

Time Budgets, Thermoregulation, and Maximal Locomotor Performance: Are Reptiles Olympians or Boy Scouts?¹

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SYNOPSIS. Do ectothermal vertebrates routinely make full use of their locomotor capacities in nature? We address this question by asking whether reptiles ever sprint at maximum burst speeds and whether they often move at speeds near maximum aerobically sustainable levels. Relevant data are largely anecdotal but suggest that lizards (and perhaps other vertebrate ectotherms) do not routinely perform at maximal capacities. They appear to do so only in situations that have a critical impact on fitness. Nevertheless, active lizards do thermoregulate carefully such that they usually maintain the *potential* for performing at maximal capacity. We consider alternative, but not exclusive, explanations for why reptiles might maintain apparently "excessive" capacities and conclude with suggestions for new field and laboratory studies that would more rigorously address these issues.

INTRODUCTION

The extent to which energetics and physiological capacities constrain the behavior and ecology of animals is a fundamental but unresolved question in physiological ecology. One initial step towards the resolution of this issue involves determining whether or not animals routinely make full use of their physiological capacities in nature. Such determinations would enable us not only to ascertain the day-to-day significance of physiological constraints on ecology and behavior, but also to evaluate whether the evolution of maximal capacities is driven by routine activities or by rare, but significant, events (Wiens, 1977; Gans, 1979; Kingsolver and Watt, 1983).

Despite their importance, these questions have been directly addressed in very few studies (Wells and Taigen, 1984; Garland, 1988). Nevertheless, the implicit assumptions that animals are active as often as possible and that they regularly use their full locomotor capacities are widespread in many ecological studies and models (see

Herbers, 1981). Although these assumptions may reflect biological reality, they might simply represent the cultural baggage of western socioeconomic traditions (Rappaport and Turner, 1977) and our fascination with maximal performance in athletics and other endeavors.

We question whether the above assumptions necessarily apply to ectothermal vertebrates such as reptiles and amphibians (Maiorana, 1977). In contrast to the endothermal vertebrates (birds and mammals), ectotherms have relatively low metabolic requirements and limited capacity for sustained (but not burst) activity (Bennett, 1978, 1980*b*; Regal, 1978, 1983; Bennett and Ruben, 1979; Pough, 1980). For example, lizards in nature have annual energy budgets that are only about one-fortieth those of birds and mammals of equivalent size (Nagy, 1982, 1983), and reptiles can often survive long periods without any energy input (Benedict, 1932; McNab, 1963; Pough, 1980).

In this paper we consider two basic issues relating to the behavior and energetics of ectotherms (especially of lizards and other reptiles) under natural conditions. First, do ectotherms maintain field active body temperatures that are *conducive* to performance at maximal capacities? Second, how

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frequently do ectotherms actually perform at maximal levels?

We focus on the intensity of activity and on locomotor performance because these characteristics may well influence an organism's fitness (*sensu* Arnold, 1983). Our analysis of available data leads to the tentative conclusion that lizards rarely perform at maximal levels. Instead, they seem to do so only in situations that are critical to fitness. However, most species do thermoregulate carefully while emergent and are therefore active at body temperatures that are conducive to maximal locomotor performance. Lizards (and perhaps other reptiles) therefore appear to be less like Olympic athletes than Boy Scouts: they may not be chronic overachievers, but at least they are almost always prepared.

ARE FIELD ACTIVE BODY TEMPERATURES CONDUCTIVE TO MAXIMAL LOCOMOTOR PERFORMANCE?

An ectotherm's physiology and thermoregulatory behavior interact with the physical environment to set limits on potential locomotor capacity (Huey, 1982, 1983; Kingsolver and Watt, 1983; Waldschmidt and Tracy, 1983). At certain body temperatures animals may be able to sprint and accelerate at maximum rates or to sustain activity for extended periods. Such maximal capacities potentially enhance the rate, duration, and intensity of prey capture activities, the ability to escape from predators, and possibly the ability to dominate social interactions (Greenwald, 1974; Webb, 1976; Huey and Stevenson, 1979; Christian and Tracy, 1981; Huey and Hertz, 1984*b*). Available data (summarized below) on field activity temperatures and on the thermal dependence of locomotor performance support the hypothesis that most active lizards maintain temperatures that are conducive to maximal locomotor performance.

Although sprint speeds of lizards show a strong temperature dependence, the temperature performance profile for many species has a broad plateau over which nearly maximal speeds can be attained (Bennett, 1980*a*; Hertz *et al.*, 1983). Data on the temperature dependence of locomotor stamina are more limited than those

on sprint speed. Maximal distance running capacity appears to be relatively insensitive to temperature over a broad range of temperatures in lizards (Bennett, 1980*a*) and perhaps anurans (Putnam and Bennett, 1980). Treadmill endurance may be more strongly temperature dependent in lizards (Moberly, 1968*b*; John-Alder and Bennett, 1981; van Berkum *et al.*, 1986; see also Brett *et al.*, 1958).

But are the *field active* body temperatures of ectotherms really conducive to maximal locomotor performance? With regard to sprint speed, the answer is yes. In the vast majority of 50 species surveyed, the mean field active body temperature (as well as the central 50% of individual temperature records) allows a sprint capability that is within 10% of the maximum sprint speed recorded in the laboratory (R. B. Huey, F. van Berkum, P. E. Hertz, and A. F. Bennett, in preparation). Similarly, four thermophilic lizard species (Bennett, 1980*a*), as well as two anuran species (Putnam and Bennett, 1980), show maximal distance running capacity within the range of body temperatures that they usually experience in nature.

A few exceptions to this generality are notable. For example, high altitude and high latitude populations frequently are active at body temperatures low enough to impair sprint performance, especially during the early morning warmup (Hertz *et al.*, 1983; Huey, 1983; Crowley, 1985; Stevenson *et al.*, 1985; van Berkum, 1986). In addition, some nocturnal, crepuscular, forest, and cryptic lizards are routinely active at temperatures suboptimal for sprinting (van Berkum, 1986; Huey and Bennett, 1987; R. B. Huey, F. van Berkum, P. E. Hertz, and A. F. Bennett, in preparation). Similarly, two lizard species that are typically active at low body temperatures would apparently function with less than maximal stamina under natural conditions (Bennett, 1980*a*).

DO MOST LIZARDS ROUTINELY USE MAXIMAL LOCOMOTOR CAPACITIES?

A direct answer to the question of whether reptiles frequently use their maximal locomotor capacities is presently impossible, simply because continuous,

long-term data on movement speeds of active lizards are unavailable. (Garland [1988, Table 1] summarizes the available data on *average* movement rates in lizards.) Ideally we would like to know the number, duration, and intensity (speed) of movements under natural conditions as well as the maximal sprint speed and stamina for the same individuals. In the absence of such data, we rely on two inexact estimators. First, mostly anecdotal accounts provide some indication of whether reptiles routinely move quickly or often. Second, data on lactic acid concentration can suggest recent burst activity, for such activity is fueled largely by anaerobic metabolism (Bennett, 1978).

Sprinting

Accounts of how frequently lizards sprint are rarely quantitative, but our interpretation of these accounts and our own field observations suggest that sprinting at near maximal speeds is infrequent. Maximal accelerations and sprints are used rarely during feeding (*e.g.*, van Berkum *et al.*, 1986) and in social encounters (Huey, 1974; Bickler and Anderson, 1986), but more frequently in predator avoidance (Belkin, 1961; Moberly, 1968a; Schall and Pianka, 1980; Christian and Tracy, 1981; Vitt and Price, 1982; van Berkum *et al.*, 1986; reviewed in Greene, 1988). Running speeds of *Amblyrhynchus cristatus* fleeing the attack of Galapagos hawks (Gleeson, 1980) approached the experimentally determined maximum average burst speed (2.5 m/sec) measured by chasing animals in the field (Gleeson, 1979). Whether sprints by other ectotherm species are undertaken at maximal speed remains an open question. Some tadpoles are thought to use maximal burst speed in predator avoidance maneuvers (Feder, 1983; Gatten *et al.*, 1984). However, some predatory fish swim at substantially less than maximal speeds when pursuing prey (Webb, 1986), and migrating salmon use maximum burst speeds for only short periods of time (Brett *et al.*, 1958).

Anaerobiosis

Anaerobic metabolism is used to support burst activity and to augment aerobic

metabolism during locomotion above the maximal aerobic speed (*i.e.*, the speed at which VO_{2max} is attained [John-Alder and Bennett, 1981]) or above the "anaerobic threshold" (see Taigen and Beuchat, 1984). But the use of anaerobic metabolism can quickly lead to exhaustion and to a period of enforced inactivity necessary to repay the oxygen debt (Bennett, 1978). Interestingly, both anaerobic scope (*i.e.*, the maximal rate of lactate production) and anaerobic capacity (*i.e.*, the maximal amount of lactate produced) show very low thermal dependence (Bennett, 1982); as a result, most ectotherms have the potential to use maximal anaerobic response at the lower end of the range of body temperatures experienced while active in nature.

Anaerobic metabolism is readily indexed by the concentration of lactate (Bennett and Licht, 1972), the endpoint of anaerobic glycolysis; but the interpretation of such data is difficult in the absence of information about the type, duration, and level of prior activity as well as resting and maximal lactate levels (Gatten, 1985). High levels of lactate indicate recent burst activity, but the implications of low to intermediate lactate levels is unclear.

In 10 laboratory studies researchers have measured lactate levels in vertebrate ectotherms induced to perform natural behaviors that required at least some locomotor movement. In many cases the animals experienced no lactate accumulation above resting levels, indicating that activity levels were probably below maximal aerobic capacity: burrowing by *Scaphiopus hammondi* (Seymour, 1973), diving in *Chelydra serpentina* (Gatten, 1980) and *Sternotherus minor* (Gatten, 1984), vigorous swimming in tadpoles of *Rana berlandieri* (Feder, 1983), *Hyla gratiosa*, *R. catesbiana*, and *R. utricularia* (Gatten *et al.*, 1984). In other cases, animals experienced significant elevation of lactate above resting levels, but the levels were well below maximum (hence, the animals were not near exhaustion): feeding by *Chalcides ocellatus* (Pough and Andrews, 1985a) and *Thamnophis elegans* (Feder and Arnold, 1982), threat-induced diving by *Chrysemys picta* (Gatten, 1981), courtship by *Desmognathus ochrophaeus* (Bennett and Houck, 1983). In only

three instances among these 10 studies did lactate levels possibly approach exhaustion levels: anti-predator behavior by *Plethodon jordani* (Feder and Arnold, 1982) and active swimming during threat-induced dives by *Iguana iguana* (Moberly, 1968b) and by *Sternotherus minor* (Gatten, 1984).

Several studies of field-active ectotherms suggest that anaerobic metabolism is often used in nature but that the animals are rarely near exhaustion. Normal underwater feeding activity and return to shore by *Amblyrhynchus cristatus* produced no significant increase in lactate concentration (Gleeson, 1979; but see Bartholomew *et al.*, 1976, p. 719). Only slight to moderate increases over resting lactate levels were produced by territorial behavior in *Anolis bonairensis* (Bennett *et al.*, 1981) and *Sceloporus jarrovi* (Pough and Andrews, 1985b), nesting by *Chelonia mydas* (Jackson and Prange, 1979), normal feeding activities on land by *Sceloporus virgatus* (Pough and Andrews, 1985b), routine activity by *Cnemidophorus exsanguis*, *C. sonorae*, *Sceloporus virgatus*, and *S. jarrovi* (Pough and Andrews, 1985b), swimming by *Hydrophis cyanocinctus* and *H. belcheri* (Seymour, 1979) and diving by *Laticauda laticauda* and *L. colubrina* (Seymour, 1979). Although emergence from the nest and the subsequent hatchling frenzy lead to a substantial increase in lactate concentration in *Caretta caretta*, it is unclear whether anaerobic scope or capacity is reached (Dial, 1987). Indeed, the only field-active animals in which lactate levels clearly approached the anaerobic capacity of the species were two *L. laticauda* captured after making natural dives (Seymour, 1979); because a majority of snakes in the sample did not have elevated lactate levels (see above), Seymour concluded that only a small fraction of the dives by this snake require significant anaerobic energy input.

These data suggest that exhausting burst activity by vertebrate ectotherms is relatively rare under natural conditions. We do not doubt that reptiles sometimes do utilize their full anaerobic capacities, most likely when they are attempting to escape from predators. (It would be extremely interesting to examine lactate levels in reptiles that had just been captured by pred-

ators [*cf.* Feder and Arnold, 1982; Bennett *et al.*, 1985].) For those critical circumstances, anaerobiosis provides an undeniably vital energetic boost (Bennett, 1983). Our point is not to deny the ecological significance of anaerobiosis, but instead to argue that available measurements of lactate support the field anecdotes (above) that near-maximal burst activities may generally represent rare events in the lives of most reptiles.

Time budgets

Partial time budgets have been constructed for 18 lizard species, and these data provide information about the levels of activity in which individuals engage (Table 1). Because of enormous differences in the ways researchers have defined activities and constructed time budgets, the least common denominator for evaluating activity is the percentage of emergent time lizards devote to vigorous activities (prey capture and handling, patrolling territories, social interactions, courtship) as opposed to being nearly immobile (resting or monitoring from a display perch). Lizards vary widely in the percentage of the time that they spend moving. Herbivores and most sit-and-wait predators spend relatively little time in vigorous activity, whereas active foragers spend more than half of their emergent time in movement (Huey and Pianka, 1981).

Time budget data must be interpreted cautiously, however, and in relation to data on daily and annual periods of activity. For example, *Cnemidophorus tigris* has been observed to spend more than 90% of its emergent time moving. However, this species is "active" approximately 5 hr per day for about 6 mo of the year (Pianka, 1970; Anderson and Karasov, 1981). An individual therefore spends a maximum of 10% of a year's time emergent, of which 90% is spent in vigorous activity. If, for the sake of comparison, we assume that a female *Anolis polylepis* is "active" for 10 hr per day for 12 mo of the year, she is emergent for about 40% of a year's time, of which about 10% is spent in vigorous activity. Overall, the *Cnemidophorus* spends only twice as much time (and, perhaps, energy)

TABLE 1. The proportion of emergent time that lizards spend in vigorous activities (i.e., those requiring locomotor movements).

Species	Proportion of time	Reference
Herbivores:		
<i>Egernia cunninghami</i>	0.08	Wilson and Lee, 1974
<i>Iguana iguana</i>	0.10	Moberly, 1968a
Ambushing predators:		
<i>Anolis bonairensis</i>	0.32	Bennett and Gorman, 1979
<i>Anolis cupreus</i> —males	0.60	Fleming and Hooker, 1975
—females	0.22	Fleming and Hooker, 1975
<i>Anolis polylepis</i> —males	0.55	Andrews, 1971
—females	0.12	Andrews, 1971
<i>Callisaurus draconoides</i>	0.02	Anderson and Karasov, 1981
<i>Eremias lineoocellata</i>	0.14	Huey and Pianka, 1981
<i>Meroles suborbitalis</i>	0.14	Huey and Pianka, 1981
<i>Sceloporus occidentalis</i>		
Infected with <i>Plasmodium</i>	0.05	Schall and Sarni, 1987
Uninfected	0.07	Schall and Sarni, 1987
<i>Uta stansburiana</i>	0.30	Alexander and Whitford, 1968
Widely foraging predators:		
<i>Ameiva quadrilineata</i>	0.75	Hillman, 1969
<i>Cnemidophorus murinus</i>	0.77	Bennett and Gorman, 1979
<i>Cnemidophorus tigris</i>	0.91	Anderson and Karasov, 1981
<i>Eremias lugubris</i>	0.57	Huey and Pianka, 1981
<i>Eremias namaquensis</i>	0.54	Huey and Pianka, 1981
<i>Ichnotropis squamulosa</i>	0.55	Huey and Pianka, 1981
<i>Nucras tessellata</i>	0.50	Huey and Pianka, 1981

in vigorous activity as does the anole, despite the ninefold difference that is "apparent" in Table 1.

Locomotor stamina

Stamina per se can be measured in different, but still ecologically relevant, ways, and laboratory data on capacities can be compared with movement rates in the field. "Treadmill endurance," the length of time that an animal can run at a fixed, low speed, has been used in numerous studies, including attempts to evaluate physiological constraints on sustained foraging movements or social interactions (e.g., John-Alder and Bennett, 1981; Garland, 1984, 1988; Huey *et al.*, 1984; van Berkum *et al.*, 1986). "Distance running capacity," the total distance run (in a fixed time or until exhaustion) at high speed has also been used, but primarily to assess capacities for stamina during escape from predators (Bennett, 1980a; Putnam and Bennett, 1980; Garland, 1984, 1988; Huey *et al.*, 1984).

Several integrated field and laboratory

studies suggest that many species—even the most active ones—routinely move at rates below their maximal aerobic speeds (*Cnemidophorus murinus*, Bennett and Gleeson, 1979 and Bennett and Gorman, 1979; *C. tigris*, Garland, 1988; *Ameiva festiva*, van Berkum *et al.*, 1986; *Trachydosaurus rugosus*, John-Alder *et al.*, 1986). *Cnemidophorus tigris* is striking in this regard (Garland, 1988). This species is the archetypal widely-foraging lizard (Pianka, 1970), and individuals may spend up to 91% of their emergent time moving (Table 1). However, their normal movement speeds are often substantially below their known capacities. Similar results were observed for foraging movements of another teiid (*Ameiva festiva*, van Berkum *et al.*, 1986) and for movements of a toad (*Bufo americanus*) during breeding choruses (Wells and Taigen, 1984). In laboratory studies, some amphibians also move at rates well below their sustainable limits during predator escape (tadpoles of *Rana berlandieri*, Feder, 1983), mating (*Desmognathus ochrophaeus*, Bennett

and Houck, 1983), and burrowing (*Scaphiopus hammondi*, Seymour, 1973).

On the other hand, some lacertid lizards (*Eremias* spp., Huey and Pianka, 1981 and Huey *et al.*, 1984; *Lacerta vivipara* and *Podarcis muralis*, Avery *et al.*, 1987), three iguanids (*Amblyrhynchus cristatus*, Gleeson, 1979; *Conolophus subcristatus* and *Dipsosaurus dorsalis*, Garland, 1988), and an agamid (*Ctenophorus nuchalis*, Garland, 1988) often move at speeds that approach or exceed maximal sustainable or maximal aerobic speeds. However, activity at these relatively high levels generally does not last for more than a few second or minutes and is punctuated by pauses. Whether such pauses allow for the metabolism of accumulated lactate is unknown (Pough, 1980; see Jackson and Prange, 1979 on "phasic exercise"). In any case, rapid movements occur most frequently when lizards cross open spaces between bushes (see van Berkum *et al.*, 1986; Garland, 1988).

An alternative approach, involving interspecific comparisons, is to ask whether quantitative measures of locomotor performance in the lab are correlated with natural activity in the field (see Bennett *et al.*, 1984). Available data from a taxonomically limited array of lizard species show an ambiguous relationship between average daily movement distance in the field and treadmill endurance at 1.0 km/hr (Table 2). Although the two measures are significantly correlated among nine species from four lizard families ($r = 0.690$, $P < 0.05$), they are not significantly correlated among the five species of Iguanidae ($r = 0.412$, $P > 0.05$), the only family from which data are available for more than two species. (Daily movement distance and treadmill endurance are not significantly *rank* correlated for all nine species [$r_s = 0.308$, $P > 0.05$] nor for the five iguanids [$r_s = 0.500$, $P > 0.05$].) Hence, it is unclear whether the data in Table 2 reflect a general correlation among lizard species (and across lizard families) or, alternatively, merely illustrate the distinctive locomotor performance and behavior of teiids. Additional data from a variety of lizard families should help to distinguish between these explanations.

Several reports suggest that ectotherms do operate at the limits of their aerobic capacity under exceptional circumstances. Crawling to nest sites, nest excavation, and emergence of hatchlings may require the maximum sustainable levels of activity of sea turtles (Jackson and Prange, 1979; Dial, 1987). Similarly, migrating salmon are almost certainly swimming at the limits of their physiological capacity (Brett, 1972). These species would presumably expend much less energy during any of their routine activities at other stages of their life cycles.

Recent studies on lizards infected with malaria demonstrate that reduced stamina may have subtle but important consequences. Infected lizards (*Sceloporus occidentalis*) have significantly reduced aerobic scopes, probably because the parasites disrupt oxygen transport (Schall *et al.*, 1982). Even so, infected and uninfected lizards had generally similar time budgets and activity patterns (our Table 1; Schall and Sarni, 1987). However, infected lizards engaged in significantly *fewer* social interactions than did non-infected lizards (Schall and Sarni, 1987). Thus, physiological capacities may well limit social interactions and potential fitness in some (see also Garland, 1988), but not all (Bennett and Houck, 1983), species. This is an important finding, and its generality must be tested.

CONCLUSIONS

Our analysis of the literature suggests that taxonomically diverse reptiles do not routinely use their maximal capacities for locomotion. In this section we first address two related questions. 1) Why aren't reptiles more active than they are in nature? 2) Why do they support apparently "excessive performance" capacities? Because our analysis and conclusion are based on circumstantial data, we also describe the types of field and laboratory data that are needed to evaluate these issues fully.

Why aren't reptiles more active?

The potential advantages of increasing locomotor performance are evident (see Introduction), but we have demonstrated that lizards are rarely active to the extent

TABLE 2. Average daily movement distance (m) and average treadmill endurance (min, running at 1.0 km/hr) for nine lizard species differing in body mass (g).

Family: Species	Mass	Distance moved	References*	Endurance time	References*
Iguanidae:					
<i>Callisaurus draconoides</i>	15	250	1, 5	7.1	5
<i>Ctenosaura similis</i> (juveniles)	23	53	5, 6	5.9	4
<i>Dipsosaurus dorsalis</i>	60	169	5, 6	15.0	9
<i>Gambelia wislizenii</i>	32	314	5, 11	32.2	5, 6
<i>Uta stansburiana</i>	3	200	5, 8	2.2	6
Lacertidae:					
<i>Eremias lineocellata</i>	4	171	7	4.6	6
Scincidae:					
<i>Egernia cunninghami</i>	268	84	5, 12	7.0	10
Teiidae:					
<i>Cnemidophorus murinus</i>	55	768	3, 5	3.0	2
<i>Cnemidophorus tigris</i>	23	900	1, 5	> 120.0	5

* Key to references: 1, Anderson and Karasov, 1981; 2, Bennett and Gleeson, 1979; 3, Bennett and Gorman, 1979; 4, Garland, 1984; 5, Garland, 1988 (includes calculations or original data); 6, T. Garland, unpublished; 7, R. B. Huey, unpublished; 8, Irwin, 1965; 9, John-Alder, 1984; 10, John-Alder *et al.*, 1986; 11, Tollestrup, 1979; 12, Wilson and Lee, 1974.

that they could be. (This finding may not apply to flying insects with short adult life-spans [J. Kingsolver, personal communication].) An obvious explanation involves the risk of predation (Maiorana, 1977; Herbers, 1981). Although frequent activity might often increase net energy gains (Schoener, 1974; Norberg, 1977), it might also advertise an animal's availability to its predators (Gerritsen and Strickler, 1977; Huey and Pianka, 1981; Vitt and Price, 1982). An alternative possibility is that speed, acceleration, and stamina are simply less important than agility, reaction time, or behavioral "choices" (Howland, 1974; Feder, 1983; Webb, 1986). In any case, we encourage additional theoretical and empirical studies of this topic.

Why do reptiles maintain capacities for high performance?

Our general conclusion is that although careful thermoregulation is conducive to maximal locomotor performance, lizards rarely take advantage of these enhanced capacities. Why do lizards thermoregulate carefully, and why do they maintain "excessive" capacities? Thermoregulation can be time-consuming and energetically expensive (Huey and Slatkin, 1976), and the development and support of structures

that maintain maximal performance are generally assumed to be costly as well (but see Garland, 1984, 1988; Garland and Else, 1987).

The "principle of excessive construction" may offer a general answer to this question. Gans (1979) notes that the phenotypic capacities of animals often exceed their routine needs and thus appear to be "excessively constructed." However, he proposes that maximal capacities are shaped, not by routine events, but by rare events that may be critical to an animal's survival. Predator escape and nest excavation are examples of relatively brief experiences that have a major impact on fitness. Our analysis suggests that animals may perform at maximum levels during just such critical activities.

By extension, careful thermoregulation and maintenance of high capacities may reflect the overriding selective importance of such rare events (van Berkum *et al.*, 1986). Of course, enhanced locomotor capacity is not the only reason for thermoregulation (review in Huey, 1982), but it may be a major determinant of field active body temperatures (van Berkum *et al.*, 1986). From this perspective, thermoregulation and high performance capacities are evidence that lizards are always pre-

pared for action, however rarely they may actually engage in vigorous activity. Hence, they are more like Boy Scouts than Olympic athletes.

Assessing the reality of this view will be especially difficult, simply because we need to monitor and evaluate *rare* events. Although we advocate following individuals for extended periods of time, this may not be an efficient or productive approach. For example, after following a lizard for a year, one might observe only a few instances of maximal performance. (On the other hand, such a finding would be concrete evidence for the conclusion that burst activities are rare.) Alternatively, following endothermal predators of lizards might be more productive (H. Snell, personal communication).

A comparative approach might provide a more viable, even if indirect, solution. One could establish *a priori* hypotheses about the effects of food availability or predator abundance on expected performance levels, and then test these hypotheses with detailed analyses from several populations or related species. This approach rephrases the question being addressed from "Do they perform at maximal levels, and if so, how commonly?" to "Under what ecological circumstances have higher performance capacities evolved?" In other words, studying the pattern or products of evolution might be more efficient than studying the process.

Another, non-exclusive reason that lizards maintain maximal locomotor performance is plausible. Consider the hypothetical possibility that maximal performance at normal activity temperatures is never used. Could this truly excessive capacity be maintained by selection even in this case? Yes, and the reason relates to the fact that ectotherms are sometimes active at temperatures *sub-optimal* for locomotion (Bennett, 1980a; Christian and Tracy, 1981; Hertz *et al.*, 1983; Crowley, 1985; van Berkum, 1986). If lizards are particularly vulnerable to predation at these times (Christian and Tracy, 1981; Hertz *et al.*, 1982; Crowley and Pietruszka, 1983), then selection could favor increased capacity at low body temperature. And if per-

formance at low temperature is genetically correlated with performance at high body temperature (Leamy and Cheverud, 1984), this would lead to the observed "excessive" performance at high body temperature. We cannot critically evaluate this second hypothesis because relevant field and genetic data are simply unavailable. However, relative locomotor performance of individual lizards is correlated across temperatures (Bennett, 1980a; Huey and Hertz, 1984a).

Types of studies needed

We have analyzed data from a series of studies, each of which addresses a small part of the overall picture. As a result, our conclusions are tentative. Here we suggest a unified approach that would provide conclusive answers to questions about how fully animals use their potential locomotor capacities.

Physiology and morphology set limits on locomotor capacities (*e.g.*, Bennett *et al.*, 1984; Garland, 1984, 1988). Consequently, to determine whether animals make full use of these capacities, we must first make laboratory measurements of maximal burst speed, acceleration, distance running, and cruising stamina (Bennett, 1980a). The particular measure used (*e.g.*, acceleration *versus* maximal speed, distance running capacity *versus* treadmill endurance, agility *versus* speed or stamina) must be ecologically relevant to the species under investigation (Huey and Stevenson, 1979). Even so, interspecific comparisons may be difficult if different measures of locomotor performance are appropriate for different species. Field data on actual movement patterns (frequency of movement, acceleration, speed, distance moved) are often difficult (and tedious) to obtain over extended periods, but casual field observations during limited time periods are sometimes misleading (Regal, 1983; R. D. Pietruszka, personal communication). Ideally, we would have continuous, detailed, long-term records of movements by individuals, obtained with an accelerometer/radiotelemeter (Dunkle, 1983). Such remote data will not eliminate the need for concomitant field observations

(Greene, 1986), for the behaviors that require maximal performance may be surprising (e.g., digging a burrow, courtship, Garland, 1988; male-male combat, Bickler and Anderson, 1986).

The study that may come closest to providing an exemplary analysis is that by Kooyman (1982) on the diving behavior of Weddell seals. These seals have the physiological capacity to dive for more than 1 hr, but they usually dive for less than 25 min, the limit of their aerobic capacities. By minimizing the time used to recover from anaerobic metabolism, this strategy may maximize underwater hunting time. Long dives are quite rare and occur primarily during emergencies.

Finally, we need explicit studies on the energetic costs (or lack thereof, Garland, 1984, 1988; Garland and Else, 1987) of developing and maintaining the anatomical and physiological machinery that allow high performance. Ideally, these data, when coupled with information on the frequency of stressful events, could be incorporated into models that predict fitness given varying rates of stressful events for animals with differing levels of maximal performance (cf. Alexander, 1981). Kingsolver and Watt (1983) have developed a formal statistical analysis of the fitness consequences of variation in the frequency of stressful events (specifically, the risk of overheating in *Colibris* butterflies), and their approach might well serve as a general model for the types of analyses we suggest here.

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REFERENCES

Alexander, C. E. and W. G. Whitford. 1968. Energy requirements of *Uta stansburiana*. *Copeia* 1968: 678-683.

- Alexander, R. McN. 1981. Factors of safety in the structure of animals. *Sci. Prog. Oxf.* 67:109-130.
- Anderson, R. A. and W. H. Karasov. 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. *Oecologia* 49:67-72.
- Andrews, R. A. 1971. Structural habitat and time budget of a tropical *Anolis* lizard. *Ecology* 52: 262-270.
- Arnold, S. J. 1983. Morphology, performance and fitness. *Amer. Zool.* 23:347-361.
- Avery, R. A., C. F. Mueller, S. M. Jones, J. A. Smith, and D. J. Bond. 1987. Speeds and movement patterns of European lacertid lizards: A comparative study. *J. Herpetol.* 21:324-329.
- Bartholomew, G. A., A. F. Bennett, and W. R. Dawson. 1976. Swimming, diving, and lactate production of the marine iguana, *Amblyrhynchus cristatus*. *Copeia* 1976:709-720.
- Belkin, D. A. 1961. The running speeds of the lizards *Dipsosaurus dorsalis* and *Callisaurus draconoides*. *Copeia* 1961:223-224.
- Benedict, F. G. 1932. The physiology of large reptiles. Carnegie Inst. Washington Publ. 425.
- Bennett, A. F. 1978. Activity metabolism of the lower vertebrates. *Ann. Rev. Physiol.* 40:447-469.
- Bennett, A. F. 1980a. The thermal dependence of lizard behaviour. *Anim. Behav.* 28:752-762.
- Bennett, A. F. 1980b. The metabolic foundations of vertebrate behavior. *BioScience* 30:452-456.
- Bennett, A. F. 1982. The energetics of reptilian activity. In C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, Vol. 13, pp. 155-199. Academic Press, New York, New York.
- Bennett, A. F. 1983. Ecological consequences of activity metabolism. In R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), *Lizard ecology: Studies of a model organism*, pp. 11-23. Harvard University Press, Cambridge, Massachusetts.
- Bennett, A. F. and T. T. Gleeson. 1979. Metabolic expenditure and the cost of foraging in the lizard *Cnemidophorus murinus*. *Copeia* 1979:573-577.
- Bennett, A. F., T. T. Gleeson, and G. C. Gorman. 1981. Anaerobic metabolism in a lizard (*Anolis bonairensis*) under natural conditions. *Physiol. Zool.* 54:237-241.
- Bennett, A. F. and G. C. Gorman. 1979. Population density and energetics of lizards on a tropical island. *Oecologia* 42:339-358.
- Bennett, A. F. and L. D. Houck. 1983. The energetic cost of courtship and aggression in a plethodontid salamander. *Ecology* 64:979-983.
- Bennett, A. F., R. B. Huey, and H. John-Alder. 1984. Physiological correlates of natural activity and locomotor capacity in two species of lacertid lizards. *J. Comp. Physiol. B* 154:113-118.
- Bennett, A. F. and P. Licht. 1972. Anaerobic metabolism during activity in lizards. *J. Comp. Physiol.* 81:277-288.
- Bennett, A. F. and J. A. Ruben. 1979. Endothermy and activity in vertebrates. *Science* 206:649-654.
- Bennett, A. F., R. S. Seymour, D. F. Bradford, and G. J. W. Webb. 1985. Mass-dependence of anaerobic metabolism and acid-base disturbance during activity in the salt-water crocodile, *Crocodylus porosus*. *J. Exp. Biol.* 118:161-171.

- Bickler, P. E. and R. A. Anderson. 1986. Ventilation, gas exchange, and aerobic scope in a small monitor lizard, *Varanus gilleni*. *Physiol. Zool.* 59:76-83.
- Brett, J. R. 1972. The metabolic demand for oxygen in fish, particularly salmonids, and a comparison with other vertebrates. *Resp. Physiol.* 14:151-170.
- Brett, J. R., M. Hollands, and D. F. Alderdice. 1958. The effect of temperature on the cruising speed of young sockeye and coho salmon. *J. Fish. Res. Bd. Canada* 15:587-605.
- Christian, K. A. and C. R. Tracy. 1981. The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. *Oecologia* 49:218-223.
- Crowley, S. R. 1985. Thermal sensitivity of sprint-running in the lizard *Sceloporus undulatus*: Support for a conservative view of thermal physiology. *Oecologia* 66:219-225.
- Crowley, S. R. and R. D. Pietruszka. 1983. Aggressiveness and vocalization in the leopard lizard (*Gambelia wislizenii*): The influence of temperature. *Anim. Behav.* 31:1055-1060.
- Dial, B. E. 1987. Energetics and performance during nest emergence and the hatchling frenzy in loggerhead sea turtles (*Caretta caretta*). *Herpetologica* 43:307-315.
- Dunkle, T. 1983. Talking potatoes. *Science* 83 4:86.
- Feder, M. E. 1983. The relation of air breathing and locomotion to predation on tadpoles, *Rana berlandieri*, by turtles. *Physiol. Zool.* 56:522-531.
- Feder, M. E. and S. J. Arnold. 1982. Anaerobic metabolism and behavior during predatory encounters between snakes (*Thamnophis elegans*) and salamanders (*Plethodon jordani*). *Oecologia* 53:93-97.
- Fleming, T. H. and R. S. Hooker. 1975. *Anolis cupreus*: The response of a lizard to tropical seasonality. *Ecology* 56:1243-1261.
- Gans, C. 1979. Momentarily excessive construction as the basis for protoadaptation. *Evolution* 33:227-233.
- Garland, T., Jr. 1984. Physiological correlates of locomotor performance in a lizard: An allometric approach. *Amer. J. Physiol.* 247:R806-R815.
- Garland, T., Jr. 1988. Locomotor performance and activity metabolism of *Cnemidophorus tigris* in relation to natural behaviors. In J. Wright (ed.), *Biology of Cnemidophorus*. Los Angeles County Museum and University of Washington Press, Seattle, Washington. (In press)
- Garland, T., Jr. and P. L. Else. 1987. Seasonal, sexual, and individual variation in endurance and activity metabolism in a lizard. *Amer. J. Physiol.* 252 Regulatory Integrative Comp. Physiol. 21):R439-R449.
- Gatten, R. E., Jr. 1980. Aerial and aquatic oxygen uptake by freely-diving snapping turtles (*Chelydra serpentina*). *Oecologia* 46:266-271.
- Gatten, R. E., Jr. 1981. Anaerobic metabolism in freely diving painted turtles (*Chrysemys picta*). *J. Exp. Zool.* 216:377-385.
- Gatten, R. E., Jr. 1984. Aerobic and anaerobic metabolism of freely-diving loggerhead musk turtles (*Sternotherus minor*). *Herpetologica* 40:1-7.
- Gatten, R. E., Jr. 1985. The uses of anaerobiosis by amphibians and reptiles. *Amer. Zool.* 25:945-954.
- Gatten, R. E., Jr., J. P. Caldwell, and M. E. Stockard. 1984. Anaerobic metabolism during intense swimming by anuran larvae. *Herpetologica* 40:164-169.
- Gerritsen, J. and J. R. Strickler. 1977. Encounter probabilities and community structure in zooplankton: A mathematical model. *J. Fish. Res. Bd. Canada* 34:73-82.
- Gleeson, T. T. 1979. Foraging and transport costs in the Galapagos marine iguana, *Amblyrhynchus cristatus*. *Physiol. Zool.* 52:549-557.
- Gleeson, T. T. 1980. Lactic acid production during field activity in the Galapagos marine iguana, *Amblyrhynchus cristatus*. *Physiol. Zool.* 53:157-162.
- Greene, H. W. 1986. Natural history and evolutionary biology. In M. E. Feder and G. V. Lauder (eds.), *Predator-prey relationships: Perspectives and approaches from the study of lower vertebrates*, pp. 99-108. University of Chicago Press, Chicago, Illinois.
- Greene, H. W. 1988. Antipredator mechanisms in reptiles. In C. Gans and R. B. Huey (eds.), *Biology of the Reptilia*, Vol. 16, pp. 1-152. John C. Wiley and Sons, New York, New York.
- Greenwald, O. E. 1974. Thermal dependence of striking and prey capture by gopher snakes. *Copeia* 1974:141-148.
- Herbers, J. M. 1981. Time resources and laziness in animals. *Oecologia* 49:252-262.
- Hertz, P. E., R. B. Huey, and E. Nevo. 1982. Fight versus flight: Body temperature influences defensive responses of lizards. *Anim. Behav.* 37:676-679.
- Hertz, P. E., R. B. Huey, and E. Nevo. 1983. Homage to Santa Anita: Thermal dependence of sprint speed in agamid lizards. *Evolution* 37:1075-1084.
- Hillman, P. E. 1969. Habitat specificity of three sympatric species of *Ameiva* (Reptilia: Teiidae). *Ecology* 50:476-481.
- Howland, H. C. 1974. Optimal strategies for predator avoidance: The relative importance of speed and manoeuvrability. *J. Theor. Biol.* 47:333-350.
- Huey, R. B. 1974. Winter thermal ecology of the iguanid lizard *Tropidurus peruvianus*. *Copeia* 1974:149-155.
- Huey, R. B. 1982. Temperature, physiology, and the ecology of reptiles. In C. Gans and F. H. Pough (eds.), *Biology of the Reptilia*, Vol. 12, pp. 25-92. Academic Press, New York, New York.
- Huey, R. B. 1983. Natural variation in body temperature and physiological performance in a lizard (*Anolis cristatellus*). In A. G. J. Rhodin and K. I. Miyata (eds.), *Advances in herpetology and evolutionary biology: Essays in honor of Ernest E. Williams*, pp. 484-490. Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts.
- Huey, R. B. and A. F. Bennett. 1987. Phylogenetic studies of coadaptation: Preferred temperatures

- versus optimal performance temperatures of lizards. *Evolution* 41:1098-1115.
- Huey, R. B., A. F. Bennett, H. John-Alder, and K. A. Nagy. 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. *Anim. Behav.* 32:41-50.
- Huey, R. B. and P. E. Hertz. 1984a. Is a jack-of-all-temperatures a master of none? *Evolution* 38: 441-444.
- Huey, R. B. and P. E. Hertz. 1984b. Effects of body size and slope on acceleration of a lizard (*Stellio (Agama) stellio*). *J. Exp. Biol.* 110:113-123.
- Huey, R. B. and E. R. Pianka. 1981. Ecological consequences of foraging mode. *Ecology* 62:991-999.
- Huey, R. B. and M. Slatkin. 1976. Costs and benefits of lizard thermoregulation. *Q. Rev. Biol.* 51:363-384.
- Huey, R. B. and R. D. Stevenson. 1979. Integrating thermal physiology and ecology of ectotherms: A discussion of approaches. *Amer. Zool.* 19:357-366.
- Irwin, L. N. 1965. Diel activity and social interaction of the lizard *Uta stansburiana stejnegeri*. *Copeia* 1965:99-101.
- Jackson, D. C. and H. D. Prange. 1979. Ventilation and gas exchange during rest and exercise in adult green sea turtles. *J. Comp. Physiol.* 134:315-319.
- John-Alder, H. 1984. Seasonal variations in activity, aerobic energetic capacities, and plasma thyroid hormones (T3 and T4) in an iguanid lizard. *J. Comp. Physiol. B* 154:409-419.
- John-Alder, H. and A. F. Bennett. 1981. Thermal dependence of endurance and locomotory energetics in a lizard. *Amer. J. Physiol.* 241(Regulatory Integrative Comp. Physiol. 10):R342-R349.
- John-Alder, H., T. Garland, Jr., and A. F. Bennett. 1986. Locomotory capacities, oxygen consumption, and the cost of locomotion of the shingleback lizard (*Trachydosaurus rugosus*). *Physiol. Zool.* 59:523-531.
- Kingsolver, J. and W. B. Watt. 1983. Thermoregulatory strategies in *Colias* butterflies: Thermal stress and the limits to adaptation in temporally varying environments. *Amer. Nat.* 121:32-55.
- Kooyman, G. L. 1982. How marine mammals dive. In C. R. Taylor, K. Johansen, and L. Bolis (eds.), *A companion to animal physiology*, pp. 151-160. Cambridge University Press, New York, New York.
- Leamy, L. and J. M. Cheverud. 1984. Quantitative genetics and the evolution of ontogeny. II. Genetic and environmental correlations among age-specific characters in random bred house mice. *Growth* 48:339-353.
- Maiorana, V. C. 1977. Predation, submergent behavior, and tropical diversity. *Evolutionary Theory* 1:157-177.
- McNab, B. K. 1963. A model of the energy budget of a wild mouse. *Ecology* 44:521-532.
- Moberly, W. R. 1968a. The metabolic responses of the common iguana, *Iguana iguana*, to activity under restraint. *Comp. Biochem. Physiol.* 27:1-20.
- Moberly, W. R. 1968b. The metabolic responses of the common iguana, *Iguana iguana*, to walking and diving. *Comp. Biochem. Physiol.* 27:21-32.
- Nagy, K. A. 1982. Energy requirements of free-living iguana lizards. In G. M. Burghardt and A. S. Rand (eds.), *Iguanas of the world: Their behavior, ecology, and conservation*, pp. 49-59. Noyes Publications, Park Ridge, New Jersey.
- Nagy, K. A. 1983. Ecological energetics. In R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), *Lizard ecology: Studies of a model organism*, pp. 24-53. Harvard University Press, Cambridge, Massachusetts.
- Norberg, R. A. 1977. An ecological theory on foraging time and energetics and choice of optimal food-searching method. *J. Anim. Ecol.* 46:511-529.
- Pianka, E. R. 1970. Comparative autecology of the lizard *Cnemidophorus tigris* in different parts of its geographic range. *Ecology* 51:703-720.
- Pough, F. H. 1980. The advantages of ectothermy for tetrapods. *Amer. Nat.* 115:92-112.
- Pough, F. H. and R. A. Andrews. 1985a. Energy costs of subduing and swallowing prey for a lizard. *Ecology* 66:1525-1533.
- Pough, F. H. and R. A. Andrews. 1985b. Use of anaerobic metabolism by free-ranging lizards. *Physiol. Zool.* 58:205-213.
- Putnam, R. W. and A. F. Bennett. 1980. Thermal dependence of behavioural performance of anuran amphibians. *Anim. Behav.* 29:502-509.
- Rapport, D. J. and J. E. Turner. 1977. Economic models in ecology. *Science* 195:367-373.
- Regal, P. J. 1978. Behavioral differences between reptiles and mammals: An analysis of activity and mental capabilities. In N. Greenberg and P. D. MacLean (eds.), *Behavior and neurology of lizards: An interdisciplinary symposium*, pp. 183-202. Dept. of Health, Education, and Welfare Publ. No. (ADM) 77-491.
- Regal, P. J. 1983. The adaptive zone and behavior of lizards. In R. B. Huey, E. R. Pianka, and T. W. Schoener (eds.), *Lizard ecology: Studies of a model organism*, pp. 105-118. Harvard University Press, Cambridge, Massachusetts.
- Schall, J. J., A. F. Bennett, and R. W. Putnam. 1982. Lizards infected with malaria: Physiological and behavioral consequences. *Science* 217:1057-1059.
- Schall, J. J. and E. R. Pianka. 1980. Evolution of escape behavior diversity. *Amer. Nat.* 115:551-566.
- Schall, J. J. and G. A. Sarni. 1987. Malarial parasitism and the behavior of the lizard, *Sceloporus occidentalis*. *Copeia* 1987:84-93.
- Schoener, T. W. 1974. The compression hypothesis and temporal resource partitioning. *Proc. Nat. Acad. Sci., U.S.A.* 71:4169-4172.
- Seymour, R. S. 1973. Physiological correlates of forced activity and burrowing in the spadefoot toad, *Scaphiopus hammondi*. *Copeia* 1973:103-115.
- Seymour, R. S. 1979. Blood lactate in free-diving sea snakes. *Copeia* 1979:494-497.
- Stevenson, R. D., C. R. Peterson, and J. S. Tsuji. 1985. The thermal dependence of locomotion,

- tongue flicking, digestion, and oxygen consumption in the wandering garter snake. *Physiol. Zool.* 58:46-57.
- Taigen, T. L. and C. A. Beuchat. 1984. Anaerobic threshold of anuran amphibians. *Physiol. Zool.* 57:641-647.
- Tollestrup, K. 1979. The ecology, social structure, and foraging behavior of two closely related species of leopard lizards, *Gambelia silus* and *Gambelia wislizenii*. Ph.D. Diss., Univ. Calif., Berkeley.
- van Berkum, F. 1986. Evolutionary patterns of the thermal sensitivity of sprint speed in *Anolis* lizards. *Evolution* 40:594-604.
- van Berkum, F., R. B. Huey, and B. A. Adams. 1986. Physiological consequences of thermoregulation in a tropical lizard (*Ameiva festiva*). *Physiol. Zool.* 59:464-472.
- Vitt, L. J. and H. J. Price. 1982. Ecological and evolutionary determinants of relative clutch mass in lizards. *Herpetologica* 38:237-255.
- Waldschmidt, S. and C. R. Tracy. 1983. Interactions between a lizard and its thermal environment: Implications for sprint performance and space utilization in the lizard *Uta stansburiana*. *Ecology* 64:476-484.
- Webb, P. W. 1976. The effect of size on the fast-start performance of rainbow trout *Salmo gairdneri*, and a consideration of piscivorous predator-prey interactions. *J. Exp. Biol.* 65:157-177.
- Webb, P. W. 1986. Locomotion and predator-prey relationships. In M. E. Feder and G. V. Lauder (eds.), *Predator-prey relationships: Perspectives and approaches from the study of lower vertebrates*, pp. 24-41. University of Chicago Press, Chicago, Illinois.
- Wells, K. D. and T. L. Taigen. 1984. Reproductive behavior and aerobic capacities of male American toads (*Bufo americanus*): Is behavior constrained by physiology? *Herpetologica* 40:292-298.
- Wiens, J. A. 1977. On competition and variable environments. *Amer. Sci.* 65:590-597.
- Wilson, K. J. and A. K. Lee. 1974. Energy expenditure of a large herbivorous lizard. *Copeia* 1974: 338-348.