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Chapter 7

Locomotor Performance And Activity
Metabolism Of *Cnemidophorus tigris* In
Relation To Natural Behaviors

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The genus *Cnemidophorus* is characterized by active, widely-foraging species (Urban, 1965; Asplund, 1970; MacLean, 1974; Regal, 1978, 1983). The western whiptail, *Cnemidophorus tigris* (Stebbins, 1985), is no exception, and might be considered the archetypal "widely-foraging" lizard (Pianka, 1966, 1970; Vitt and Price, 1982; Pietruszka, 1986). In comparison with other lizards of similar size, *C. tigris* have relatively large home ranges, move farther, and expend more energy on a daily basis (references below). Even in comparison with other whiptails, *C. tigris* have been described as having a "nervous temperament" (Milstead, 1957a, p. 430), being "nervous and wary" (Milstead, 1957a, p. 438, 1957b, 108; Echternacht, 1967, p. 456), possessing "extreme wariness" (Scudday and Dixon, 1973, p. 286), and being the "most wary" (Mitchell, 1979, p. 1490). Their movements during foraging are described as "rapid and jerky" (Milstead, 1957b, p. 108; Echternacht, 1967, p. 456).

Enhanced stamina might be expected to evolve as an adaptation to an active, widely-foraging lifestyle. The purpose of this study was, therefore, to determine whether *C. tigris* possess high endurance capacities, as compared with other lizards. Secondly, if *C. tigris* are exceptional in this regard, what are the morphological and/or physiological bases for their high endurance capacities? I first review briefly the expected functional correlates of variation in locomotor capacity and the literature that has attempted to establish such correlates. Next, I compile the available quantitative data on natural behavior and activity of *C. tigris*, and compare this species with other lizards. Finally, I provide new data on locomotor capacity and activity metabolism of *C. tigris* and several other species. In the discussion, I attempt to evaluate the adaptive significance of the locomotor capacities of *C. tigris*, then consider some general patterns in the evolution of locomotor performance and its functional correlates.

Literature Review

Expected Functional Correlates of Variation in Locomotor Capacity

In this section I review briefly the functional bases for variation in the capacity for locomotor performance. This review suggests measurable characters that would be expected to vary with performance. Consideration of the natural activities of *C. tigris* suggests that endurance capacities, as opposed to sprint running abilities, might be exceptional. Maximal running speeds of *C. tigris*, measured in the laboratory on a photocell-timed racetrack, average < 13 km/h (F. H. van Berkum, pers. comm.), about in the middle of the range of variation seen among species of lizards, including other teiids (Urban, 1965; Bennett, 1980; Garland, 1982, 1983b, 1984, 1985, unpublished; Crowley and Pietruszka, 1983; Huey *et al.*, 1984; van Berkum *et al.*, 1986; Garland and Losos, *in press*; references therein). However, *C. tigris* may attain speeds of at least 23 km/h on a high-speed motorized treadmill (Garland, unpublished; J. A. Peterson, pers. comm.), which is relatively fast for a lizard of such size. In any case, I do not discuss factors affecting maximal running speed; such discussions may be found elsewhere (reviews and references in Howell, 1944; Bakker, 1983; Garland, 1983b, 1985; Van Valkenburgh, 1987; Gleeson and Harrison, 1988). It should be noted, however, that functional links or tradeoffs may exist between sprint and endurance capacities, because many factors that affect one capacity will also affect the other (Bennett *et al.*, 1984; Huey *et al.*, 1984; but see Garland, 1988; Garland *et al.*, 1988).

If any vertebrate engages in activity that uses ATP at a rate greater than the maximum rate at which its cells can produce it via aerobic (oxidative) pathways, additional ATP is produced through anaerobic glycolysis, with concomitant production of lactic acid. Through mechanisms as yet not fully understood, production of high amounts of lactic acid, which is related to changes in blood and intracellular pH, leads ultimately to muscular fatigue and hence exhaustion (Simonson and Weiser, 1976; Putnam, 1979a, b; Knuttgen *et al.*, 1983). Fatigue may also be related to more subtle effects of exhaustive exercise, such as fatigue of ventilatory muscles, substrate depletion, dehydration, electrolyte losses, hyperthermia, changes in muscle cell permeability, reduced motor drive ("central nervous system fatigue"), and/or failure of neuromuscular transmission (see Simonson and Weiser, 1976; Putnam, 1979a, b; Knuttgen *et al.*, 1983). Currently, no consensus exists as to what causes fatigue during various activities, but endurance capacity will likely depend on a variety of characters and capacities at several levels of biological organization.

The maximal organismal rate of oxygen consumption ($\dot{V}O_{2max}$) corresponds with the upper limit to the intensity of locomotor activity that can be supported aerobically. Supplementary anaerobic production of ATP

occurs when an animal engages in activity that exceeds its $\dot{V}O_{2max}$. The treadmill speed at which $\dot{V}O_{2max}$ is attained is termed the maximal aerobic speed (John-Alder and Bennett, 1981). In some species, blood lactate levels begin to increase at a workload significantly below that at which $\dot{V}O_{2max}$ is attained (references and discussion in Taigen and Beuchat, 1984; but see Brooks, 1985; Mazzeo *et al.*, 1986); this workload is termed the "anaerobic threshold." The maximal aerobic speed depends both on the slope of the relationship between oxygen consumption and running speed (termed the net or incremental cost of locomotion) and on $\dot{V}O_{2max}$. Both the net cost of locomotion (John-Alder *et al.*, 1986) and $\dot{V}O_{2max}$ (references below; this study) vary among species of lizards.

An animal forced to run on a motorized treadmill at a speed higher than its maximal aerobic speed eventually exhausts. The length of time the animal runs before exhaustion can be recorded as a measure of its endurance capacity (Bennett, 1989; Garland and Losos, *in press*). In lizards, fatigue is operationally defined as the point at which an individual can no longer maintain tread speed, even though given pinching and prodding (Moberly, 1968b used mild electrical shocking) as motivation (Garland, 1984; Huey *et al.*, 1984; John-Alder, 1984; John-Alder *et al.*, 1986; Garland and Else, 1987). This agrees with the definition of fatigue as "decrease of working capacity due to preceding work" (Simonson and Weiser, 1976, p. xv). In lizards, the maximal aerobic speed is a good predictor of the maximum speed that can be sustained for >15-30 min, and the applicability of the anaerobic threshold concept is unclear (John-Alder and Bennett, 1981; John-Alder *et al.*, 1983; Bennett and John-Alder, 1984; Taigen and Beuchat, 1984; John-Alder *et al.*, 1986; Garland and Else, 1987; see also Taylor *et al.*, 1981 regarding mammals).

The maximal rate of oxygen consumption ($\dot{V}O_{2max}$) depends both on the rate at which oxygen can be delivered to the tissues and on the maximal rate at which the tissues can utilize oxygen for oxidative phosphorylation. The rate at which oxygen can be delivered to tissues depends on the rate at which oxygen can diffuse from the alveoli into the blood, the amount of oxygen that a given volume of blood can carry, the rate at which blood can be pumped through the circulatory system, the fraction of oxygen that can be extracted from the blood by the tissues, and the rate at which oxygen can diffuse from capillaries into cells and then into the mitochondria (see Taylor and Weibel, 1981; Weibel *et al.*, 1981; Perry, 1983; Taylor, 1983; Hillman and Withers, 1985; Garland and Huey, 1987). The rate at which tissues can utilize oxygen will depend on the amount of tissue as well as the oxidative capacity (*e.g.*, mitochondrial volume density) per unit weight of the tissues. Exhaustion obviously does not occur immediately after an animal exceeds its anaerobic threshold and/or maximal aerobic speed. In

effect, supplementary anaerobic production of ATP extends activity capacity, but leads ultimately to exhaustion. Therefore, the capacity of muscle tissue to produce ATP anaerobically will also affect endurance capacity. In addition, the ability of an animal to cope with the deleterious consequences of lactic acid production should affect its endurance capacity.

From the foregoing, an animal adapted for high endurance capacities should possess many or all of the following characteristics — listed with characters that might be measured as indices of function:

- I. High maximal aerobic speed and/or high anaerobic threshold
 - A. Low incremental (net) cost of locomotion — limb proportions (see Myers and Steudel, 1985; Bickler and Anderson, 1986; John-Alder *et al.*, 1986)
 - B. A high maximal rate of oxygen consumption — $\dot{V}O_{2max}$
 - 1) High capacity to deliver oxygen to the tissues
 - a) Well developed lungs — lung size, volume, vascularity, size of alveoli, thickness and nature of alveolar membranes (see Perry, 1984)
 - b) Large heart — mass of heart or ventricle(s)
 - c) High maximal heart rate
 - d) High blood oxygen carrying capacity — hematocrit (Hct) or hemoglobin (Hb) content of the blood
 - e) High capacity to extract oxygen from blood — large arterial-venous difference in blood O_2 content
 - 2) High tissue capacity to utilize oxygen for oxidative phosphorylation
 - a) Massive locomotor muscles (*e.g.*, Garland, 1984)
 - b) High per gram tissue oxidative capacity — maximal *in vitro* catalytic rates of enzymes involved in the Krebs' cycle, electron transport, and/or fatty acid oxidation (see Hochachka and Somero, 1984)
 - c) High myoglobin concentrations in heart or skeletal muscle (see Bennett *et al.*, 1984; Hochachka and Somero, 1984)
- II. Capacity to tolerate high concentrations of lactic acid and metabolic acidosis
 - A. High blood buffering capacity (see Bennett, 1973)
 - B. High tissue/cellular buffering capacity — muscle buffering capacity (Castellini and Somero, 1981; Parkhouse *et al.*, 1985)
 - C. Low functional biochemical sensitivity to pH changes — *e.g.*, enzyme activity versus pH curves?

Relative development of each of these components in a given animal should depend on the capacity of that animal to perform various types of locomotor activities. In addition to differing in the total amount of ATP

they require, activities of different lengths and intensities differ also in the relative proportions of ATP derived from alternative sources (see, for example, Howald *et al.*, 1978). Endurance time at relatively low speeds, lasting many minutes or hours, will be fueled almost exclusively by the aerobic production of ATP. Short-term, intense, exhaustive activities, lasting one or a few minutes, will be fueled primarily by the anaerobic production of ATP, but may also reduce or exhaust endogenous stores of ATP and creatine phosphate (*e.g.*, see Bennett, 1982 regarding lizards), in addition to recruiting some amount of aerobically derived ATP. Hence, different types of "endurance" may be limited by different metabolic capacities, perhaps of different muscle groups, in addition to the ability of an organism to continue functioning "normally" in the face of metabolic acidosis. Moreover, many of the above components may be functionally interdependent.

Comparative Studies of Locomotor Capacity in Lizards

In this section, I review comparative studies that have looked for correlates of locomotor performance in lizards. Related studies on snakes (summarized in Pough, 1983; Ruben, 1983), amphibians (*e.g.*, Bennett, 1974; Hutchison and Miller, 1979; Taigen *et al.*, 1982; Putnam and Bennett, 1983; Taigen and Pough, 1983; Withers and Hillman, 1983; Pough and Gatten, 1984; Pough and Kamel, 1984; Taigen and Wells, 1985; Full, 1986; Gatten *et al.*, 1992), and mammals (*e.g.*, Taylor *et al.*, 1981; Pietschmann *et al.*, 1982; Yacoe *et al.*, 1982) are not discussed.

Locomotor performance is highly variable among species of lizards (Garland, 1991; Garland and Losos, *in press*) and even among populations (Garland and Adolf, 1991). Maximal (burst or sprint) running speed (Bennett, 1980; John-Alder *et al.*, 1983; Garland, 1984, 1985; John-Alder *et al.*, 1986; Avery *et al.*, 1987) and treadmill endurance (at 1.0 km/h; Moberly, 1968b; Bennett and Gleeson, 1979; Gleeson, 1979, 1980, 1981; Gleeson *et al.*, 1980; Gleeson and Bennett, 1982; Bennett and John-Alder, 1984; Garland, 1984, this study, unpublished; Huey *et al.*, 1984; John-Alder, 1984; John-Alder *et al.*, 1986; Garland and Else, 1987) both vary by more than 15-fold, whereas distance running ability varies at least 5-fold (Bennett, 1980; Huey *et al.*, 1984; Garland, 1984, this study, see RESULTS) among species of lizards. The functional correlates of interspecific variation in sprint speed in lizards are not well understood (Garland, 1985; but see Gleeson and Harrison, 1987; Losos and Sinervo, 1989; Losos, 1990a; Garland and Janis, 1993).

Maximal oxygen consumption also varies considerably among species of lizards (Gleeson, 1981; Withers, 1981; Gleeson, 1981; Bennett, 1982; Kamel and Gatten, 1983; John-Alder, 1984; Garland, 1984, this study; Garland and Else, 1987; see RESULTS), and this variation would be expected to correlate positively with variation in treadmill endurance. Some previ-

ous data on "maximal oxygen consumption" must be viewed with caution, however, because many of the values appear not to represent true $\dot{V}O_{2\max}$ (compare Moberly, 1968a with Gleeson *et al.*, 1980 for *Iguana iguana*; Asplund, 1970 with present study for *C. tigris*; Wilson, 1974 with John-Alder *et al.*, 1986 for *Trachydosaurus rugosus*). Manual stimulation of restrained animals, or electrical stimulation of animals restrained or confined to metabolic chambers, may not elicit $\dot{V}O_{2\max}$. Unless one can demonstrate that $\dot{V}O_2$ fails to increase above a certain work rate (*e.g.*, employs a "step test," Garland, 1984; John-Alder, 1984), it cannot be known with certainty that $\dot{V}O_{2\max}$ has been attained (see also Taylor *et al.*, 1981; Taigen and Wells, 1985).

Bennett and Licht (1972) concluded there was "little variation" in anaerobic scope (= maximal rate of lactic acid production) or anaerobic capacity (= total amount of lactate produced during activity to exhaustion) among several species of small lizards, although variation in the time to exhaustion was greater.

Although neither treadmill endurance nor distance running capacities have been quantified in varanid lizards, most of which are active, widely foraging carnivores, they generally seem to have greater stamina than iguanians (Gleeson *et al.*, 1980; Gleeson and Bennett, 1982; Bickler and Anderson, 1986), though this may not be true for all varanids (Gleeson, 1981). Summarizing his dissertation work, Bennett (1973, p. 686) concluded: "Varanus and *Sauromalus* (an herbivorous iguanid lizard) are almost identical in most factors affecting oxygen transport and utilization: resting metabolic rate, resting and active ventilation rate, active heart rate, hematocrit, blood oxygen capacity and affinity, resting blood pH and lactate content, blood bicarbonate and phosphate concentrations and aerobic enzymatic activities in the liver and skeletal muscle. The physiological superiorities of *Varanus* are few but critical: a complex lung structure with a much greater surface area, excellent non-carbonic blood buffers and high levels of myoglobin in the skeletal muscles." In comparison with *Iguana iguana*, *Varanus exanthematicus* has higher treadmill endurance, an increased oxygen content of arterial blood and oxygen extraction from the blood, and a greater contribution of stroke volume to increasing cardiac output during activity (Gleeson *et al.*, 1980). Varanids also have a more complete ventricular septum than do other lizards, a condition which allows higher blood pressures and hence cardiac outputs, and is presumed to be advantageous for activity metabolism (see Auffenberg, 1978; Regal, 1978; Burggren and Johansen, 1982).

Bennett *et al.* (1984) and Huey *et al.* (1984) demonstrated that *Eremias lugubris* and *E. lineocellata* differ significantly in treadmill endurance, distance running ability, sprint speed, $\dot{V}O_{2\max}$, relative heart

mass, hematocrit, and anaerobic scope and capacity — and in the directions expected — but not in relative hind limb muscle mass, myoglobin concentration or citrate synthase (a Krebs cycle enzyme) activity.

A few studies have considered intraspecific variation in activity metabolism (reviews in Bennett, 1987, 1989; Garland and Losos, *in press*). Seasonal variation in stamina, paralleled by seasonal variation in various components of activity metabolism, has been found in two species of lizards (John-Alder, 1984; Garland and Else, 1987). John-Alder (1984 and references therein) also demonstrated experimentally correlations between thyroid function and various components of activity metabolism, including endurance. Schall *et al.* (1982) examined the consequences of malarial infection for activity metabolism in fence lizards. Garland (1984), John-Alder (1984), and Garland and Else (1987) (see also Schall *et al.*, 1982) have demonstrated that individual differences in treadmill endurance and maximal distance run to exhaustion reflect individual variation in a variety of organismal and suborganismal characters. (I am currently pursuing such studies with both *Cnemidophorus tigris* and *Callisaurus draconoides*.) Finally, Gleeson and Harrison (1988) have demonstrated correlations between sprint speed and muscle fiber characteristics among individual desert iguanas.

A number of studies that have demonstrated interspecific variation in either locomotor performance or morphological, physiological or biochemical characters that would be expected to affect performance, but surprisingly few (Bennett *et al.*, 1984; Huey *et al.*, 1984) have quantified both performance and its expected correlates in different species of lizards. Furthermore, some comparisons that have been made (*e.g.*, varanids versus iguanians) may suffer from the confounding influences of phylogeny (discussions and references in Jaksic, 1981; Harvey and Mace, 1982; Ridley, 1983; Bennett *et al.*, 1984; Huey *et al.*, 1984; Felsenstein, 1985; Garland, 1985; Huey, 1987; Brooks and McLennan, 1991; Garland *et al.*, 1991; Harvey and Pagel, 1991; Martins and Garland, 1991; Garland *et al.*, 1992).

Natural Activity of *Cnemidophorus tigris*

As do other active, widely-foraging species (Huey and Pianka, 1981; Vitt and Price, 1982; Andrews, 1984; Karasov and Anderson, 1984; Nagy *et al.*, 1984), *C. tigris* has a high rate of energy expenditure in the field (Anderson and Karasov, 1981; Nagy, 1982), as compared with other lizards of similar size. This high daily energy expenditure is largely a function of the greater activity of *C. tigris* (*cf.* Bennett and Gleeson, 1979; Huey and Pianka, 1981; Karasov and Anderson, 1984), since resting metabolic rates are not exceptionally high (Asplund, 1970; Anderson and Karasov, 1981;

Bennett, 1982; Andrews and Pough, 1985; this study, see RESULTS). The high natural activity levels of *C. tigris* can be evidenced in several ways.

Home ranges of *Cnemidophorus tigris* are relatively large in comparison with other lizards of similar size. Because it is difficult to compare home ranges estimated in different studies using different techniques (Turner *et al.*, 1969; Schoener, 1981; Christian and Waldschmidt, 1984), I do not here present data on lizard home ranges; the preceding statement is a generality based on comparisons of several studies (Milstead, 1957a, b, 1961; Turner *et al.*, 1969; Werth, 1972; Kay *et al.*, 1973; Clark, 1976; Krekorian, 1976; Anderson and Karasov, 1981; Hulse, 1981; Satrawaha and Bull, 1981; Brooke and Houston, 1983; Christian and Waldschmidt, 1984; Munger, 1984; Anderson, 1986; references therein). These studies also suggest significant intraspecific variation in home range size in *C. tigris* (*cf.* Schoener and Schoener, 1982).

Another index of animal activity under natural conditions is daily movement distance (DMD, Garland, 1983a). The DMD of an animal is defined as the actual path length of an animal's movements (*i.e.*, not just the straight-line distance between points of resighting), including all daily activities. Figure 1 presents all available estimates of daily movement distances of lizards smaller than 1 kg. Some of these estimates are from direct observation of marked individuals for their entire active period, others are estimates based on measures of the mean per minute or per hour rate of movement multiplied by the average length of the active period for individual lizards. I have no reason to think that such differences in methods of estimation of DMD bias the interspecific comparisons made here.

Cnemidophorus move relatively long distances on a daily basis (Fig. 1). The highest estimated DMD is for *C. tigris*, but estimates for *C. murinus* and *C. hyperythrus* are nearly as high. In fact, DMDs of *Cnemidophorus* are similar to or greater than those of some sympatric small mammals (Garland, 1983b).

Pietruszka's (1986) data indicate that movement rates may be relatively invariant seasonally and from year-to-year within a single population of *C. tigris*. However, other studies indicate that movement rates may vary among populations. For example, Anderson and Karasov's (1981) report that *C. tigris* move an average of about 900 m/day, but Kay *et al.* (1973) observed this species to move an average of only 62 m during their entire activity period, partly because the latter whiptails were active for a much shorter period of time (and see Regal, 1983, p. 116). Moreover, Karasov and Anderson (1984) have documented approximately 2-fold differences in DMD for *C. hyperythrus* living in different habitats, due primarily to differences in total activity time. Parker (1972) noted that juvenile *C. tigris* did not move as far between recaptures as did adults. Daily movement dis-

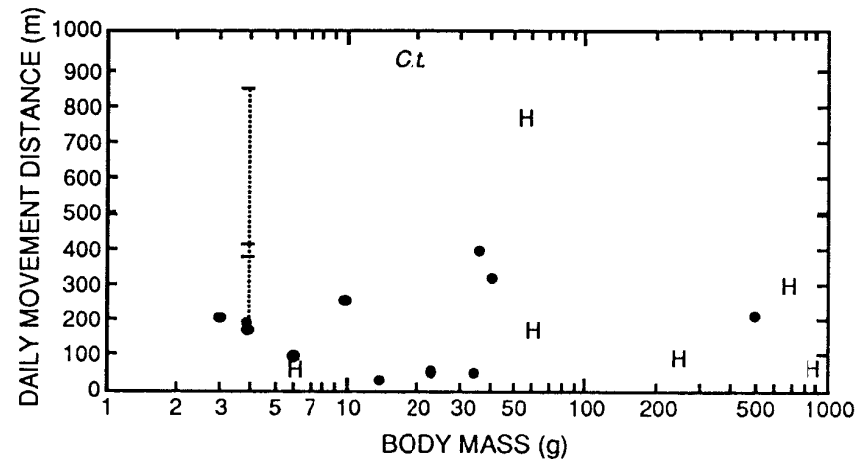


FIGURE 1. Daily movement distances (lengths of actual paths of movement) of 17 species of lizards smaller than 1 kg. Closed circles are insectivores and carnivores; herbivores are designated "H". Sources of data are as follows: *Anolis bonairensis*, 6 g, 0.13 m/min X 12 h = 94 m/day (Bennett and Gorman, 1979); *Calisaurus draconoides*, 10 g, 9.8 m/min X 5 h = 392 m/day for males, 2.7 m/min X 5 h = 108 m/day for females, \bar{x} = 250 m/day (Anderson and Karasov, 1981); *Cnemidophorus hyperythrus* in different habitats, 4 g, 56% or 78% time in locomotion X 165 or 136 m/h of locomotor time X 9 or 3.5 h = 832 or 371 m/day for males, 76% or 73% time in locomotion X 59 or 73 m/h of locomotor time X 9 or 3.5 h = 404 or 187 m/day for females (vertical dotted line with horizontal bars; Karasov and Anderson, 1984); *Cnemidophorus murinus*, 55 g, 1.6 m/min X 8 h = 768 m/day (Bennett and Gorman, 1979); *Cnemidophorus tigris*, 17 g, 3 m/min X 5 h = 900 m/day (Anderson and Karasov, 1981); *Ctenosaura similis* 23 g, 7.61 m/h X 7 h = 53 m/day (Garland, unpublished); *Cydura carinata*, 670 g, 1.93 feeding forays/day X 149 m/foray = 288 m/day (Auffenberg, 1982); *Dipsosaurus dorsalis*, 6 g, 57 m/day for juveniles, 60 g, 169 m/day for adults (2 points; direct observation of individuals for entire active period, Garland, unpublished); *Egernia cunninghami*, 240 g, 4.5 m/min X 18.7 min/day = 84 m/day (Wilson and Lee, 1974); *Eremias lineocellata*, 4 g, 171 m/day (R. B. Huey, pers. comm.); *Eremias lugubris* 4 g, 184 m/day (R. B. Huey, pers. comm.); *Cambelia silus*, 36 g, 389 m/day (Tollestrup, 1979, p. 51); *Cambelia wislizenii*, 41 g, 314 m/day (Tollestrup, 1979, p. 79); *Heloderma suspectum*, 500 g, 215 m/day (Heath, 1961; but see Jones, 1983; Bock, 1988); *Iguana iguana* on Curacao, 860 g, 69 m/day (Marken Lichtenbelt, 1961); *Phrynosoma cornutum*, 35 g, 47 m/day (Whitford and Bryant, 1979); *Sceloporus jarrovi*, 14 g, 30 m/day (Ruby, 1978); *Uta stansburiana*, 3 g, 200 m/day (Irwin, 1965).

tances of juvenile *Dipsosaurus dorsalis* are also lower than those of adults (Fig. 1; as are home range areas, Krekorian, 1976), and DMDs appear to differ significantly among habitats in this species (Garland, unpublished). The foregoing examples indicate that interspecific comparisons of indices of animal movements should be made with caution. Nevertheless, it is

apparent that such measures as DMD and home range size reveal more biological variability than can be accounted for simply by differences in observation or measurement technique.

Existing measurements of the velocities at which lizards move in nature are compiled in Appendix I. These estimates were obtained by a variety of techniques, but generally involve watching undisturbed individuals for a few or several minutes — rarely for most or all of the active period — and dividing the total distance moved by the total time of observation, termed “mean velocity” by Huey and Pianka (1981, their Table 1). If the total period of observation can be broken into periods of inactivity versus activity (locomotion), then estimates of “velocity moving” (Huey and Pianka, 1981) are available. Assuming this is done relatively accurately, then “velocity moving” is an estimate of the average speed at which lizards walk when active in nature. For some studies, it is difficult to determine whether a reported value is mean velocity or velocity moving. Probably most of the lizard movements observed in most studies were related to foraging per se, but movements related to thermoregulation (e.g., Kay *et al.*, 1973; Wilson and Lee, 1974) or home range patrolling or searching for mates (e.g., Karasov and Anderson, 1984; Garland, unpublished) may also be important.

Not surprisingly, mean velocities are generally higher for widely-foraging lizards than for those that sit-and-wait (Appendix I; see also Avery *et al.*, 1987). Widely-foraging species, including *C. tigris*, tend also to be active for shorter total periods of time each day than are sympatric sit-and-wait species (Anderson and Karasov, 1981; Huey and Pianka, 1981; Andrews, 1984; Nagy *et al.*, 1984). As compared with other widely-foraging species, *C. tigris* is not exceptional with regard to either mean velocity or velocity moving. Velocities moving of *C. tigris* often exceed 1.0 km/h over short distances as animals traverse open spaces between bushes, but are much lower as they forage under bushes (Appendix I; Anderson, this volume; Garland, personal observations).

Materials and Methods

Adult *Cnemidophorus tigris*, *Callisaurus draconoides*, and *Cambelia wislizenii* were collected by hand or by slip noose, 18-19 May, 1983 along the northern edge of Dale Dry Lake, San Bernardino Co., CA (California Scientific Collector's Permit #0746). Lizards were returned immediately to the laboratory at the University of California, Irvine, and housed in glass terraria with incandescent lamps on 12L:12D permitting behavioral thermoregulation. Water was always available, and crickets were provided periodically. All individuals appeared to remain in good health during the experiments.

All whole-animal measures were made at 40°C, near the mean or modal field body temperature of *C. tigris*, *C. draconoides*, and *G. wislizenii* (Medica, 1967; Pianka, 1970; Asplund, 1974; Muth, 1977; Anderson and Karasov, 1981; Crowley and Pietruszka, 1983). Two measures of locomotor performance were recorded. Maximal distance run was recorded by chasing individuals continually and at top speed around a circular track until exhaustion (Garland, 1984). Individuals were tested on each of two days; higher performances were analyzed. Endurance capacity was measured as the length of time individuals could maintain a constant speed on a motorized treadmill (see Garland, 1984). Initial endurance trials were conducted at 1.0 km/h, a speed that exhausts most lizards within minutes or at least within an hour (e.g., Garland, 1984; John-Alder, 1984; John-Alder *et al.*, 1986; Garland and Else, 1987). However, this speed failed to exhaust adult *C. tigris*, so all individuals were tested at a tread speed of 1.5 km/h on a 20% incline (rise/run).

Maximal rates of oxygen consumption ($\dot{V}O_{2max}$) were obtained from animals fitted with light-weight, transparent plastic masks (upstream from oxygen and carbon dioxide analyzers) as they ran on the treadmill through a stepped series of increasing speeds (Garland, 1984; John-Alder, 1984). Maximal oxygen consumption was judged to have been obtained when further increases in tread speed produced no further increases in $\dot{V}O_2$. A continual record of % oxygen was made on a strip chart recorder; the highest stable segment of at least two minutes in length was analyzed by planimetry (Garland, 1984). Each individual was tested on two days; higher values are reported as $\dot{V}O_{2max}$.

Maximal aerobic speeds (MAS = speed at which $\dot{V}O_{2max}$ is attained) were estimated by noting the lowest treadmill speed above which $\dot{V}O_2$ did not increase. The higher speed from the two trials is reported as MAS. Because *C. draconoides* and *G. wislizenii* generally would not maintain even, constant paces at various speeds while wearing a mask, MASs could not be determined.

Standard rates of oxygen consumption (SMR) were recorded as animals (fasted 2 days) rested overnight (> 12 h), in the dark, in flow-through metabolism chambers (details in Garland, 1984).

Animals were sacrificed by decapitation, and hematocrit (Hct) and hemoglobin (Hb) content of the blood were determined in duplicate from blood samples taken from the severed neck (Garland, 1984). Whole hearts, livers (minus contents of gall bladder), and the entire mass of right thigh muscle were dissected free and weighed.

All data (except MAS, Hct, and Hb) were log-transformed before statistical analysis. This procedure helped to achieve homogeneity of

variances (e.g., Fig. 2) and/or linearity on log-log plots (e.g., Fig. 4) versus body mass. Reported means are antilogs of means of logs.

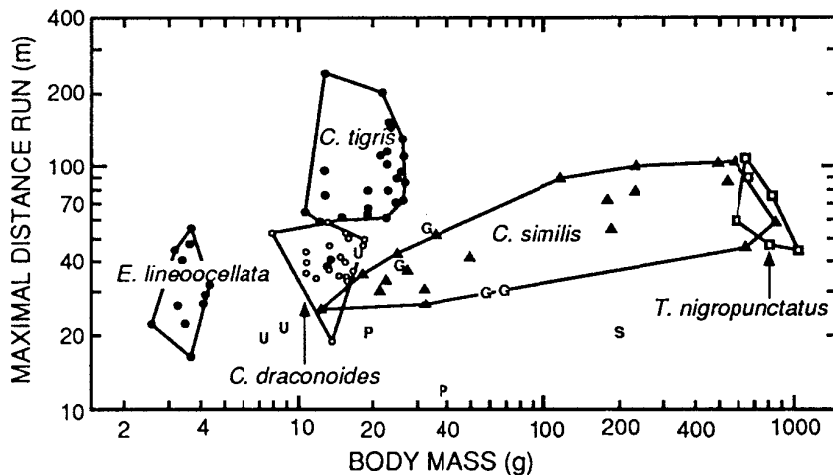


FIGURE 2. Maximal distances run around a circular track when chased to exhaustion for 10 species of lizards: *Callisaurus draconoides*, *Cnemidophorus tigris*, *Ctenosaura similis*, *Eremias lineoocellata*, four *Gambelia wislizenii* ("G"), one *Phrynosoma coronatum* ("P"), one *Phrynosoma platyrhinos* ("P"), one *Sauromalus obesus* ("S"), *Tupinambis nigropunctatus*, three *Uma inornata* ("U").

Results

The average distance running ability of *C. tigris* is higher than that of any species yet tested, including the much larger teiid *Tupinambis nigropunctatus* (Fig. 2). When chased continually around the circular track, *C. tigris* ran an average of 93 m (Fig. 2; $n=24$, range = 58 to 239 m). These trials lasted an average of 3.63 min ($n=23$, range = 1.75 to 18.3 min). Distance running abilities of other species, including *C. murinus*, reported by other workers using slightly different methods, are also less than those reported here for *C. tigris* (Bennett, 1980; Huey *et al.*, 1984).

Treadmill endurance capacities of *C. tigris* are also high. Preliminary tests indicated that adult *C. tigris* could maintain a speed of 1.0 km/h indefinitely, *i.e.*, for one or two hours or more. Subsets of individual *C. tigris* were tested at higher tread speeds: several individuals could maintain 1.5 or 2.0 km/h for more than one hour, and one individual maintained 1.5 km/h for 2 hours and 34 min. Finally, all individuals were tested twice each at 1.5 km/h with the treadmill inclined 20%. Endurance times at this

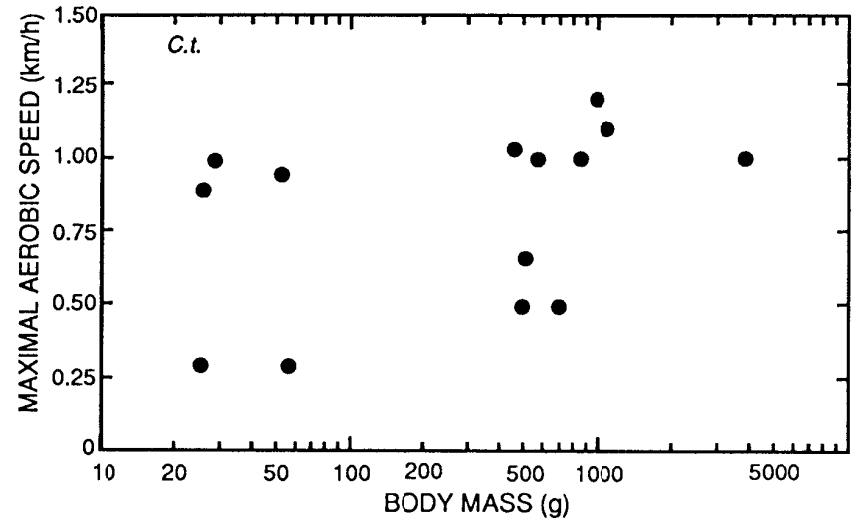


FIGURE 3. Maximal aerobic speeds of 15 species of lizards. The regression of maximal aerobic speed on log 10 body mass is not significant either for all 15 species ($r^2 = 0.019$, $P > 0.50$) or for 14 species, excluding *C. tigris* ($r^2 = 0.139$, $P > 0.10$). Sources of data are as follows: *Ameiva festiva*, 25 g, 0.9 km/h (B. A. Adams, pers. comm.); *Amblyrhynchus cristatus*, 580 g juvenile, 1.0 km/h (Gleeson, 1979); *Amphibolurus nuchalis*, 28 g, 1.0 km/h (Garland and Else, 1987); *Cnemidophorus murinus*, 55.2 g, 0.3 km/h (Bennett and Gleeson, 1979); *Cnemidophorus tigris*, 21.8 g, 1.46 km/h (this study); *Conolophus subcristatus*, 3,885 g, 1.0 km/h (Gleeson, 1979); *Dipsosaurus dorsalis*, 51.3 g, 0.96 km/h (John-Alder and Bennett, 1981); *Gerrhonotus multicarinatus*, 25 g, 0.3 km/h (John-Alder, unpublished, cited in Bennett, 1983); *Heloderma suspectum*, 464 g, 1.03 km/h (John-Alder *et al.*, 1983); *Iguana iguana*, 709 g, 0.5 km/h (Gleeson *et al.*, 1980); *Trachydosaurus rugosus*, 526 g, 0.67 km/h (John-Alder *et al.*, 1986); *Tupinambis nigropunctatus*, 865 g, 1.0 km/h (Bennett and John-Alder, 1984); *Uromastix aegyptius*, 1,103 g, 1.1 km/h (Dmit'el and Rapoport, 1976); *Varanus exanthematicus*, 1,025 g, 1.2 km/h (Gleeson *et al.*, 1980); *Varanus salvator*, 505 g, 0.5 km/h (Gleeson, 1981).

workload ranged from 7.3 to 69 min ($n=23$, $\bar{x} = 23$ min). An approximately 10-fold range of individual variation in treadmill endurance is common for lizards (Garland, 1984, unpublished; John-Alder, 1984; Garland and Else, 1987).

Callisaurus maintained a treadmill speed of 1.0 km/h for an average of only 7.1 min ($n=20$, range = 3.4-18.3 min). *Gambelia* were generally uncooperative on the treadmill, often turning to bite; the best individual that ran to apparent exhaustion maintained 1.0 km/h for 53 min. Most other species of lizards I have tested exhaust within minutes at this speed (Car-

land, 1984, unpublished; John-Alder *et al.*, 1986; but see Bickler and Anderson, 1986; Garland and Else, 1987). Even *T. nigropunctatus* exhausts within about 5-30 min or more at 1.0 km/h (Bennett and John-Alder, 1984); however, the *Tupinambis* measured were captive animals that may have experienced a decrease in activity capacity (Bennett and John-Alder, 1984; but see Gleeson, 1979; Taigen *et al.*, 1992; Garland *et al.*, 1987). *Cnemidophorus murinus* exhausts in less than 5 min at only 0.5 km/h (Bennett and Gleeson, 1979). *Ameiva festiva* also appears to have lower endurance capacities than does *C. tigris* (van Berkum *et al.*, 1986 and R. B. Huey, pers. comm.).

Estimated maximal aerobic speeds of *C. tigris* averaged 1.46 ± 0.347 km/h (\pm SD, $n = 21$, range = 0.9 to 2.3 km/h; 95% confidence interval = 1.30 - 1.62), which is higher than for any lizard yet tested, including three teiids (Fig. 3). Maximal rates of oxygen consumption averaged 86.2 ml O_2/h ($n = 20$, \bar{x} body mass = 22.5 g), also significantly higher than for any lizard yet measured at 40°C (Fig. 4; but see Bickler and Anderson, 1986). Analysis of covariance comparing *C. tigris* with *A. nuchalis* ($n = 57$, Garland and Else, 1987), *C. draconoides* ($n = 17$, this study), *C. similis* ($n = 18$, Garland, 1984), and *A. festiva* ($n = 8$, van Berkum *et al.*, 1986 and B. A. Adams, pers. comm.) indicated no significant heterogeneity in slopes among species, but significant differences in elevation, with *C. tigris* being significantly higher than any other species ($P < 0.001$). *Dipsosaurus dorsalis* and *C. murinus* were not included in the ANCOVA because original data were unavailable and *G. wislizenii* was excluded because $n = 3$, but these species clearly have a lower $\dot{V}O_{2max}$ than does *C. tigris* (Fig. 4).

Standard metabolic rates (Fig. 5) averaged 6.29 ml O_2/h ($n = 20$, \bar{x} body mass = 20.9 g). The SMR of *C. tigris* is higher than in the sympatric iguanians *C. draconoides* and *D. dorsalis*, higher than an Australian desert iguanian (*A. nuchalis*), and higher than the general allometric equation for lizards (Andrews and Pough, 1985). However, the SMR of *C. tigris* is not significantly different from that of sympatric leopard lizards or juvenile *C. similis*, a tropical iguanian (see Fig. 5).

Hematocrit and hemoglobin content of the blood of *C. tigris* fall in the upper 1/3 of the range of variation found among lizards (Fig. 6). Hematocrit (31.8%) is higher than reported for *Tupinambis nigropunctatus* (25%; Illastala *et al.*, 1985), the only other teiid for which data are available. However, *C. tigris* does not have a large heart for its size (Fig. 7). The thigh muscles of *C. tigris* are also not unusually large. Thigh muscle masses (in % body mass) for 20 g (unless otherwise noted) lizards are as follows: *Amphibolurus nuchalis*, 2.13% (Garland and Else, 1987); *Ctenosaura similis*, 2.49% (Garland, 1984); *Callisaurus draconoides*, 3.48%, *Gambelia wislizenii*, 3.00%, *C. tigris*, 2.59% (this study); *Cyclura nubila*, 3.03%

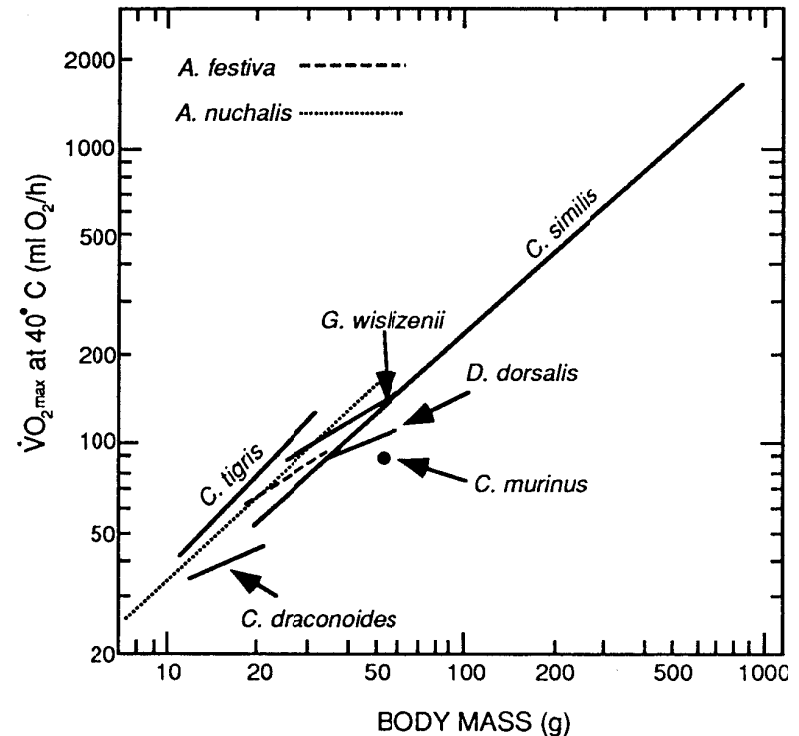


FIGURE 4. Maximal rates of oxygen consumption for eight species of lizards measured at 40°C. Lines represent intraspecific allometric equations where body mass and $\dot{V}O_{2max}$ ranges were available. Sources of data are as follows: *Ameiva festiva*, 24.1, 73.9 ml O_2/h (van Berkum *et al.*, 1986 and B. A. Adams, pers. comm.); I used highest $\dot{V}O_2$ for each individual at either 35, 38 or 40°C); *Amphibolurus nuchalis* (Garland and Else, 1987); *Callisaurus draconoides*, 17.2 g, 40.7 ml O_2/h (his study); *Cnemidophorus murinus* 55.2 g, 90.0 ml O_2/h (Bennett and Gleeson, 1979); *Cnemidophorus tigris*, 22.5 g, 86.2 ml O_2/h (this study); *Ctenosaura similis* (Garland, 1984); *Dipsosaurus dorsalis* (Bennett and Dawson, 1972; John-Alder and Bennett, 1981); *Gambelia wislizenii*, 38.4 g, 111.0 ml O_2/h (this study).

(1,176 g, K. A. Christian, pers. comm.); *Dipsosaurus dorsalis*, 2.44% (46.9 g, Garland, unpublished); *Sceloporus magister*, 2.57% (31.0 g adult, one individual, Garland, unpublished), *Varanus olivaceus*, 3.70% (2,031 g, Auffenberg, 1988). Finally, liver size of *C. tigris* is not outstanding. Liver masses (in % body mass) for 20 g lizards are as follows: *Amphibolurus nuchalis*, 2.53% (Garland and Else, 1987); *Amphibolurus vitticeps*, 2.55% for 298 g animals (P. L. Else, pers. comm.); *Anolis carolinensis*, 1.8-3.9% for 1-8.5 g animals Dessauer, 1955); *C. draconoides*, 1.02% (this study);

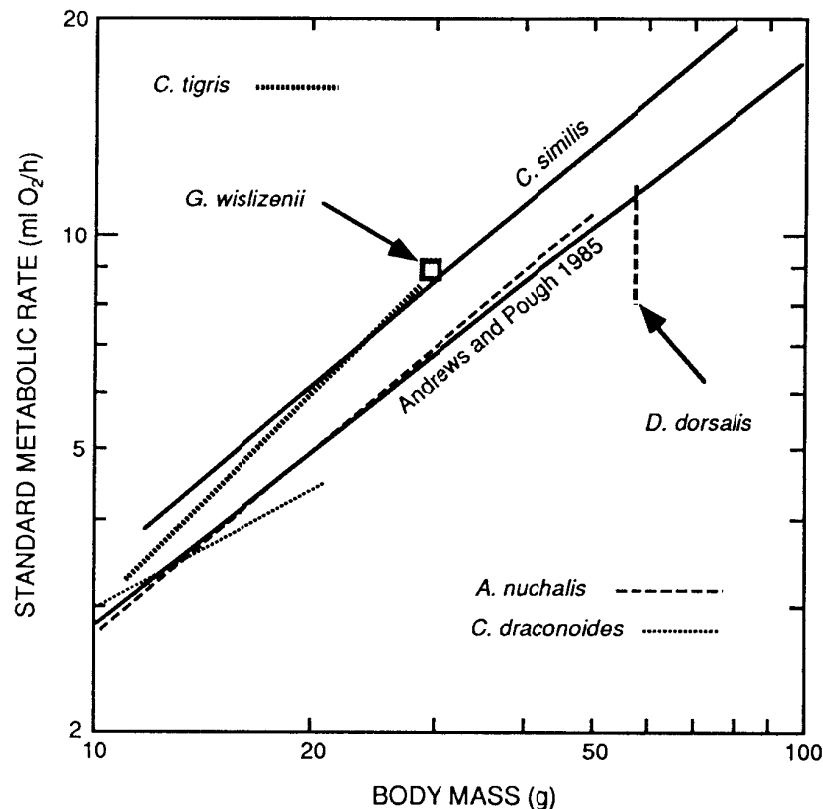


FIGURE 5. Standard rates of oxygen consumption of lizards at 40°C. Lines represent intraspecific allometric equations where ranges of body mass and SMR were available. Andrews and Pough (1985) is for all lizards under standard conditions at 40°C. Sources of data are as follows: *Amphibolurus nuchalis* (Garland and Else, 1987); *Callisaurus draconoides*, 17.2 g, 3.98 ml O₂/h (this study); *Cnemidophorus tigris*, 20.9 g, 6.29 ml O₂/h (this study); *Ctenosaura similis* (Garland, 1984); *Dipsosaurus dorsalis* (John-Alder, 1983, 1984); *Cambelia wislizenii*, 29.6 g, 8.91 ml O₂/h (this study).

Cnemidophorus sexlineatus, 2.51% for 5.5 g animals (Bracklin, 1978); *C. tigris*, 1.98% (this study); *Ctenosaura similis*, 2.21% (Garland, 1984); *Cyclura nubila*, 2.92% (1,176 g, K. A. Christian, pers. comm.); *Dipsosaurus dorsalis*, 1.54-1.77% for 56 g animals (John-Alder, 1984); *Egernia cunninghami*, 2-3% (all sizes, Barwick and Bryant, 1966); *G. wislizenii*, 1.58% (this study); *Hydrosaurus pustulosus*, 1.6% for ≈ 750 g animals (Auffenberg,

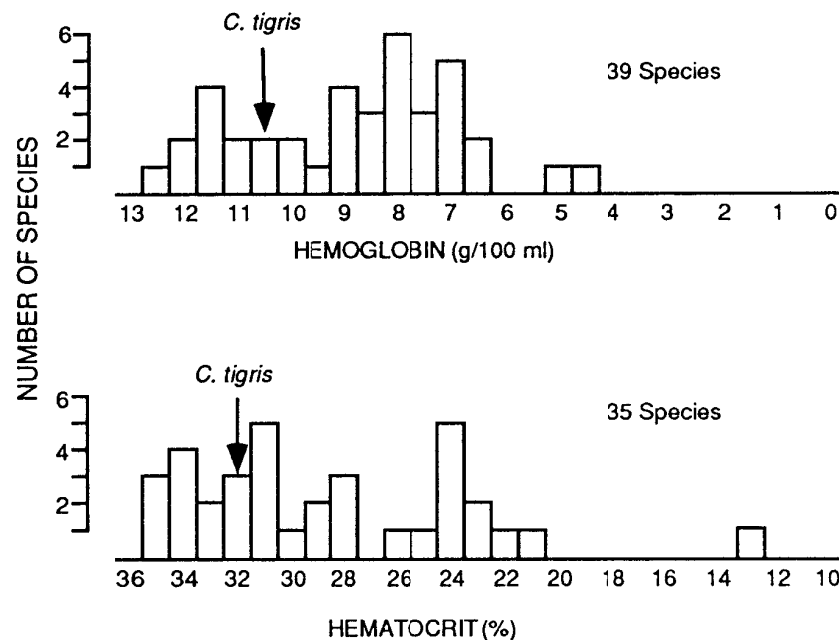


FIGURE 6. Histograms of hematocrit and hemoglobin content of lizard blood. Data are from Pough (1979, 1980) with the following additions; hematocrit in %, hemoglobin in g/100 ml of blood: *Amphibolurus nuchalis*, 20.7, 6.95 (Garland and Else, 1987); *Callisaurus draconoides*, 29.2, 10.86 (this study); *Cnemidophorus tigris*, 31.8, 10.69 (this study); *Ctenosaura similis*, 27.9, 7.06 (Garland, 1984); *Eremias lineoocellata*, 24.4, no data (Bennett *et al.*, 1984); *Eremias lugubris*, 30.1, no data (Bennett *et al.*, 1984); *Cambelia wislizenii*, 23.3, 9.83 (this study); *Sceloporus occidentalis*, 32.3, 7.3 (Schall *et al.*, 1982; I used overall literature mean values of 34.1 and 8.7 for this species); *Tupinambis nigropunctatus*, 25, no data (Hlastala *et al.*, 1985); *Uta stansburiana*, 3 4.7, 10.28 (Hadley and Burns, 1968); *Varanus exanthematicus*, 31, no data (Gleeson *et al.*, 1980). *Agama agama* (not included in histograms) also have higher hematocrits and hemoglobin levels than do *C. tigris* (J. J. Schall, pers. comm.).

1988); *Sceloporus jarrovi*, 1.35-4.1% for 7-30 g animal (Goldberg, 1972); *Sceloporus magister*, 0.95% for one 31 g animal (Garland, unpublished); *Sceloporus occidentalis*, 3.06% (Garland, unpublished); *Takydromus tachydromoides* (see Telford, 1970); *Varanus olivaceus*, 1.89% (see Auffenberg, 1988, p. 58); *Varanus salvator*, 2.64% (see Auffenberg, 1988, p. 58).

Relative hindlimb lengths (Pianka and Parker, 1972) and hindlimb spans ($152 \pm 1.6\%$ of snout-vent length, $\bar{x} \pm \text{SEM}$, Garland, unpublished)

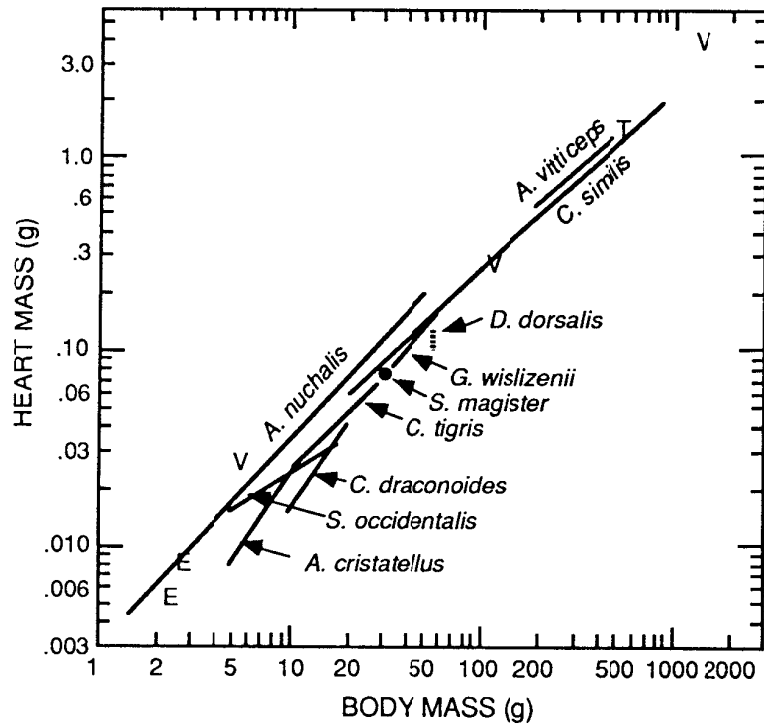


FIGURE 7. Log-log plot of heart mass versus body mass for lizards (cf. Seymour, 1987). Lines represent intraspecific allometric equations where body mass and heart mass ranges were available. Sources of data are as follows (mean body mass in g, mean heart mass in g): *Amphibolurus nuchalis*, 9.71, 0.0330 (Garland and Else, 1987); *Amphibolurus vitticeps*, 298, 0.833 (P. L. Else, pers. comm.); *Anolis cristatellus*, 7.84, 0.0141 (Garland, unpubl.); *Callisaurus draconoides*, 14.31, 0.0275 (this study); *Cnemidophorus tigris*, 20.43, 0.0496 (this study); *Dipsosaurus dorsalis*, 56, 0.104-0.125 (seasonal variation, John-Alder, 1984); *Eremias lineocellata*, 2.29, 0.0052 (Bennett *et al.*, 1984, "E"); *Eremias lugubris*, 2.76, 0.0077 (Bennett *et al.*, 1984, "E"); *Gambelia wislizenii*, 38.35, 0.0967 (this study); *Sceloporus magister*, 31.0, 0.0765 (one individual, Garland, unpublished); *Sceloporus occidentalis*, 10.04, 0.0228 (Garland, unpublished); *Trachydosaurus rugosus*, 508, 1.429 (John-Alder and Garland, unpublished, "T"); *Varanus gilleni*, 5.54, 0.0266, *Varanus mertensi*, 1320, 3.98, *Varanus tristis*, 114, 0.288 (John-Alder and Garland, unpublished, one individual of each species, "V").

of *C. tigris* are also unexceptional for lizards (cf. Garland, 1984, 1985; John-Alder *et al.*, 1986).

Discussion

Endurance capacities of *C. tigris*, as measured in the laboratory, are high in comparison with other lizards (Fig. 2), including three other teiids. I therefore conclude that *C. tigris* does in fact possess an exceptional endurance capacity, which is not always characteristic of its clade. It should be remembered, however, that in comparison with the total number of extant lizard species, the available data base is very limited! Clearly, data on other arid habitat *Cnemidophorus* are needed. Maximal sprint speeds of *C. tigris* are probably higher than average for lizards in general (compared with > 100 lizard species for which data are available; Garland, unpublished), but probably are not as exceptional as their endurance capacities.

The high endurance capacities of *C. tigris* are at least partly attributable to a high maximal rate of oxygen consumption. A high $\dot{V}O_{2max}$ leads to a high maximal aerobic speed, and hence a greater range of speeds that can be sustained aerobically. It would be of interest to determine whether *C. tigris* also has a low net cost of transport, which would contribute further to a high maximal aerobic speed (cf. John-Alder *et al.*, 1986).

Is there an obvious energetic cost associated with the high $\dot{V}O_{2max}$ of *C. tigris*? An affirmative answer to this question has been suggested by comparisons among species and among higher taxa of vertebrates, because such comparisons suggest a necessary correlation between standard and maximal metabolic rates (Bennett and Ruben, 1979; Taigen, 1983; Walton, *in press*). Standard rates of oxygen consumption of *C. tigris* are higher than average for lizards in general, but similar to those of some other lizards with lower endurance and $\dot{V}O_{2max}$ (cf. Figs. 4 and 5). Loumbourdis and Hailey (1985) report a positive correlation between resting and "active" rates of oxygen consumption among species of lizards; however, many of the values for "active" O_2 consumption clearly did not represent $\dot{V}O_{2max}$. Taigen (1983) reports a positive correlation between resting and "maximum" (but see Taigen and Wells, 1985) rates of oxygen consumption among 17 species of anuran amphibians, and Walton (*in press*) obtained a similar result. Consequently, I am currently gathering data to examine further the relationship between SMR and $\dot{V}O_{2max}$ in lizards. After removing correlations with body mass, individual differences in SMR and $\dot{V}O_{2max}$ are not significantly correlated within any of three species of lizards that have been tested (Garland, 1984; John-Alder, 1984; Garland and Else, 1987; see also Pough and Andrews, 1984). Moreover, acclimation studies of salamanders suggest no necessary relationship between standard and maximal rates of oxygen consumption (Feder, 1987).

Hematocrit and hemoglobin content of the blood of *C. tigris* are higher than average for lizards (Fig. 6), but perhaps not as high as might

have been predicted considering the high stamina and $\dot{V}O_{2\max}$ of *C. tigris*. Also somewhat surprising is the relatively small heart of *C. tigris*, as compared with some other species that have lower stamina and $\dot{V}O_{2\max}$ (Fig. 7). Relative thigh muscle and liver sizes of *C. tigris* are not unusual for lizards.

Any or all of the foregoing characters might be expected to be high in an animal with a high endurance capacity and $\dot{V}O_{2\max}$. Because this study is only correlational, demonstrating that a given character (e.g., hemoglobin content of the blood) is not exceptionally high does not establish that its role in determining the activity capacity of *C. tigris* is unimportant. Furthermore, most of the characters measured serve other functions in addition to their role in activity metabolism. For example, the liver does play a role in activity metabolism (see Garland, 1984), but because the liver also serves as a major detoxification center, liver size may be responsive to other selective factors, such as those related to dietary composition (see Jaksic *et al.*, 1979; Boxenbaum, 1980; Auffenberg, 1988). Furthermore, the liver is a major storage site for lipids and glycogen used during hibernation and for development of reproductive tissues, and may undergo dramatic seasonal variations in overall weight and composition (e.g., Des-sauer, 1955; Barwick and Bryant, 1966; Telford, 1970; Gaffney and Fitzpatrick, 1973), which are not necessarily related to its clearance function (*cf.* Regoczi and Chindemi, 1981). Hemoglobin and hematocrit (Pough, 1969) and standard metabolic rate (e.g., see Kamel and Gatten, 1983; Andrews and Pough, 1985; Hinds and MacMillen, 1985) may also be shaped by selective pressures unrelated to activity per se.

Finally, many characters of perhaps crucial importance in determining endurance capacity (e.g., maximal heart rate) are not considered herein. Data on tissue oxidative and glycolytic capacities of *C. tigris* will be presented elsewhere. Other factors that would be of particular interest to measure in *C. tigris* include anaerobic capacity (Bennett and Licht, 1982; Loumbourdis and Hailey, 1985) and blood (Bennett, 1973) and muscle (Castellini and Somero, 1981; Parkhouse *et al.*, 1985) buffering capacities.

The Adaptive Significance of Locomotor Performance

Is the high endurance capacity of *Cnemidophorus tigris* an adaptation for foraging widely? An affirmative answer to this question would require (at least) demonstrating that high endurance capacities are not merely a characteristic of *Cnemidophorus* or macroteiids in general, and hence not merely attributable to "phylogenetic inertia." I think this has been provisionally demonstrated. Further supporting evidence would include discovering that other, unrelated, active, widely-foraging animals also possess high endurance capacities. Finally, it must be demonstrated that

performance capacities in the laboratory coincide with what *C. tigris* are actually doing in the field during foraging.

Widely-foraging species with exceptional capacities for endurance and/or aerobic metabolism occur in several other taxa: the Gila monster (John-Alder *et al.*, 1983), varanid lizards (Bennett, 1972; Gleeson, 1981), lacertid lizards (Huey *et al.*, 1984), snakes (Ruben, 1983 and references therein), anuran amphibians (Putnam, 1979a, b; Taigen *et al.*, 1982; Taigen and Pough, 1983; Taigen and Beuchat, 1984; Pough and Kamel, 1984), canids (Weibel *et al.*, 1985). However, either low-level endurance capacity (e.g., on the treadmill) or maximal, short-term activity capacity, or both, have been correlated with activities other than foraging in both reptiles and amphibians; for example, mode of locomotion, defensive mechanisms, escape from predators, intraspecific or interspecific combat, subduing large prey, burrowing, calling (in anurans), and reproductive behavior (e.g., Tucker, 1967; Bennett, 1972, 1973, 1978, 1980, 1982, 1983; Regal, 1978, 1983; Gleeson, 1981; Bucher *et al.*, 1982; Taigen *et al.*, 1982; John-Alder *et al.*, 1983; Pough, 1983; Taigen and Pough, 1983; Hailey, 1984; John-Alder, 1984; Pough and Gatten, 1984; Wells and Taigen, 1984; Loumbourdis and Hailey, 1985; Pough and Andrews, 1985; Taigen and Wells, 1985; Bickler and Anderson, 1986).

Treadmill endurance capacities and the maximal aerobic speed of *C. tigris* appear to exceed what is required for average rates of travel (Appendix I). However, although the overall average rate of movement while foraging (*i.e.*, mean velocity) is only about 0.1 to 0.3 km/h, walking speeds between bushes may exceed 1.0 km/h (Appendix I). Foraging behaviors of *Ameiva festiva* (van Berkum *et al.*, 1986; Garland, pers. observation; and see Hirth, 1963 for *A. quadrilineata*) and *C. murinus* (Bennett and Gorman, 1979; Bennett and Gleeson, 1979), species with lower stamina than *C. tigris*, appear generally to be less strenuous than in *C. tigris* (Milstead, 1957a, b; Echternacht, 1967; Scudday and Dixon, 1973; Case, 1979; Garland, pers. observation).

Although *C. tigris* do not generally pursue their prey, they occasionally do so and may jump to heights of 18 inches in an attempt to capture insects (Milstead, 1957b, p. 110; Echternacht, 1967). Scudday and Dixon (1973, p. 281) report that "...one *C. inornatus* took 17 minutes to capture, subdue and swallow a large grasshopper nymph." Such activities may well be associated with some anaerobic metabolism (*cf.* Pough and Andrews, 1985). Whiptails, including *C. tigris* (Scudday and Dixon, 1973, p. 285; Anderson, this volume) dig a considerable amount during foraging (e.g., Milstead, 1957; Scudday and Dixon, 1973; Case, 1979). The energetic cost of digging has not been measured in lizards, but burrowing can be quite costly in toads (Seymour, 1973) and gophers (Vleck, 1979). Conceivably, digging

could lead to fatigue in animals of limited endurance capacity. *Cnemidophorus tigris* dig also to construct burrows, to lay eggs, and sometimes while searching for mates (T. J. Case, pers. comm.; R. A. Anderson, pers. comm.).

The foregoing suggests that exceptional endurance capacities may in fact play a permissive role in the foraging behavior of *C. tigris*. Moreover, periodic decreases in food abundance, either seasonally or year-to-year (e.g., during droughts, Boag and Grant, 1981), might force *C. tigris* to move at even higher speeds and/or over longer distances than typically observed (Appendix 1; but see Pietruszka, 1986).

However, several other activities in which *C. tigris* engages may also require high endurance capacities. For example, searching for and finding mates can be a major component of reproductive success, as can persistence in courtship leading to copulation (e.g., Wade and Arnold, 1980, p. 449). Case (1979, p. 249) noted that "persistent male (*C. tigris*) will follow specific females for hours" (see also Kennedy, 1968, p. 94), and males may pursue females at speeds "more rapid than the usual foraging speed" (Milstead, 1957b, p. 118; R. A. Anderson, pers. comm.; see also Fitch, 1958, for *C. sexlineatus*). Interestingly, Ruby (1981) found that the single best predictor of reproductive success in *Sceloporus jarrovi* was an index of activity, and Bracklin (1978) notes that a positive relationship between dominance and activity levels has been reported in a number of vertebrates (cf. Garland *et al.*, 1990).

Many lizards engage in intense territorial battles, especially during the reproductive season. Success in these battles may depend on overall body size, strength, and/or stamina, and losers may be killed (Auffenberg, 1981). With regard to the importance of stamina, Fitch (1940) reports fights lasting 45 min in fence lizards. In Galapagos land iguanas, Christian and Tracy (1982) report fights lasting > 4 h (*Conolophus pallidus*) and, amazingly, Werner (1982, p. 353) reports that "in one case two males fought for up to eight hours per day on more than 40 days in a two month period" (*C. subcristatus*). Although *Cnemidophorus* are often noted for a "remarkable lack of overt aggressive interspecific (or intraspecific) interactions" (Case, 1979, p. 249; Parker, 1972), both inter- and intraspecific combat has been reported in several species (e.g., Fitch, 1958; Kennedy, 1968; Vitt, 1983a). In *C. tigris*, "intraspecific meetings... resulted in fast, furious chases which ended when the pursued out-distanced the pursuer" and "usually covered from 15 to 60 feet" (Milstead, 1957a, p. 430), and Echternacht (1967, p. 456) noted "violent chases and sometimes fighting." R. A. Anderson (pers. comm.) reports that intraspecific interactions may occur as often as once per hour, and may result in chases of 2-60 m. In *C. inornatus*, intraspecific meetings usually resulted in "brief wrestling matches which ended when

one participant lost the tip of its tail" (Milstead, 1957a, p. 429 as *C. perplexus*). Intraspecific chases of 5-10 m are reported for *Dipsosaurus dorsalis* (Krekorian, 1976) and of 15 m for *Egernia cunninghami* (Wilson and Lee, 1974). Interspecific chases between adult *Cnemidophorus* have been described as generally short (2-8 m, Case, 1979), but they may occur frequently (Barbault and Maury, 1981, p. 341). Bickler and Anderson (1986) and Beck (1988) suggest that male-combat behavior may require high aerobic capacity in *Varanus gilleni* and *Heloderma suspectum*, respectively.

The evolution of a particular foraging strategy may have important consequences for the type and frequency of predators encountered during foraging (Huey and Pianka, 1981; Vitt, 1983b). Hence, as a widely-foraging behavior evolves, selection would be expected also to favor the evolution of appropriate anti-predator behaviors and performance capacities (cf. Vitt and Price, 1982). Maximal (sprint) speeds are important for predator avoidance in many lizards (e.g., Hardy, 1962; Hirth, 1963; Kennedy, 1968; Tanner and Krogh, 1974; Schall and Pianka, 1980; Vitt and Price, 1982), but stamina may also be important. Relatively prolonged chases of lizards by predators have rarely been reported, and such maximal exertion exhausts lizards within a few minutes (Bennett and Licht, 1972; Bennett, 1980; Huey *et al.*, 1984; Garland, 1984; this study). Nevertheless, some species — and *C. tigris* in particular (Fig. 2) — can run for considerable distances before exhausting. Several known predators of *C. tigris*, e.g., roadrunners, racers, whipsnakes (Pianka, 1970; Schall and Pianka, 1980; H. W. Greene, pers. comm.), may on occasion chase whiptails for many meters. Although it has never been quantified with "natural" predators, some *C. tigris* do run considerable distances when approached and/or chased by humans (Schall and Pianka, 1980). Roadrunners may chase desert iguanas for many meters (H. B. John-Alder, pers. comm.) and van Berkum *et al.* (1986) report a small *A. festiva* sprinting > 6 m before being captured by a snake. I have witnessed a colubrid snake chase a juvenile *Ctenosaura similis* for > 10 m. Juvenile *C. similis* are rarely found more than a few meters from cover (Garland, unpublished), which seems consistent with their limited stamina (Fig. 2 and Garland, 1984).

In summary, a variety of activities other than foraging may require some aspect of endurance capacity. Moreover, it may be rare events, rather than routine activities, through which natural selection has acted to shape the locomotor capacities of some animals (cf. Van Berkum *et al.*, 1986). Consequently, the primary adaptive significance of the high endurance capacity of *C. tigris* is unclear.

Balancing Field Behavior and Performance Capacities

A general unresolved issue is the strategy employed by animals in nature with regard to balancing their physical activities with their locomotor capacities (Hertz *et al.*, 1988; Pough *et al.*, 1992). For example, do animals normally limit the intensity and duration of their activities so as to avoid exceeding their anaerobic threshold and hence accumulating an oxygen debt (Regal, 1978, 1983; Gatten, 1985; Taigen and Beuchat, 1985; Marken and Lichtenbelt, 1991, p. 120)? Or do they just try to avoid fatigue and exhaustion *per se*? Alternatively, animals might routinely engage in activities that exceed their anaerobic threshold, or even the workload at which they attain $\text{VO}_{2\text{max}}$, resulting in exhaustion which forces the animal to stop and rest. Presumably, an animal so incapacitated by exhaustion would face an enhanced risk of predation, unless it compensated behaviorally by seeking a safe retreat in which to recover. Exhaustive activity may also impair subsequent performance by reducing glycogen stores, as suggested by Gleeson (1985) and Pough and Andrews (1985).

Examples compiled by Taigen and Beuchat (1985) suggest that vertebrates generally avoid exceeding their anaerobic threshold. Such is not always the case, however. For example, Galapagos marine iguanas "are occasionally exhausted by the strenuous swimming required to get through the heavy surge ... and can be seen drifting almost helpless in the wave currents" (Bartholomew *et al.*, 1976, p. 719). Furthermore, recent studies have found that both lizards (Pough and Andrews, 1985) and anuran amphibians (Pough and Gatten, 1984) may use anaerobic metabolism more commonly than previously thought (Gatten, 1985; Pough *et al.*, 1992).

Maximal aerobic speeds average about 20-fold slower than burst speeds in lizards (Garland, 1982), and comparisons of data presented in Figure 3 and Appendix I indicate that *A. festiva*, *A. cristatus*, *C. murinus*, *C. tigris*, and *T. rugosus* all typically walk at speeds below their maximal aerobic speeds. However, at certain times, as when searching for or pursuing mates (R. A. Anderson, pers. comm.), *C. tigris* may sustain speeds that exceed the anaerobic threshold, and hence would lead eventually to exhaustion. It should also be noted that the "endurance capacity" of a whiptail moving in nature, at widely varying velocities, with periodic rests, and over various surfaces, may be quite different from its capacity to run on a treadmill at a single speed (*cf.* Marken and Lichtenbelt, 1991, p. 121). Such comparisons of treadmill endurance with field behavior are especially problematical for some species. For example, *A. nuchalis* and *D. dorsalis* often run quickly across open spaces between bushes, exceeding their maximal aerobic speeds, but move at much slower speeds while

beneath bushes (*cf.* Werner, 1983, on land iguanas walking to nesting areas).

The Evolution of Locomotor Performance and its Functional Correlates

The results of the present study and others discussed in the Introduction (*e.g.*, Bennett, 1983; Bennett *et al.*, 1984) indicate that exceptional capacities for locomotor performance are generally reflected in high capacities of one or more, but not all, components that should affect performance. Apparently, the evolution of enhanced locomotor performance can occur by augmentation of capacities at any of several levels of biological organization, but does not necessarily require that capacities of all components be enhanced. This implies that in a given (ancestral) species, at a given point in evolutionary time, capacities of some components may have been in excess of what is used during maximal locomotor exertion (*cf.* Withers and Hillman, 1983; Hillman and Withers, 1985). Put another way, there may be "weak links" within the chain of components that potentially are limiting to performance. Such a view is contrary to the expectations of "symmorphosis ... a state of structural design commensurate to functional needs resulting from regulated morphogenesis, whereby the formation of structural elements is regulated to satisfy but not exceed the requirements of the functional system" (Taylor and Weibel, 1991, p. 3; Weibel *et al.*, 1991; for a contrasting view see Hillman and Withers, 1985; Withers and Hillman, 1988). Instead, capacities of one or more elements in the overall functional system of activity metabolism may exceed the energetic (and other) requirements of maximal locomotor performance, at various times during the evolution of a clade (Garland and Huey, 1987). (These conclusions assume that "noise" introduced by comparing data from different studies has not obscured real correspondence among functional capacities.) In addition, components or links that appear to have excessive capacity or construction (Gans, 1979) for one function may actually be used in (adapted for) some other functional context as well, in which their capacity is not excessive (see also Dudley and Gans, 1991).

Concluding Remarks

Endurance capacities may be important in a variety of natural activities (*cf.* Pough *et al.*, 1992). The relative importance of these different activities in selecting for the evolution of a high endurance capacity in *Cnemidophorus tigris* is unclear. Quantitative data on natural behaviors are required. How often and during what activities are the endurance capacities of *C. tigris* (or any other animal) actually put to the selective test (van Berkum *et al.*, 1986; Hertz *et al.*, 1988)? How often is behavior actually constrained by physiological capacities (Wells and Taigen, 1984)? What are the strongest ecological or behavioral correlates of interspecific variation in locomotor performance? Does interpopulation variation in, for example,

anti-predator behaviors (Schall and Pianka, 1980 for *C. tigris*) or home range size (e.g., Schoener and Schoener, 1982) predict variation in speed or stamina (cf. Garland and Adolf, 1991; Sinervo and Losos, 1991)? Can individual differences in laboratory performance abilities be found to correlate with components of individual fitness (Walton, 1988; Garland *et al.*, 1990)? The time seems ripe for studies that quantify field behaviors with the purpose of elucidating the adaptive significance of performance capacities as measured in the laboratory (cf. Garland and Losos, *in press*).

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APPENDIX I: Average rates of movement (mean velocity) and walking speeds (velocity moving) of lizards in nature (see text for further explanations).

Species	Mean Velocity (km/h)	Velocity Moving (km/h)	Length of Observation	Reference
Sit-and-Wait Foragers				
IGUANIA				
<i>Anolis aeneus</i>	.0013	---	>1 h	Magnusson <i>et al.</i> , 1985
<i>Anolis bonariensis</i>	.0078	.0234	20 min	Bennett and Corman, 1979
<i>Anolis coelestinus</i>	.0032	---	"varying length of time"	Moermond, 1979
<i>Anolis cybotes</i>	.0029	---	"	"
<i>Anolis distichus</i>	.0055	---	"	"
<i>Anolis hendersoni</i>	.0026	---	"	"
<i>Anolis koopmani</i>	.0019	---	"	"
<i>Anolis menticola</i>	.0012	---	"	"
<i>Anolis semilineatus</i>	.0018	---	"	"
<i>Callisaurus draconoides</i>	.0392 males .0108 females	---	15-30 min	Anderson and Karasov, 1981
<i>Ctenosaura similis</i> (juveniles)	.00671	.269	> 5 min \bar{x} = 21 min	Garland, unpublished
<i>Phrynosoma cornutum</i>	.0085	---	all day	Whitford and Bryant, 1979
<i>Sceloporus occidentalis</i>	.006-.009	---	\bar{x} = 82 min	C. A. Boot and S. Rubenstein, pers. comm.
<i>Sceloporus jarrovi</i>	.0055 males .0027 females	---	≥ 1 h	Ruby, 1978
<i>Sceloporus virgatus</i>	.0054	---	30 min	Pough and Andrews, 1985
<i>Uta stansburiana</i>	.0233 males .0100 females	---	minutes to hours	Irwin, 1965
<i>Cnemidophorus hyperythrus</i>	---	.14	.5-3 min	Casc, 1979

† Huey and Pianka (1981) categorize these two species as sit-and-wait foragers, in comparison with other, sympatric lacertids. Note, however, that their movement rates are perhaps more similar to mem-

APPENDIX I. (cont.)

Species	Mean Velocity (km/h)	Velocity Moving (km/h)	Length of Observation	Reference
"	.0209 males .0160 females	---	> 30 min	Bound, 1977
LACERTIDAE				
<i>Eremias lineoocellata</i> †	.074	.477	\bar{x} = 10 min	Huey and Pianka, 1981
<i>Meroles suborbitalis</i> †	.061	.461	\bar{x} = 8.2 min	"
Widely-Foraging Species				
HELODERMATIDAE				
<i>Heloderma horridum</i>	.3	.45	extended	D. Beck, pers. comm.
<i>Heloderma suspectum</i>	.107; .24	.35	3 h; extended	Heath, 1961; D. Beck, pers. comm.
IGUANIA				
<i>Gambelia silus</i> *	.0694	---	all day	Tollestrup, 1979
<i>Gambelia wislizenii</i> *	.0629	---	all day	Tollestrup, 1979
LACERTIDAE				
<i>Eremias lugubris</i>	.315	.561	\bar{x} = 4.8 min	Huey and Pianka, 1981
<i>Eremias namaquensis</i>	.282	.488	\bar{x} = 5.3 min	"
<i>Ichnotropis squamulosa</i>	.192	.378	\bar{x} = 4.2 min	"
<i>Nucras tessellata</i>	.378	.719	\bar{x} = 5.4 min	"
<i>Nucras intertexta</i>	.536	---	\bar{x} = 3.0 min	Pianka <i>et al.</i> , 1979
TEIIDAE				
<i>Ameiva ameiva</i>	.0726	---	> 1 h	Magnusson <i>et al.</i> , 1985
<i>Ameiva festiva</i>	---	.16 (up to 0.65)	minutes	van Berkum <i>et al.</i> , 1986

bers of other families that are classified as widely-foraging.

APPENDIX I (cont.)

Species	Mean Velocity (km/h)	Velocity Moving (km/h)	Length of Observation	Reference
<i>Varanus rosenbergi</i>	---	.38-1.57 \bar{x} = .812	<1 min	Garland and John-Alder, unpublished
<i>Varanus varius</i>	.297-.579 \bar{x} = .475	---	1-4 h	Stebbins and Barwick, 1968
Herbivores or Omnivores				
IGUANIA				
<i>Amblyrhynchus cristatus</i>	---	.78-1.0	20 min	Gleeson, 1979
<i>Conolophus subcristatus</i>	.3	<2-3 over <20 m	all day	Werner, 1983
<i>Dipsosaurus dorsalis</i>	.0163 6g juv. .0412 60g adult	---	all day \bar{x} = 230 min	Garland, unpublished
<i>Iguana iguana</i>	---	.51	all day	Marken Lichtenbelt, 1991
SCINCIDAE				
<i>Egernia cunninghami</i>	--	.18-.36	all day	Wilson and Lee, 1974
<i>Trachydosaurus rugosus</i>	---	.15-.72 \bar{x} = .369	<30 sec	Garland, unpublished
TEIIDAE				
<i>Cnemidophorus murinus</i>	.096	.125	10 min	Bennett and Gorman, 1979
"	---	.151 males. 066 females	15 min	Karasov and Anderson, 1984
<i>Cnemidophorus inornatus</i>	.022	---	\bar{x} = 113 min	Kay <i>et al.</i> , 1973
"	.146	---	?	Milstead, 1957

* Tollestrup (1979) considers both *Gambelia* species to be intermediate between sit-and-wait and widely foraging.

APPENDIX I (cont.)

Species	Mean Velocity (km/h)	Velocity Moving (km/h)	Length of Observation	Reference
<i>Cnemidophorus lemniscatus</i>	.0346	---	> 1 h	Magnusson <i>et al.</i> , 1985
<i>Cnemidophorus sacki</i>	.183	---	?	Milstead, 1957
<i>Cnemidophorus sexlineatus</i>	---	.226 juveniles .522 adults	?	M.A. Paulissen, pers.comm.
<i>Cnemidophorus tessellatus</i>	.183	---	?	Milstead, 1957
<i>Cnemidophorus tigris</i>	.192	.576-2.52 \bar{x} = .864-1.368 between bushes	\bar{x} = 30 min	Anderson, this volume
"		.022-.216 \bar{x} = .097 under bushes	\bar{x} = 30 min	Anderson, this volume
"	.180	---	15-30 min	Anderson and Karasov, 1981
"	---	.22	.5-3 min	Case, 1979
"	---	.56-1.45 \bar{x} = 1.17 between bushes	.60-3.0 min \bar{x} = 1.79 min	Garland, unpublished
"	.049	---	\bar{x} = 113 min	Kay <i>et al.</i> , 1973
"	.275	---	?	Milstead, 1957
<i>Kentropyx striatus</i>	.0102	---	>1 h	Magnusson <i>et al.</i> , 1985
VARANIDAE				
<i>Varanus komodoensis</i>	---	4.8	?	Auffenberg, 1981
<i>Varanus olivaceus</i>	---	.49-.77	?	Auffenberg, 1988

PLEASE NOTE

During the final production of this volume, the positions of some of the entries for individual species in APPENDIX I were transposed.

Bottom of page 207: *Cnemidophorus hyperythrus* should be listed as a "Widely-Foraging Species"

Top of page 208: the first entry represents a continuation of values for *Uta stansburiana*

Middle of page 208: The entry for *Heloderma suspectum* should also cite Beck (1990)

Bottom of page 209: The second entry under *Cnemidophorus murinus*, citing Karasov and Anderson (1984), actually should be the second entry under *Cnemidophorus hyperythrus*

Bottom of page 209: *Cnemidophorus inornatus* should be listed as a "Widely-Foraging Species"

Page 210: *Kentropyx* and all *Cnemidophorus* species except *Cnemidophorus murinus* should be listed under "Widely-Foraging Species"

Bottom of page 210: *Varanus komodoensis* should be listed under "Widely-Foraging Species." *Varanus olivaceus* is correctly listed as an "Herbivore or Omnivore"

Finally, Cuellar (this volume, page 369) provides information on movements of *C. tigris* that can yield an estimate of Daily Movement Distance that is consistent with the value given in my Figure 1 (page 171).