# LOCOMOTORY CAPACITIES, OXYGEN CONSUMPTION, AND THE COST OF LOCOMOTION OF THE SHINGLE-BACK LIZARD (TRACHYDOSAURUS RUGOSUS)[1]

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*Trachydosaurus rugosus* is a large, slow-moving Australian skink. The maximal sprint velocity of this species averages only 2.7 km/h and is apparently limited by short limbs that have relatively little muscle mass. Standard metabolic rate at 35 C is $0.073 \pm 0.009$ ml $O_2/(g \cdot h)$, and the maximal rate of $O_2$ consumption is $0.722 \pm 0.019$ ml $O_2/(g \cdot h)$. The maximal aerobic speed is 0.67 km/h, and endurance at 1.0 km/h is $23 \pm 7$ min. The net cost of locomotion ($C_N$) is 0.921 ml $O_2/(g \cdot km)$ (95% confidence limit [C.L.]: 1.133, 0.709). This value is tabulated together with all other data available for lizards, and a new allometric equation describing net cost of locomotion as a function of body mass is presented. For all lizards, $C_N$ (ml $O_2/(g \cdot km)$) = 4.22 (body mass, g)$^{-0.282}$. The locomotory and energetic capacities of *Trachydosaurus* describe an unusually slow lizard with limited stamina.

## INTRODUCTION

Lizards have relatively limited capacity for aerobic energetic support of activity compared to mammals (Bennett 1978, 1982; Bennett and Ruben 1979; Pough 1980). Consequently, these animals can generally sustain low levels of activity (John-Alder and Bennett 1981; Garland 1982; John-Alder, Lowe, and Bennett 1983). Nevertheless, lizards vary considerably in natural behavioral levels (Stamps

1977; Huey and Pianka 1981; Vitt and Price 1982; Garland 1985), in abilities to sustain activity (Garland 1982, 1985), and in physiological capacities to support activity (Bennett 1982). Several recent studies have demonstrated that interspecific differences in locomotory capacities are correlated with differences in underlying energetic support. For example, some widely foraging species of Kalahari lacertids have higher aerobic capacity, greater endurance, and lower sprint capacity than closely related sit-and-wait foragers (Bennett, Huey, and John-Alder 1984; Huey et al. 1984). Correlates of these behavioral and energetic limitations are obvious. Widely foraging lacertids may be too slow to be ambush predators, and sit-and-wait lacertids may not be effective at widely foraging (Huey et al. 1984).

The present study is an analysis of some aspects of the locomotory performance and the physiological basis of activity of *Trachydosaurus rugosus*. *Trachydosaurus* is a large, slow-moving skink distributed widely in the southern half of Australia. This lizard is the sole representative of its monotypic genus (Cogger 1983) and is easily recognized by its short, rounded tail and greatly enlarged, rugose dorsal scales (thus, the colloquial names: shingle-back, sleepy, or stumpy-tailed lizard). *Trachydosaurus* is a diurnal lizard with a moderately low preferred body temperature of 32–36 C (War-

burg 1965; Licht et al. 1966; Wilson 1974; Bennett and John-Alder 1986). In general appearance, *Trachydosaurus* is somewhat similar to the Gila monster, *Heloderma suspectum*, a distantly related lizard of North American deserts. Both species have robust bodies, short tails, and relatively short limbs, and adult body masses frequently exceed 500 g. We have previously reported that *Heloderma* has a relatively high aerobic capacity and a relatively low net cost of locomotion (John-Alder et al. 1983), two qualities that appear to be adaptive for this widely foraging, carnivorous species (Heath 1961; Jones 1983). *Trachydosaurus* is omnivorous, and its home range is only about 10% of that expected for a carnivorous lizard of similar size (Satrawaha and Bull 1981). Thus, despite its morphological similarity to *Heloderma*, *Trachydosaurus* might be expected on the basis of ecological observations to have a much more limited ability to sustain locomotion. We report here the performance of *Trachydosaurus* in sprint and sustainable locomotion together with an analysis of aerobic locomotory energetics for this species. We compare our results to those obtained previously for the Gila monster (John-Alder et al. 1983) and to limited data we have obtained on two other large Australian skinks (*Tiliqua scincoides* and *Egernia cunninghami*). In addition, we present a new allometric equation for the net cost of locomotion in lizards.

## MATERIAL AND METHODS

Lizards used for most aspects of this study were captured by hand during the austral spring in the vicinity of Wilmington, South Australia, under South Australian National Parks and Wildlife Permit 918 issued to A.F.B. Animals were transported to the laboratory at the University of Adelaide and then held on a natural photoperiod in cages equipped with high-wattage incandescent bulbs to permit daily behavioral thermoregulation. Some determinations of endurance and SMR were made by one of us (T.G.) in A. J. Hulbert's laboratory at the University of Wollongong. Animals used in Wollongong were collected under New South Wales National Parks and Wildlife Service Permit B185. Dog food and mixed fruits were provided twice

weekly, and water was available at all times. All animals maintained body mass and remained in good health throughout the study. All measurements were made at a body temperature of 35 C, which is within the normal activity range (Bennett and John-Alder 1986).

### LOCOMOTORY PERFORMANCE

Burst speeds of *Tiliqua scincoides* ($n = 6$; body mass = $438 \pm 26.2$ g [mean $\pm$ SEM]) and *Egernia cunninghami* ($n = 9$; $268 \pm 11.5$ g) were obtained on a photocell-timed racetrack as previously described (Huey et al. 1984; Garland 1985). Each individual was run a total of eight times over 2 days, and the single fastest 0.5-m interval for each individual was entered into the analysis.

*Trachydosaurus rugosus* consistently refused to run on the racetrack, choosing instead to turn and threaten the investigator with an open mouth and hissing sounds. We therefore obtained maximal running speeds of this species on a motorized treadmill. Eleven lizards with an average body mass of $432 \pm 27.6$ g were used for these measurements. The treadmill had a speed range of 0.1–3.6 km/h, and the top surface was 170 cm long and 40 cm wide. A radiant heater was suspended above the tread belt, and the entire treadmill was enclosed in a polyethylene tent open only to the investigator for the maintenance of desired thermal conditions. Body temperatures were adjusted to 35 C prior to measurements. Deep cloacal temperatures were measured before and after a running trial, and the average temperature was recorded. When maximal running velocity was to be measured, an animal was placed on the motionless tread belt, and its tail and hind limbs were tapped and squeezed to encourage the animal to begin walking. The velocity of the tread belt was then adjusted to match that of the walking lizard. The lizard's tail and hind limbs were repeatedly tapped and squeezed to encourage the lizard to walk progressively faster, and the treadmill was continually accelerated to match the velocity of the lizard. This procedure was continued until the lizard was no longer able to move faster than the tread velocity. The lizard was then removed, and the tread velocity was recorded as the maximal run-

ning velocity for that determination. Seven lizards were used for duplicate measurements on separate days to assess the reproducibility of measured velocities.

Locomotory endurance at 1.0 km/h was measured on six *T. rugosus* (542 ± 28.3 g), three *T. scinccides* (475 ± 41.4 g), and eight *E. cunninghami* (270 ± 11.6 g). Body temperatures were maintained as described previously. Endurance was measured as the length of time a lizard maintained station at 1.0 km/h on the treadmill with tapping and squeezing as encouragement (Garland 1984). Trials were terminated when an individual did not maintain station after 10 consecutive taps at ≤1-s intervals. Animals were usually exhausted at this point.

### METABOLISM AND LOCOMOTORY ENERGETICS

Standard metabolic rate (SMR) (Garland 1984; Andrews and Pough 1985) was measured during the austral summer. Standard metabolic rate was measured as the rate of $O_2$ consumption using a Taylor Servomex type OA-272 $O_2$ analyzer in an open-flow system as animals rested in a dark, temperature-regulated cabinet at 35 C. Dry air was metered through metabolic chambers at a flow rate of about 150 ml/min (STPD). Each animal's metabolic rate was measured for 8–10 min each hour from dusk until dawn, and the lowest reading was used to calculate SMR.

Rates of $O_2$ consumption and $CO_2$ production ($\dot{V}O_2$ and $\dot{V}CO_2$) during locomotory activity at 35 C were measured over a range of velocities on the treadmill at the University of Adelaide, using 14 lizards (474 ± 29.9 g). A lizard was removed from the temperature-regulated cabinet and was fitted with a lightweight, transparent plastic mask through which room air was drawn. An animal was encouraged to walk as above. When an even-paced locomotory velocity was attained, $\dot{V}O_2$ and $\dot{V}CO_2$ were measured for 10–30 min until a 5-min record of stable $O_2$ consumption had been obtained. Subsequently, the animal was encouraged to walk at a higher velocity for a second measurement. When these efforts were successful, gas exchange at the higher velocity was measured for 10 min. While most trials consisted of one walking velocity, as many as three velocities per trial were occasionally obtained. For measurements

of maximal rates of $O_2$ consumption ($\dot{V}O_2max$), lizards were encouraged to accelerate quickly to a high velocity, and gas exchange was measured at the highest attained velocity for 10 min or until exhaustion. Trials were rejected in the absence of a stable $\dot{V}O_2$ for >90 s. Measurements of gas exchange were made and analyzed as described previously (John-Alder and Bennett 1981; John-Alder et al. 1983). The rate of $O_2$ consumption was calculated using equation (3b) in Withers (1977), and $\dot{V}CO_2$ was calculated using equation (2) in Gleeson (1979*b*).

### MORPHOLOGY

Morphological measurements were made on animals sacrificed by a blow to the head in preparation for studies on contractile properties of limb skeletal musculature (John-Alder and Bennett, unpublished). Snout–vent length was measured to the nearest millimeter, and hind limb length was measured as the distance from the body wall to the end of the longest toe along the anterior surface of a leg extended at a right angle from the body (Pianka 1969). Hind limb span was measured on living animals as the length between toe tips (exclusive of claws) on limbs extended perpendicularly from the body (Garland 1984).

### STATISTICS

Statistical analyses were done using a Stat I statistics module for a Hewlett-Packard HP41-CX hand-held computer and STATPRO (Blue Lakes Computing).

### RESULTS

The average SMR for six individuals was 41.70 ± 5.20 ml $O_2$/h or 0.073 ± 0.009 ml $O_2$/(g · h). A value of 46.23 ml $O_2$/h is predicted by equation (1) in Andrews and Pough (1985). Skinks as a family tend to have somewhat lower SMRs than do other squamates (Andrews and Pough 1985), and adding the mean skink residual (−0.049) from table 2 in Andrews and Pough (1985) to their equation (1) yields a predicted SMR of 41.30 ml $O_2$/h. Thus, SMR of *Trachydosaurus* seems typical for skinks.

Rates of $O_2$ consumption during treadmill locomotion are reported in figure 1. These data are described by two equations derived through least-squares linear regres-
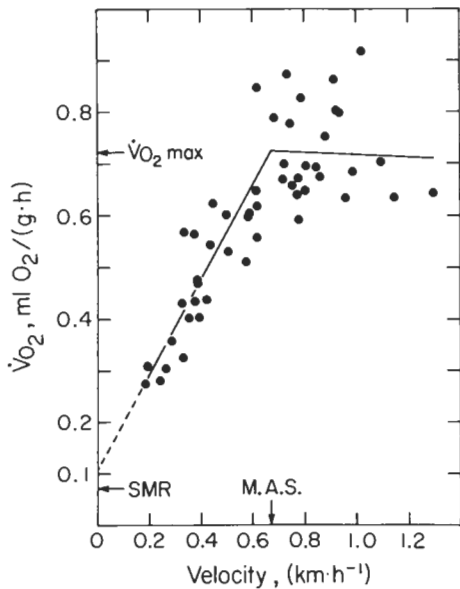
FIG. 1.—Rates of $O_2$ consumption as a function of walking velocity on a motorized treadmill. Maximal $\dot{V}O_2$, SMR, and MAS are indicated on the appropriate axes. See text for details of statistical analysis.

sion analysis as described by John-Alder and Bennett (1981). For the purpose of finding the two best-fitting equations (by the criterion of minimizing the sum of the residual sums of squares), the data were divided into two subsets at intervals of 0.05 km/h. The two best-fitting equations are:

$$\dot{V}O_2 = 0.107 + 0.921 \ (V),$$

$$V = \text{velocity} < 0.7 \text{ km/h}, \qquad (1)$$

$$n = 27 \text{ observations on 14 individuals};$$

$$r^2 = .762; \ P < .001,$$

and

$$\dot{V}O_2 = 0.746 - 0.027 \ (V),$$

$$V = \text{velocity} > 0.7 \text{ km/h}, \qquad (2)$$

$$n = 23 \text{ observations on 14 individuals};$$

$$r^2 = .002; \ P > .5.$$

The slope of equation (2) is not significantly different from zero ($P > .5$). Maximal $\dot{V}O_2$, estimated as the average of $\dot{V}O_2$'s attained at $V > 0.7$ km/h, is $0.722 \pm 0.019$ ml $O_2/$ $(g \cdot h)$ ($\bar{X} \pm 1$ SE). The net cost of locomotion (Schmidt-Nielsen 1972), given by the slope of $\dot{V}O_2$ on $V$ in equation (1), is

0.921 ml $O_2/(g \cdot km)$ (95% C.L.: 1.133, 0.709). The maximum aerobic speed (MAS), given by the intersection of equations (1) and (2) (John-Alder and Bennett 1981), is 0.67 km/h. Respiratory exchange ratios were significantly lower below than above MAS ($1.17 \pm 0.04$ vs. $1.44 \pm 0.05$; $P < .001$).

The average maximal running velocity for 11 individuals was 2.70 km/h (table 1). The average duration of a running trial was 3.21 min (range 1.50–6.65). Duration was not correlated with peak velocity ($r = .078$; $n = 11$; $P > .50$). Thus, peak velocity was not limited by stamina in a trial. Determinations of maximal running velocity on the treadmill were repeatable: the first and second measurements on seven individuals on 2 days were significantly correlated ($r = .870$; $P < .05$). The first and second measurements on individuals did not differ significantly (two-way ANOVA; $P > .5$). Sprint velocities of *Tiliqua scincoides* and *Eqernia cunninghami* are also reported in table 1.

Endurance of *T. rugosus* (mean = 23 min) was intermediate to that of *T. scincoides* (75 min) and *E. cunninghami* (7.0 min) (table 1). Endurance was not correlated with body mass in any species, but the range of body masses was small in all three.

The average snout–vent length of *T. rugosus* used for studies on muscle contractile properties (John-Alder and Bennett, unpublished) was $269 \pm 4.9$ mm ($n = 4$), and average hind limb length was $56.8 \pm 2.0$ mm. On average, hind limb length was 21.1% (range: 19.4%–23.1%) of snout–vent length. Hind limb spans of all three species are reported in table 1.

## DISCUSSION

The $\dot{V}O_2$max reported here for *Trachydosaurus rugosus* is in the lower 50% of all values that have been reported for lizards at 35 C (Gleeson 1981; John-Alder et al. 1983). This comparison is achieved by adjusting measured $\dot{V}O_2$max's for size-related differences among species (Bennett 1982), i.e., by dividing $\dot{V}O_2$ (ml/h) by body mass (g) raised to the 0.76 power ($g^{0.76}$) (= $\dot{V}O_2$max,corr). The $\dot{V}O_2$max,corr for *Trachydosaurus* is 3.27 ml $O_2/(g^{0.76} \cdot h)$.

TABLE 1

LOCOMOTORY PERFORMANCE AND HIND LIMB PROPORTIONS OF THREE LARGE
AUSTRALIAN SKINKS AND THE GILA MONSTER

| Species | Burst Speed (km/h) | Endurance at 1 km/h (s) | Hind Limb Span (mm) (% snout–vent length) | | Body Mass[a] (g) |
|---|---|---|---|---|---|
| *Trachydosaurus rugosus* .......... | 2.70 ± .148, 11 (1.78–3.6) | 23.1 ± 6.13, 6 (11.5–45.4) | 158 ± 7.8, 3 | 54.9 ± 4.38 | 560 ± 89.7 |
| *Tiliqua scincoides* ........ | 3.85 ± .220, 6 (3.32–4.68) | 74.6 ± 12.0, 3 (54.9–96.3) | 149 ± 7.1, 6 | 47.0 ± 2.33 | 438 ± 64.2 |
| *Egernia cunninghami* ...... | 9.69 ± .442, 9 (7.56–11.2) | 7.0 ± .60, 8 (3.9–9.3) | 192 ± 8.1, 9 | 88.7 ± 3.33 | 268 ± 34.2 |
| *Heloderma suspectum* ........ | 2[b] | No data (see text) | . . . | 69[b] | . . . |

NOTE.—All values are $\bar{X} \pm$ SD; $n$ is number following; range in parentheses.

[a] Body masses are for those individuals used to measure hind limb proportions; body masses for individuals used in speed and endurance trials are given in Results.

[b] From Bogert and Martin del Campo, 1956; see also John-Alder et al. 1983.

Wilson (1974) reported $\dot{V}O_2$max,corr = 2.13 ml $O_2/(g^{0.76} \cdot h)$, only 65% of the value reported here. Reasons for this discrepancy are uncertain. Wilson (1974) used electrical stimulation to elicit vigorous activity in his animals, and this procedural difference is known to contribute to differences in reported $\dot{V}O_2$max's. Similarly, $\dot{V}O_2$max's for *Amblyrhynchus cristatus, Cnemidophorus tigris,* and *Iguana iguana* were substantially higher for animals running on a treadmill (Gleeson 1979b; Garland 1985; Gleeson, Mitchell, and Bennett 1980, respectively) than for animals stimulated electrically (Bennett, Dawson, and Bartholomew 1975; Asplund 1970; Moberly 1968, respectively). However, $\dot{V}O_2$max's attained during forced locomotory activity are not higher than those via electrical stimulation in *Dipsosaurus dorsalis* (cf. Bennett and Dawson [1972] with John-Alder and Bennett [1981]) or in *Sceloporus occidentalis* (Bennett and Gleeson 1976; Gleeson 1979a, 1982). Thus, these two procedural variations do not consistently bias measured $\dot{V}O_2$max's one way or the other. However, obviously "$\dot{V}O_2$max's" determined by different techniques should be compared with caution. Intraspecific differences in $\dot{V}O_2$max have also been reported

as a function of season (John-Alder 1984; Garland 1985). However, as Wilson (1974) did not report collection dates, this explanation cannot be evaluated in the present case.

The net cost of locomotion for *Trachydosaurus* and other lizards is tabulated in table 2. Using these values, we have computed a new allometric relationship between net cost of locomotion and body mass in lizards:

$C_N$, ml $O_2/(g \cdot km)$

$$= 4.22 \, (\text{body mass, g})^{-0.282}, \quad (3)$$

$$n = 19; \, r^2 = .873; \, P < .0001.$$

This relationship is reported in figure 2. The 95% confidence limit for the slope is −0.227–0.337, and for the constant, 0.493–0.756. The slope of a previously formulated equation is −.25 (Gleeson 1979b), within the 95% confidence limit reported here. We did not wish our equation to be biased by the inclusion of several points for a single species. Therefore, we have calculated species means (table 2), except where the range of body masses was > fourfold (*Amblyrhynchus cristatus, Tupinambis nigropunc-*

TABLE 2

Net cost of locomotion ($C_N$) of lizards

| Species | Body Mass (g) | $C_N$ (ml O$_2$/g × km) | Reference |
|---|---|---|---|
| Gerrhonotidae: | | | |
|   Gerrhonotus sp. ............ | 14 | 1.91[a] | Bakker 1972 |
| Helodermatidae: | | | |
|   Heloderma suspectum ........ | 464 | .616[a] | John-Alder et al. 1983 |
| Iguanidae: | | | |
|   Amblyrhynchus cristatus ...... | 580 | .749[a] | Gleeson 1979b |
| | 2,885 | .373[a] | |
|   Conolophus subcristatus ...... | 2,369 | .527 | Gleeson 1979b |
| | 4,731 | .299 | |
| | 4,556 | .256 | |
|   $\bar{X}$ ..................... | 3,885 | .3607[a] | |
|   Ctenosaura sp. ............. | 126 | 1.09[a] | Bakker 1972 |
|   Dipsosaurus dorsalis ........ | 51.3 | 1.38[a] | John-Alder and Bennett 1981 |
|   Iguana iguana ............. | 900 | 1.07 | Gleeson 1979b |
| | 1520 | .83 | |
|   $\bar{X}$ ..................... | 1210 | .95[a] | |
| Lacertidae: | | | |
|   Lacerta vivipara ............ | 3.4 | 3.6[a,b] | |
|   L. sicula ................. | 6.4 | 2.05 | |
| | 10 | 1.95 | |
|   $\bar{X}$ ..................... | 8.2 | 2.0[a] | |
|   L. viridus ................ | 26 | 1.3[b] | |
| | 35 | 1.1[b] | |
|   $\bar{X}$ ..................... | 30.5 | 1.2[a,b] | |
| Scincidae: | | | |
|   Trachydosaurus rugosus ...... | 541 | .921[a] | Present study |
| Teiidae: | | | |
|   Cnemidophorus murinus ...... | 70.7 | 3.68 | Bennett and Gleeson 1979 |
|   Tupinambis nigropunctatus[c] ... | 16 | 1.66[a] | Bakker 1972 |
| | 1,200 | .35 | Bakker 1972 |
| | 865 | .521 | Bennett and John-Alder 1984 |
| | 1,089 | .373 | Bennett and John-Alder 1984 |
|   $\bar{X}$ ..................... | 1,051 | .4147[a] | |
| Varanidae: | | | |
|   Varanus sp. "1" ............. | 26 | 1.86[a] | Bakker 1972 |
| | 230 | 1.24[a] | |
|   Varanus sp. "2" ............. | 145 | 1.28[a] | Bakker 1972 |
| | 630 | .56[a] | |
|   V. exanthematicus ........... | 990 | .62[a] | Gleeson 1979b |

[a] Denotes 19 values used for regression analysis; see text and fig. 2.

[b] Cragg, reported in Hughes 1977, fig. 8; species designations assumed, given body mass ranges reported in Cragg 1978.

[c] Species assumed to be *nigropunctatus* for Bakker (1972).

*tatus, Varanus* sp. "1" and "2"). In these cases, we used two values for each species. We have excluded *Cnemidophorus murinus* from the analysis because of uncertainty regarding the estimation of $C_N$ (see Bennett and Gleeson 1979). Similarly, we did not include the value of *T. nigropunctatus* measured at 25 C (Bennett and John-Alder 1984). The corresponding slope for mammals is −0.316 (Taylor, Heglund, and Ma-

loiy 1982), which is within the 95% confidence limit of our equation (3).

Although $C_N$ of *Trachydosaurus* is somewhat higher than predicted, it does not fall outside the 95% confidence limit of equation (3). However, we have compared $C_N$'s for *Trachydosaurus* and *Heloderma suspectum* using original data in a multiple-regression model with dummy variables (Kleinbaum and Kupper 1978). The rela-
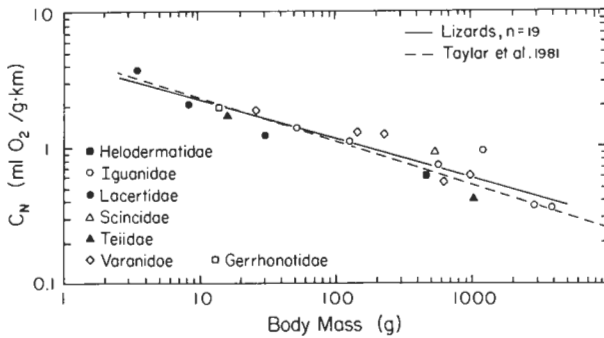
FIG. 2.—Log-log plot of net cost of locomotion ($C_N$) of lizards (data from table 2). Solid line is least-squares regression equation (see text). Broken line is equation for mammals from Taylor et al. 1981.

tionship between $\dot{V}O_2$ and velocity for *Heloderma* is:

$$\dot{V}O_2 = 0.258 + 0.617\ (V),$$

$$0.3 \leq V \leq 0.9\ \text{km/h},$$    (4)

  $n = 30$ observations on 11 individuals;

  $r^2 = .539;\ P < .001$

(Eq. [3] in John-Alder et al. 1983).

Using data obtained on groups of lizards in which body masses are not significantly different ($P > .2$), we found that the net cost of locomotion is significantly higher in *Trachydosaurus* than in *Heloderma*, i.e., the slope of equation (1) > the slope of (4) ($P < .05$). The same result is obtained if rates of $O_2$ consumption are expressed as ml $O_2/(g^{0.76} \cdot h)$ before the comparison is made (see Bennett and John-Alder 1984). The basis of this higher cost in *Trachydosaurus* is uncertain. The morphological similarities between these two species might suggest that mechanical differences in gait or posture are not responsible for the difference in locomotory costs. Fundamental differences in the efficiencies of muscular contraction, as seen among different mammalian fiber types (see Rall 1983), may give rise to these differences.

In addition to having a significantly higher net cost of locomotion than *Heloderma, Trachydosaurus* has a significantly lower $\dot{V}O_2$max,corr [3.27 vs. 3.75 $O_2/$ $(g^{0.76} \cdot h)$; $P < .05$]. As a consequence of these differences in aerobic capacity and locomotory energetics, the maximum aerobic speed (MAS) of *Trachydosaurus* (0.67 km/ h) is only 61% that of *Heloderma* (1.1 km/ h) (John-Alder et al. 1983). The endurance of *Heloderma* at 1.0 km/h would therefore be predicted to exceed 30 min at 1.0 km/h (John-Alder, Lowe, and Bennett 1983) versus only $23 \pm 6.7$ min ($n = 6$) for *Trachydosaurus* at 35 C.

Maximal running velocities of *Trachydosaurus*, about 2.7 km/h, are only about $^1/_{10}$ those reported for many other species of lizards (Garland 1982, 1984, 1985). Sprint velocities of *Trachydosaurus* are probably limited by the short length and small muscle mass of this species' limbs. The ratio of hind limb length to snout–vent length is only 0.21 in *Trachydosaurus;* in many other species, this ratio varies from 0.35 to 0.90 (Pianka 1969; John-Alder and Bennett, unpublished). Although relative hind limb length generally decreases with increasing body mass (see Garland 1984, 1985), the limb length of *Trachydosaurus* appears to be exceptionally short for a lizard of this mass. In comparison, the ratio of hind limb to snout–vent length is 0.39 in *Varanus mertensi* (body mass = 1,178 g) and 0.41 in *V. tristis* (body mass = 106 g) (see also table 1). *Heloderma,* which is also characterized by short hind limbs, has an exceptionally low maximal sprint velocity, less than 2 km/h (John-Alder et al. 1983). The only other species of lizards for which similarly low sprint velocities have been measured are small, reduced-limbed skinks (Huey and Bennett, unpublished). Limi-

tations on muscle contractile kinetics may also contribute to the low sprint velocities of *Trachydosaurus*. For example, although the maximal velocity of muscle shortening is not slower than predicted for a lizard of comparable mass, it is slower than predicted on the basis of muscle length (John-Alder et al., unpublished). Furthermore, the time required for the development of peak twitch tension in *Trachydosaurus* is longer than predicted for a lizard of comparable mass.

Our observations on aerobic energetics and locomotory capacities of *Trachydosaurus* describe an unusually slow lizard with limited stamina. We have recorded locomotory velocities ranging from 0.15 to 0.72 km/h ($\bar{X} \pm$ SEM $= 0.37 \pm 0.060$ km/h; distances $= 0.6$–2.3 m; $n = 8$) in undisturbed individuals in the field, values that are all below or near MAS (0.67 km/h). Velocities of two presumably frightened lizards crossing roads in front of approaching cars averaged 2.1 km/h. These observations indicate that our experimentally determined MAS and sprint velocities are ecologically relevant values. It has been suggested that good sprinters are likely to have limited endurance and that lizards with high endurance will not be able to run fast. Data presented for Kalahari lacertids substantiate that expectation (Huey et al. 1984). *Trachydosaurus* is exceptional in this regard, as it is characterized by both low sprint capacity and a low MAS, the latter particularly in comparison with *Heloderma* (John-Alder et al. 1983).

The suite of physiological and locomotory qualities that characterize *Trachydosaurus* do not appear to be adaptive for either the widely foraging or sit-and-wait modes of predation (Huey and Pianka 1981; Huey et al. 1984). One correlate, perhaps consequence, of this is the dietary generality of *Trachydosaurus*. Whereas *Heloderma*, which is a widely foraging species (Heath 1961; Jones 1983), preys mainly on bird eggs plus occasional juvenile mammals, *Trachydosaurus* is omnivorous (Wilson 1974) and traverses only a small fraction of the area expected for a comparably sized, carnivorous lizard (Satrawaha and Bull 1981; see also Christian and Waldschmidt 1984). However, the omnivory of *Trachydosaurus* is not a necessary consequence of its inability to forage either widely or by sit-and-wait predation. *Phrynosoma cornutum*, another unusual lizard that fits neither of the extremes of foraging mode (Whitford and Bryant 1979; Huey and Pianka 1981), is an ant specialist under very different circumstances of foraging ecology. The dichotomy between widely foraging versus sit-and-wait predation adequately characterizes many species of lizards (Huey and Pianka 1981; but see Magnusson et al. 1985), and general consequences with regard to prey selection can be predicted for these species. In species that fit neither category, however, uniquely divergent behaviors and foraging ecology are likely to have evolved in close association with physiological and morphological features.

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