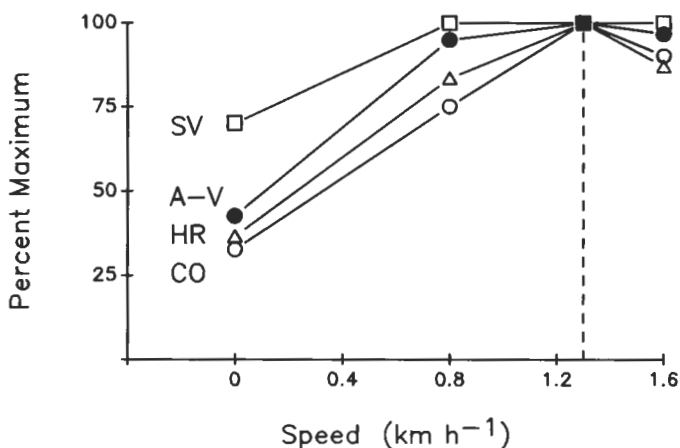
FIG. 7. Cardiovascular function in the lizard *Varanus exanthematicus* walking at different speeds (body temperature = 35°C). Maximal aerobic speed (vertical dashed line) is 1.3 km h^{-1}. Values are plotted as a percentage of maximal value measured at any speed: maximal heart rate (open triangles) = 115 beat min^{-1}, maximal stroke volume (open squares) = 3.0 ml beat^{-1}, maximal cardiac output (open circles) = 350 ml min^{-1}, and maximal oxygen extraction (A–V difference) (solid circles) = 0.61 ml O_2 ml blood^{-1}. Cardiovascular function is maximized at maximal aerobic speed. Data recalculated from Gleeson *et al.* (1980).

turtles (Jackson and Prange, 1979) or physiological thermoregulation during incubation in pythons (Hutchison *et al.*, 1966; Vinegar *et al.*, 1970), sustained levels of oxygen consumption are quite high, probably at or approaching maximal oxygen consumption. Interspecific comparisons generally show a positive association between aerobic capacity and level of foraging intensity, but their interpretation is complicated by phylogenetic diversity (Hertz *et al.*, 1988). For instance, varanid and teiid lizards generally have greater maximal oxygen consumption and endurance than do iguanid and agamid lizards (e.g., Bartholomew and Tucker, 1964; Gleeson, 1981; Anderson and Karasov, 1981; John-Alder *et al.*, 1983; Garland, 1993). These former groups tend to have more continuous patterns of foraging than do the latter. Such comparisons, however, are complicated by many factors. Comparative measurements among closely related species that differ in level of natural activity are more useful in eliminating extraneous factors from these comparisons. One such study compares the ecology, behavior, and physiology of two closely related (congeneric) lacertid lizards (Table I) (Nagy *et al.*, 1984; Huey *et al.*, 1984, Bennett *et al.*, 1984). *Eremias lugubris* is a continuous forager and *E. lineoocellata* is an ambush

TABLE I

FIELD METABOLIC RATES AND BEHAVIORAL AND PHYSIOLOGICAL CAPACITIES
OF TWO SMALL LACERTID LIZARDS[a]

	Eremias lugubris	*Eremias lineoocellata*
Foraging mode	Widely foraging	Sit-and-wait
Field metabolic rates		
Cost of foraging ($J\ h^{-1}$)	214	44
Daily energy use ($J\ day^{-1}$)	800	544
Behavioral capacities		
Sprint speed ($m\ s^{-1}$)	1.58	2.63
Maximal exertion (m)	70.8	29.9
Endurance (min at $0.5\ km\ h^{-1}$)	>30	7
Physiological capacities		
Maximal oxygen consumption (ml $O_2\ g^{-1}\ h^{-1}$)	3.22	2.49
Anaerobic scope (mg lactate $g^{-1}\ min^{-1}$)	2.12	2.56
Anaerobic capacity (mg lactate g^{-1})	1.40	1.81
Heart mass (mg)	7.7	5.2
Hematocrit (%)	30.1	24.4

[a] Body temperature = 35–37°C. All differences between species are significant. Data from Bennett *et al.* (1984), Huey *et al.* (1984), and Nagy *et al.* (1984).

predator, and both live together in the same desert habitat. The former has higher maximal oxygen consumption, endurance, and field metabolic rate than does the latter. Field metabolic rate measurements indicate that *E. lugubris* forages at or close to its maximal aerobic limits. Its greater maximal oxygen consumption is correlated with cardiovascular factors, but not with differences in skeletal muscle physiology. Greater aerobic capacities as detected in the laboratory for this species may, therefore, both reflect and permit its greater level of field foraging intensity. Measurements of daily field metabolic rate indicate that lizards utilize about 100–200% more energy that can be accounted for by their resting (or standard) metabolic rates alone (Bennett and Nagy, 1977; Nagy, 1982).

How important are these capacities for sustainable activity to reptiles in nature? Are high capacities for endurance useful in promoting survival or enhanced growth and reproduction? Research on these questions has only recently begun and is confined to few studies. It has concentrated on the correlation between endurance and survivorship among individual animals in natural populations (garter snakes, Jayne and Bennett, 1990b; sceloporine lizards, unpublished observa-

tions of R. B. Huey and others cited in Bennett and Huey, 1990). None of these studies has found a significant association between endurance and survivorship (although the correlation is marginally significant, $0.1 > P > 0.05$, for older snakes), indicating no detectable natural selection on endurance. None of the species examined are widely foraging or highly active reptiles, and the generality of these results is unknown. Hertz *et al.* (1988) consider several alternative explanations for the maintenance of physiological capacities that may not be used frequently under field conditions, such as endurance. Among those proposed are the relatively rare (and therefore generally unobserved) nature of an appropriate selective event or the possibility that the trait in question is correlated with performance that is only adequate in some other condition (e.g., at lower body temperatures). However, the survivorship studies cited should, within statistical limits, encompass these possibilities in natural populations (Bennett and Huey, 1990). Maybe circumstances requiring the trait are truly rare, that is, not encountered every generation but only once in every ten or hundred generations, and therefore not detected easily even in multiyear studies. At present, the significance and maintenance of endurance capacities in reptiles are not understood.

III. Burst and Exertion Activity

A. Anaerobic Glycolysis and Metabolic Support

Most reptiles are capable of very intense, short-lived bursts of activity. These bouts are not supported through oxygen consumption, but rather by anaerobic metabolic pathways. As in aerobic exercise physiology, comparative studies of metabolism during burst activity were first undertaken in fish, particularly by Black and his co-workers (1961). This research showed that intense activity is accompanied by the catabolism of muscle glycogen and the appearance of large quantities of lactic acid in the blood. Studies on reptiles (e.g., Austin *et al.*, 1927; Moberly, 1968a; Gatten, 1975) also found very large increments in blood lactate as a result of brief struggling activity. [It is now clear that use of anaerobic glycolysis in support of intense struggling is nearly universal among the vertebrates and is probably a primitive character of the chordate and perhaps deuterostome lineage (Ruben and Bennett, 1980; Bennett, 1991).] However, measurement of changes in blood lactate concentration in exercise physiology has interpretive limitations. Because of the compartmentalization of lactate within the

body and long lags associated with intercompartmental transfers (e.g., muscle to blood), blood lactate concentrations cannot be used to quantify the total amount of anaerobic metabolism or its contribution to activity energetics. The analytical development of whole-body lactate analysis (Bennett and Licht, 1972) permitted the quantification of the anaerobic energetic contribution to activity. It became possible to estimate directly the contribution of anaerobiosis to activity and to measure the maximal rate of lactic acid formation (anaerobic scope) and the amount formed during activity to exhaustion (anaerobic capacity). It also became possible to compare simultaneously aerobic and anaerobic metabolic support for any behavior or sequence of behaviors of brief duration. In the first experiments undertaken, the level or amount of burst activity was not quantified: reptiles were stimulated manually or electrically. Later, locomotor performance was measured directly as maximal speed attained on a racetrack ("burst speed," Bennett, 1980; Hertz *et al.*, 1982) or as distance covered during several minutes or to exhaustion ("maximal exertion" *sensu* Bennett, 1989) (Bennett, 1980).

Bursts of intense activity in reptiles are fueled primarily through anaerobic glycolysis, resulting in lactic acid formation. For example, during burst activity in a small lizard, about 60% of energy utilized is derived from lactate formation, about 6% from catabolism of adenosine triphosphate and creatine phosphate, and only 1% from other anaerobically formed compounds; the balance is aerobic (Table I). High levels of lactate formation during activity have been found in all groups of extant reptiles examined (squamates, turtles, and crocodilians) (reviewed in Bennett, 1978, 1982; Gatten, 1985), with blood lactate concentrations sometimes exceeding 50 mM (Bennett *et al.*, 1985). Simultaneous measurement of oxygen consumption and lactic acid formation (Table II and Fig. 8) indicates that the latter accounts for 60–90% of the ATP formed during 2-min bouts of intense activity, aerobic metabolism playing a relatively minor energetic role (Bennett and Dawson, 1972; Bennett and Gleeson, 1976). This balance results from the combination of high anaerobic and low aerobic capacities in reptiles. In mammals, in contrast, 75–92% of the ATP equivalents formed during 2 min of burst activity are derived aerobically (Ruben and Battalia, 1979). Anaerobic metabolic support in reptiles assumes an even greater fraction of total energy production as body temperature decreases (Fig. 8). The aerobic contribution is more strongly temperature dependent, with a temperature coefficient (Q_{10}) of approximately 2 (reviewed in Bennett, 1982), in comparison to temperature coefficients of 1.1–1.3 for lactic acid formation (Bennett and Licht,

TABLE II

ATP EQUIVALENTS GENERATED BY THE LIZARD
SCELOPORUS OCCIDENTALIS DURING 2 MIN
OF BURST ACTIVITY[a]

	Micromole ATP $(g \text{ body mass}^{-1})$	Percent (total)
Aerobic		
Oxygen consumption	12.7	33
Anaerobic		
Production of		
Lactic acid	22.5	59
Pyruvic acid	0.2	<1
Alanine	0.2	<1
Succinic acid	0	0
Catabolism of		
ATP	0.9	2
Creatine phosphate	1.6	4

[a] Body temperature = 35°C. Unpublished data from
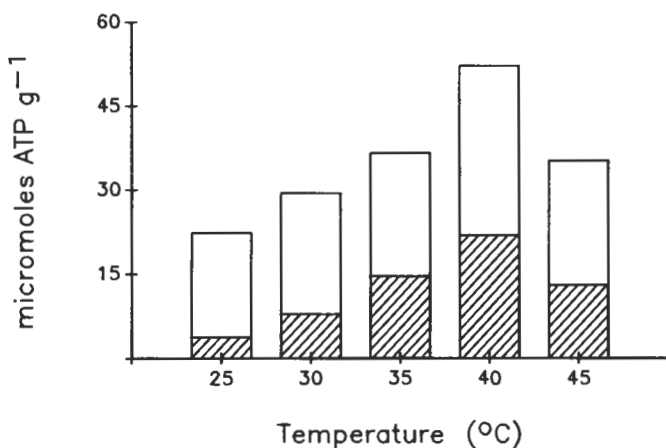A. F. Bennett and T. T. Gleeson.

FIG. 8. Thermal dependence of aerobic and anaerobic contributions to energy production during 2 min of burst activity by the lizard *Dipsosaurus dorsalis*. Aerobic metabolism (hatched bar) is measured by oxygen consumption; anaerobic contribution (open bar) by whole-body lactic acid accumulation. The aerobic contribution has a stronger thermal dependence ($Q_{10} = 3.23$ versus anaerobic $Q_{10} = 1.39$ from 25° to 40°C), resulting in a diminished percentage contribution at low body temperatures. Data from Bennett and Dawson (1972).

1972; Bennett, 1982). Anaerobiosis thus ensures a capacity for intense exercise and resulting escape or pursuit behavior over a relatively wide range of body temperatures, even during seasons of low activity (Gatten *et al.*, 1988). For this reason and for its very rapid mobilization and intensity, anaerobic glycolysis has been referred to as the Smith and Wesson, the great equalizer of the ectotherms and endotherms (Coulson, 1979).

The large amounts of lactic acid formed during activity in reptiles are highly physiologically disruptive (see Bennett, 1982, for a discussion). Blood and tissue can experience pronounced acidosis, with blood pH values declining as low as 6.79 in snakes (Ruben, 1979) and 6.42 in crocodiles (Bennett *et al.*, 1985). This acidosis may disrupt enzyme (Hochachka and Somero, 1984) and hemoglobin (Bennett, 1973) function and perturb blood calcium homeostasis (Ruben and Bennett, 1981). The relatively low ATP yield per carbohydrate molecule catabolized requires extensive depletion of muscle glycogen (Gleeson, 1991). These physiological disruptions are associated with pronounced and prolonged exhaustion after a bout of intense exertion. Physiological factors responsible for this exhaustion are not known. Physiological recovery by reptiles from intense activity (reviewed by Gleeson, 1991) takes a long time, as much as several hours, and rate of recovery is greatly retarded by low body temperatures.

B. ANAEROBIC METABOLISM UNDER NATURAL CONDITIONS

In view of its potential for physiological disruption and exhaustion, we might well consider the extent to which anaerobic metabolism is normally used during natural activities by reptiles (e.g., Hertz *et al.*, 1988). A number of studies have examined the extent of lactic acid formation during staged behaviors in the laboratory or under natural conditions in the field. In several species of lizards sampled in the field without regard to their prior behavior, lactate concentrations are moderately elevated in comparison to resting or preemergence values (Bennett *et al.*, 1981; Pough and Andrews, 1985a), indicating general increase associated with routine activity. Some species show no such elevation (Pough and Andrews, 1985a). Lactic acid is formed during conspecific agonistic encounters by lizards (Bennett *et al.*, 1981; Pough and Andrews, 1985a; Wilson and Gatten, 1989; Wilson *et al.*, 1990), and accumulation is correlated with the intensity of the aggression (e.g., Fig. 9). Moderate amounts of glycolysis are observed in snakes feeding on salamanders (Feder and Arnold, 1982); significant but relatively lower levels have been measured in lizards eating insects (Pough
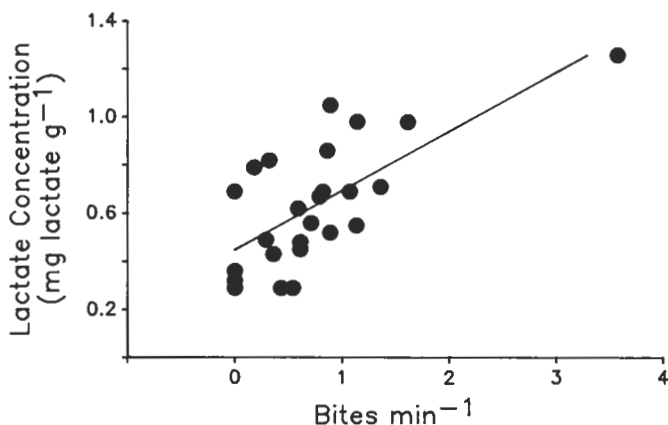
Fig. 9. Lactate contents of resident lizards (*Sceloporus jarrovi*) resulting from territorial defense against an experimentally placed intruder. Intensity of defense activity was measured as the rate of bites inflicted on the intruder. Intensity is directly correlated with lactate formation. Lizards at morning emergence and during routine daily activity have average lactate concentrations of 0.26 and 0.31 mg lactate g^{-1}, respectively. Data redrawn from Pough and Andrews (1985a).

and Andrews, 1985a,b). Lactate accumulation occurs during egg laying by sea turtles in the field (Jackson and Prange, 1979) and in hatchling sea turtles during digging out of the nest, crawling across the beach, and swimming through the surf (Dial, 1987; Baldwin *et al.*, 1989). Turtles hibernating underwater utilize anaerobic metabolism (Gatten, 1981, 1985; Ultsch and Jackson, 1982), accumulating phenomenal concentrations of lactate (up to 5.5 mg g^{-1}; Gatten, 1981). Lactate accumulation also occurs in reptiles during forced diving in the laboratory, but is usually avoided during free diving behavior in the field (reviewed by Seymour, 1982; Gatten, 1985), a situation similar to that observed in diving mammals and birds. Hertz *et al.* (1988) concluded that reptiles frequently utilize anaerobic metabolism during natural activities, but rarely do so to the point of exhaustion. Anaerobic metabolism appears to be particularly useful in and used for fueling intense activities of short duration but great ecological importance (e.g., territorial defense, nest emergence).

C. Ecological and Evolutionary Consequences

What are the ecological and evolutionary consequences of burst speed and maximal exertion capacities for reptiles? Both factors have been demonstrated to be heritable (van Berkum and Tsuji, 1987; Gar-

land, 1988; Tsuji *et al.*, 1989; Jayne and Bennett, 1990a,b), indicating a genetic basis and potential to respond to natural selection (Bennett and Huey, 1990). In staged laboratory encounters, individual male lizards with greater burst speeds (but not endurance) were dominant in social interactions (Garland *et al.*, 1990). Reptiles fleeing predators in nature appear to do so at the maximal speeds they can attain (Greene, 1988; Hertz *et al.*, 1988). For example, marine iguanas observed while naturally escaping from hawks ran as fast as when they were pursued experimentally (Gleeson, 1979, 1980). Burst speed capacity (and body-size-adjusted burst speed capacity) has been significantly and positively associated with survivorship among individuals in natural populations of garter snakes (Jayne and Bennett, 1990b) and tree lizards (Miles, 1989), indicating that it is under directional selection in these populations. Other studies (R. B. Huey and co-workers, as cited in Bennett and Huey, 1990) on fence lizards and canyon lizards have found no significant association between survivorship and speed. Thus, the ecological and microevolutionary significance of these factors apparently may vary among populations, at least among species, and perhaps with time and environment within a single population.

IV. Summary

From the vantage point of thirty years of study, we can sketch the general features of activity capacity and performance ability in reptiles. Extant reptilian groups all share low levels of maintenance metabolism and ectothermy, with their consequent advantages (Pough, 1980) and disadvantages. Among the latter is a limited capacity to expand aerobic metabolism, limited in comparison to the relatively great costs of terrestrial locomotion. Particularly at low body temperatures, reptiles outstrip their aerobic capacities with any exercise more intense than a slow walk. Anaerobic metabolism, particularly anaerobic glycolysis, can be used to fuel bursts of intense activity. As a consequence, however, physiological disruption and exhaustion are entailed. Under field conditions, many reptiles alternate long periods of quiescence or slow movement with very brief bursts of exertion. Other ectotherms with a similar pattern of metabolism have been shown thereby to extend performance beyond that supportable by either aerobic or anaerobic metabolism alone (Weinstein and Full, 1992). Even with careful alternation between these metabolic modes, reptiles remain particularly prone to exhaustion during vigorous activity, as least as judged by our mammalian frame of reference. Their capacities

for burst activity and exertion have been shown, at least in some species, to be important determinants of their natural survival.

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