

## Locomotor Performance and Activity Energetics of Helodermatid Lizards

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Locomotor performance and activity energetics were analyzed in 19 individual helodermatid lizards ranging in mass from 24.5–1220 g. We measured maximum sprint speeds, endurance on a treadmill, cost of transport, and aerobic capacity ( $\dot{V}O_{2\max}$ ) at a mean body temperature of 30.8 C. The maximum sprint speed for both *Heloderma* species averaged 1.7 km/h, which is among the lowest recorded for lizards. A typical *Heloderma* had an endurance time of 16.0 min at 1.0 km/h, which is higher than expected for a lizard of this size at 31 C. At lower speeds, adult *Heloderma* could run for prolonged periods. The cost of transport for a 500 g *Heloderma* at 0.4 km/h was 0.46 ml  $O_2 g^{-1} km^{-1}$ , which is comparable to the cost of transport in other lizards. The two *Heloderma* species showed no significant differences in  $\dot{V}O_{2\max}$ , cost of locomotion, endurance, or sprint speeds. Neither cost of locomotion nor aerobic capacity differed between captive and wild *Heloderma*. At 31 C, helodermatids had a high  $\dot{V}O_{2\max}$ , resulting in the highest factorial aerobic scope (30.4) of any lizard measured to date. The high aerobic capacity of *Heloderma* seems surprising for a sedentary lizard but may be advantageous during intensive male-male agonistic behaviors. Males had significantly higher  $\dot{V}O_{2\max}$  than did females, suggesting that sexual selection may favor males with high aerobic capacities.

PATTERNS of variation in locomotor and aerobic capacities of lizards have generated considerable interest in the past decade (Bennett, 1983; Pough, 1983; Garland, 1993). A principal goal of previous studies has been to determine what behavioral, ecological, and evolutionary factors influence performance measures such as endurance and aerobic capacity. For example, Garland (1994) documented considerable variation in treadmill endurance capacities among 57 lizard species/subspecies. About half of this variation could be explained by body mass and temperature, but phylogenetic affinity and ecology were also suggested as important correlates. High endurance capacities have been identified in a number of lizard families, including helodermatids, and are usually interpreted as adaptations for high activity levels or widely foraging behaviors (Bennett, 1983; John-Alder et al., 1983; Garland, 1994). In this paper, we examine activity energetics and locomotor performance in helodermatid lizards. We draw on information from field studies to propose that factors other than those related to foraging behavior and general activity levels can account for high aerobic capacities of lizards.

*Heloderma* (Helodermatidae) belongs to the Varanoidea, which includes *Varanus* and *Lanthanotus* (Varanidae) as the only other living genera (Pregill et al., 1986; Estes et al., 1988).

Both helodermatid species, *H. horridum*, the Mexican beaded lizard, and *H. suspectum*, the Gila monster, are large, stout lizards that inhabit desert and dry tropical regions of the southwestern United States, western Mexico, and Guatemala (Bogert and Martín del Campo, 1956; Campbell and Lamar, 1989). Helodermatids are the only venomous lizards and forage for vertebrate eggs and young in nests (Lowe et al., 1986; Beck, 1990; Beck and Lowe, 1991). Although finding such prey requires considerable searching (i.e., a widely foraging strategy), helodermatids spend the vast majority of their time at rest in shelters (Lowe et al., 1986; Beck, 1990; Beck and Lowe, 1991). During their activity seasons, both species allocate less than 1 h/day to surface activity (121 h/yr for *H. horridum*, and 65–75 h/yr for *H. suspectum*), and forage at a slow pace (0.25 km/h for *H. suspectum*, 0.35 km/h for *H. horridum*; Beck, 1990; Beck and Lowe, 1991). In addition, helodermatids have very low metabolic rates during rest (Beck and Lowe, 1994).

In contrast to its sedentary habits and low resting metabolic rate, *H. suspectum* has a high capacity for sustained aerobic activity (John-Alder et al., 1983). Aerobic and endurance capacities have not been investigated in *H. horridum*, nor have they been reported for helodermatids at 30 C, the body temperature at which both species of *Heloderma* are normally active

in nature (Beck, 1990; Beck and Lowe, 1991). *Heloderma horridum* is larger, has proportionately longer limbs (Campbell and Lamar, 1989), and is more active than is the Gila monster (Beck and Lowe, 1991). If aerobic capacity is related to activity levels, *H. horridum* might be predicted to have higher capacities for aerobic activity and endurance than those of its congener.

Male helodermatids engage in strenuous fights (Demeter, 1986; Ramírez-Velazquez and Guichard-Romero, 1989; Beck and Ramírez-Bautista, 1991). Individuals with greater aerobic capacities and/or endurance may have an advantage in these tests of dominance (Beck, 1990). If aerobic capacities are related to success in male-male agonistic behaviors, then males might be expected to have higher aerobic capacities than do females.

We address the following questions: Is a high aerobic capacity in *H. suspectum* matched by a high endurance capacity? Do *H. horridum* and *H. suspectum* differ in aerobic and endurance capacities? Do endurance and aerobic capacities of male helodermatids differ from those of females? What are the behavioral and ecological correlates of aerobic capacities in helodermatid lizards? To address these questions, we measured sprint speeds, treadmill endurance, cost of transport, and aerobic capacity ( $\dot{V}O_2\text{max}$ ) of both *Heloderma* species at 31 C.

#### MATERIALS AND METHODS

*Animal collection and maintenance.*—Twelve Mexican beaded lizards and 10 Gila monsters, some wild-caught and some captive, were used in this study (Appendix). Mean body mass was 617.9 g (SD = 341.4, range = 24.5–1220 g). Four *H. horridum* were collected during May 1990 in Jalisco, Mexico, and returned to their capture location in late June 1990. Permits were issued by the Mexican Secretaria de Desarrollo Urbano y Ecología to AR-B and CHL and by the United States Fish and Wildlife Service to CHL. Individuals of *H. suspectum* were collected during May 1990 near Tucson (Arizona Game and Fish Department permits to CHL). Lizards were transported to the American Museum of Natural History Southwestern Research Station near Portal, AZ. All measurements were made during May and June 1990. Food was withheld for the duration of the study, but water was always available. Lizards were held in cages and allowed to thermoregulate in the sun prior to measurements. All measurements were made at body temperatures of approximately 31 C, which is within the normal activity range of helodermatid lizards in nature (Beck, 1990; Beck and Lowe, 1991). Internal body temperatures were

measured at the beginning and end of each trial with a Schultheis quick-registering mercury thermometer inserted 5 cm into the cloaca. Ambient temperatures were regulated with an incandescent light above the treadmill.

*Sprint speed.*—We measured maximum sprint speed on a motorized treadmill with a rubberized cloth belt (John-Alder et al., 1986). Lizards were placed on the tread belt and induced to walk by lightly prodding and pinching the tail and hind limbs. Tread speed was matched to lizard walking speed, then quickly increased until the lizard could no longer make forward progress. The highest speed sustained for 3–5 sec was interpreted as maximum sprint speed.

*Endurance.*—Treadmill endurance was measured using techniques similar to those of John-Alder et al. (1983), Tsuji et al. (1989), and Garland (1993). Endurance capacity was defined as the length of time lizards could maintain a given speed (1.0, 0.8, or 0.6 km/h) on the treadmill. Trials were terminated when lizards failed to maintain pace following 10 consecutive taps or pinches to the tail and hind limbs. All individuals were tested twice, on separate days, and only the higher endurance time was analyzed.

*Cost of transport and aerobic capacity.*—The cost of transport at 0.4 km/h and aerobic capacity ( $\dot{V}O_2\text{max}$ ) were measured as lizards walked on the motorized treadmill using techniques similar to those of John-Alder et al. (1983), Garland (1984, 1993), and Garland and Else (1987). Before trials, lizards were fitted with light-weight, transparent acetate masks. Each mask had a large opening at one end that was slipped over the head of the lizard. Foam rubber was attached around this opening to prevent the mask from slipping off the head during trials. A Tygon tube extended from a small opening at the opposite end of the mask, nearest the lizard's snout. Air was drawn from the mask into the Tygon tube and through a column of Drierite-Ascarite-Drierite to remove water vapor and carbon dioxide. Air then passed through a thermal mass flow controller (Sierra Instruments, Inc., Monterey, CA, Model 844) at a rate ranging from 500–3500 ml/min, STP (depending on lizard size), and through an airtight diaphragm pump. High flow rates were used to ensure rapid wash-out. Oxygen concentration was then subsampled from the air through an additional column of Drierite-Ascarite-Drierite and recorded every second with an Applied Electrochemistry S-3A/II oxygen analyzer interfaced to a computer.

After gathering 2–3 min of baseline data, a

running trial consisted of masking a lizard, placing it on the treadmill, and allowing it to remain stationary for up to 5 min or until it began to walk voluntarily. Tread speed was gradually increased to 0.4 km/h and maintained for 20–30 min. The lizard was encouraged to walk by tapping and lightly squeezing the tail and hind limbs as necessary to maintain an even gait. After a lizard had been walking at 0.4 km/h for 20 min, tread speed was increased by 0.2 km/h every 5 min up to a maximum of 1.0 km/h and maintained at this speed until the lizard was no longer able to maintain pace. This procedure allowed us to determine both the cost of transport at an ecologically relevant speed (0.4 km/h) and  $\dot{V}O_{2\max}$  (see below) during the same trial.

Rates of  $O_2$  consumption ( $\dot{V}O_2$ ) were calculated using equation 4a in Withers (1977). A BASIC program was used to calculate 5- and 10-min intervals of lowest oxygen consumption (corrected for baseline drift) for locomotion at 0.4 km/h. Oxygen consumption rates were assessed during running trials on each of two consecutive days. Aerobic capacity was interpreted as the highest 2-min interval of oxygen consumption from either of the two trials. Cost of transport at 0.4 km/h was taken as the lowest rate of oxygen consumption over a 5-min interval from either of the two trials.

*Statistical analyses.*—Data were used only from animals that cooperated during trials (Appendix). Data were analyzed using SPSS/PC+ (Norris, 1988) and BIOM-PC (Sokal and Rohlf, 1981). Analysis of covariance (ANCOVA), with body mass and/or temperature as the covariates, was used for between-group comparisons. Statistical significance was judged at  $P < 0.05$ .

## RESULTS

Because conditions in the laboratory were less than ideal for temperature control, lizard body temperatures varied somewhat during trials (mean = 30.8, range = 28.5–33.2, SD = 1.27; Appendix). Given that metabolic rate can increase two- to threefold with an increase of 10 C (i.e.,  $Q_{10} = 2$ –3, Beck and Lowe 1994), variation in  $T_b$  might significantly affect our results. Maximum sprint speed, however, was not correlated with body temperature ( $F = 0.04$ ,  $P > 0.50$ ,  $df = 1,16$ ). The cost of locomotion at 0.4 km/h was not significantly correlated with final body temperatures (ANCOVA,  $F = 3.49$ ,  $P = 0.08$ ,  $df = 1,15$ ) nor with the change in body temperatures (ANCOVA,  $F = 1.19$ ,  $P = 0.29$ ,  $df = 1,15$ ). Furthermore, temperature did not significantly affect maximal rates of  $O_2$  consumption ( $F = 1.02$ ,  $P = 0.33$ ,  $df = 1,16$ ). There-

fore, the minor variation in lizard  $T_b$  during the performance trials had a negligible effect on locomotor performance and activity energetics.

*Sprint speed.*—Maximum sprint speed averaged 1.65 km/h for *H. horridum* ( $n = 11$ , SD = 0.26, range = 1.41–2.26, Table 1), and 1.56 km/h for *H. suspectum* ( $n = 6$ , SD = 0.17, range = 1.39–1.88, Table 1). Sprint speeds did not differ significantly between the two species ( $F = 0.85$ ,  $P > 0.50$ ,  $df = 1,11$ ) or sexes ( $F = 0.68$ ,  $P > 0.50$ ,  $df = 1,11$ ). Maximum sprint speed was not correlated with body mass ( $F = 0.40$ ,  $P > 0.50$ ,  $df = 1,16$ ).

*Endurance.*—Analysis of covariance indicated no significant differences in endurance (i.e., duration that a pace of 1 km/h could be maintained) between the two *Heloderma* species ( $F = 0.11$ ,  $P = 0.75$ ,  $df = 1,11$ ); therefore, endurance data for both species were combined. Endurance at 1.0 km/h was significantly correlated with body mass in *Heloderma*, yielding the following allometric equation:

$$\log_{10} \text{Endurance (min)}$$

$$= 0.156 + 0.376 \log_{10} \text{Body Mass (g)} \quad (1)$$

( $r^2 = 0.41$ , S.E.E. = 0.283). The slope differed significantly from zero ( $F = 12.64$ ,  $P = 0.003$ ). A *Heloderma* of mean body mass from this study (618 g) could maintain a pace of 1.0 km/h for an average of 16.0 min ( $n = 13$ , range = 2.92–45.25 min). Data on walking times at 1.0 km/h were obtained from only three females, so differences between sexes could not be tested.

Of 13 individuals (both species) tested at 0.8 km/h, six maintained pace for over 1 h, at which time trials were terminated; one *H. horridum* (1220 g) walked for 3 h 40 min before its trial was terminated. The remaining seven individuals walked for an average of 26.0 min (Appendix). At 0.6 km/h, all 12 lizards measured maintained pace for over one hour, at which time trials were terminated. Therefore, endurance of *Heloderma* is prolonged (i.e., several hours) between 0.6 and 0.8 km/h or at lower speeds.

*Cost of transport.*—The cost of transport (sustained rates of  $O_2$  consumption at 0.4 km/h) for *H. horridum* and *H. suspectum* are summarized in Table 1. Values for  $\dot{V}O_2$  at 0.4 km/h were determined as the lowest sustained  $O_2$  consumption over 5-min intervals. Similar results were obtained over 10-min intervals; however, values were about 7% higher over 10-min intervals (see Hayes et al, 1992). The correlation between 10- and 5-min intervals was 0.98. Anal-

TABLE 1. LOCOMOTOR PERFORMANCE AND ACTIVITY ENERGETICS OF HELODERMATID LIZARDS MEASURED AT 31 C (MEANS  $\pm$  1 SD, RANGES IN PARENTHESES).

	<i>H. horridum</i>	n	<i>H. suspectum</i>	n
Mass, g	803 $\pm$ 294 (194–1220)	12	396 $\pm$ 256 (24.5–673)	10
Sprint speed, km/h	1.70 $\pm$ 0.263 (1.41–2.26)	11	1.56 $\pm$ 0.165 (1.39–1.88)	6
Endurance time, min				
1.0 km/h	20.43 $\pm$ 12.70 (5.08–45.25)	7	10.94 $\pm$ 6.84 (2.92–17.37)	6
0.8 km/h	>61 (10.92–220+)	7	28.45 $\pm$ 8.67 (14.52–40.93)	6
0.6 km/h	>61	6	>61	6
$\dot{V}O_2$ at 0.4 km/h	329.2 $\pm$ 191.4 (106.9–646.9)	11	223.6 $\pm$ 123.9 (46.0–409.8)	7
$\dot{V}O_{2max}$	811.2 $\pm$ 284.0 (251.5–1188.5)	12	447.0 $\pm$ 188.8 (54.2–597.0)	7

\* Only running trials >20 min at 0.4 km/h were used. Values were determined as the lowest sustained  $O_2$  consumption (ml  $O_2$ /h) over 5-min intervals.

<sup>b</sup>  $\dot{V}O_{2max}$  was taken as the highest  $O_2$  consumption over a 2-min interval measured on either of two consecutive days.

yses of covariance indicated no significant differences between captive and wild-caught lizards ( $F < 0.01$ ,  $P = 0.95$ ,  $df = 1,16$ ) or between *H. horridum* and *H. suspectum* ( $F = 0.22$ ,  $P = 0.88$ ,  $df = 1,16$ ), so all individuals were pooled. The pooled allometric equation describing the relationship between body mass and oxygen consumption at 0.4 km/h was as follows:

$$\log_{10} \dot{V}O_2(\text{ml } O_2/\text{h}) = 0.839 + 0.564 \log_{10} \text{Body Mass (g)} \quad (2)$$

( $r^2 = 0.44$ , S.E.E. = 0.231). The slope of this equation differed significantly from zero ( $F = 12.42$ ,  $P = 0.003$ ,  $df = 1,16$ ).

**Aerobic capacity.**—Maximal rates of  $O_2$  consumption for *H. horridum* and *H. suspectum*, especially captive lizards, were generally higher for the second trial (Appendix), although repeatability between trials was highly significant ( $r = 0.89$ ,  $P < 0.001$ ). As with sustained  $\dot{V}O_2$  at 0.4 km/h, there were no significant differences in  $\dot{V}O_{2max}$  between captive and wild-caught lizards ( $F = 2.90$ ,  $P = 0.11$ ,  $df = 1,17$ ), or between species ( $F = 2.15$ ,  $P = 0.16$ ,  $df = 1,17$ ). However, males had significantly higher  $\dot{V}O_{2max}$  than did females (ANCOVA for species pooled,  $F = 15.81$ ,  $df = 1,14$ ,  $P = 0.002$ , Fig. 1). A 3-way ANCOVA with species, wild vs captive, and sex as main factors and body mass and body temperature as covariates confirmed these results: only sex and mass had significant effects on  $\dot{V}O_{2max}$ , and this result held whether or not  $\dot{V}O_{2max}$  and body mass were log transformed.

Considering all 19 individuals, the relationship between mass and aerobic capacity was described by the pooled allometric equation:

$$\log_{10} \dot{V}O_{2max} (\text{ml } O_2/\text{h}) = 0.455 + 0.841 \log_{10} \text{Body Mass (g)} \quad (3)$$

( $r^2 = 0.95$ , S.E.E. = 0.068). The slope was significantly different from zero ( $F = 320.2$ ,  $P < 0.001$ ,  $df = 1,17$ ).

Levels of maximal and sustained  $O_2$  consumption (ml  $O_2$ /h) on a whole-animal basis were significantly correlated ( $r = 0.68$ ,  $P < 0.05$ ). However, after accounting for mass effects by computing residuals from the regression equations, sustained  $\dot{V}O_2$  at 0.4 km/h and  $\dot{V}O_{2max}$  were uncorrelated ( $r = 0.20$ ,  $P > 0.05$ ). Therefore, lizards with higher  $\dot{V}O_{2max}$  did not necessarily exhibit higher oxygen consumption levels while walking at 0.4 km/h.

## DISCUSSION

**Sprint speed and endurance.**—Helodermatid lizards are not swift runners. The mean maximum sprint speed of 1.7 km/h for *Heloderma* in this study is somewhat higher than 1.27 km/h observed for *H. suspectum* by Bogert and Martín del Campo (1956) but is still only about 10% of that reported for many other species of lizards (Garland, 1982; John-Alder et al., 1986; Garland and Losos, 1994). For example, some iguanid lizards of similar size can attain sprint speeds of at least 25 km/h (Garland, 1984). *Heloderma* is relatively unique among lizards in its inability to engage in quick-burst locomotor activity (see

also John-Alder et al., 1983). This lack of sprinting ability may be related to the defensive adaptations of these lizards. Helodermatids are the only venomous lizards. They do not use speed to escape predation but rely instead upon their secretive habits, cryptic nature, and venom (Beck, 1985; Lowe et al., 1986; Greene, 1988). Some large Australian skinks that use open-mouth defensive displays also have low sprinting abilities (John-Alder et al., 1986).

The endurance of *Heloderma* walking on a treadmill at 1.0 km/h (16.0 min for a 618 g lizard) is not exceptional compared to some other lizards (e.g., 40 min for a 30 g *Amphibolurus nuchalis*, Garland and Else, 1987; and over 2 h for *Cnemidophorus tigris*, Garland, 1993) but is higher than predicted for a lizard of this size and temperature (Garland, 1994). At 0.8 km/h, many *Heloderma* in this study showed considerable stamina by continuing on the treadmill for over one hour, at which time trials were terminated (Appendix). At lower speeds, *Heloderma* could maintain pace for prolonged periods. These results correspond with the maximum aerobic speed (speed at which  $\dot{V}O_2\text{max}$  is attained) of 0.7 km/h measured for *H. suspectum* at 25 C by John-Alder et al. (1983). These speeds are considerably higher than the typical speeds of 0.25 to 0.35 km/h at which *Heloderma* travels in the wild (Beck, 1990; Beck and Lowe, 1991).

A potential problem with measuring sprint speeds and endurance on a treadmill is the difficulty in distinguishing between actual locomotor abilities and psychological factors such as motivation and defensive behavior. Defensive behaviors (most notable in wild juveniles) and lack of motivation to perform on a treadmill (most notable in captive lizards in our sample) may be more pervasive in *Heloderma* than in other lizards. Unless they were gradually brought up to sustainable speeds over several minutes, many *Heloderma* in this study performed a defensive response by turning, hissing, and attempting to bite (Garland, 1994). Because of this, nine lizards were excluded from analyses of endurance time at 1.0 km/h, and five would not sprint. Once they became accustomed to walking on the treadmill, however, lizards exhibited reliable locomotor behaviors. During trials designed to measure  $\dot{V}O_2\text{max}$ , they were brought gradually (> 25 min) to speeds at which they exhibited maximal oxygen consumption.

*Cost of transport and aerobic capacity.*—Our sample included 11 captive and 10 "field fresh" *Heloderma* (Appendix). Several captive lizards were initially more reluctant than were wild-

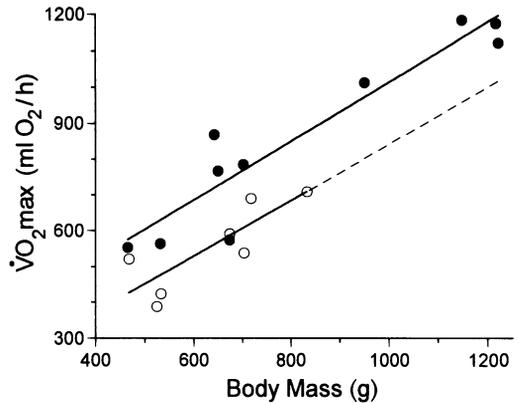


Fig. 1. Relationship between aerobic capacity ( $\dot{V}O_2\text{max}$ ) and body mass in male and female *Heloderma*. Males (closed circles)  $\dot{V}O_2\text{max} = 0.82 \times \text{Body Mass} + 192$  ( $r^2 = 0.88$ , 95% confidence limits for slope are  $\pm 0.25$ ); females (open circles)  $\dot{V}O_2\text{max} = 0.77 \times \text{Body Mass} + 66$  ( $r^2 = 0.68$ , 95% confidence limits for slope are  $\pm 0.60$ ). The slopes of the two regression lines do not differ significantly, but males have significantly higher  $\dot{V}O_2\text{max}$  than do females (ANCOVA,  $F = 15.81$ ,  $df = 1, 14$ ,  $P = 0.002$ ). See equation 3 (text) for pooled relationship between  $\dot{V}O_2\text{max}$  and body mass.

caught lizards to perform on the treadmill. This behavior may have been responsible for captives having a greater tendency to show an increase in  $\dot{V}O_2\text{max}$  between the two experimental trials than did the wild-caught lizards (see Appendix). However, captive and wild *Heloderma* showed no differences in oxygen consumption rates at 0.4 km/h, or in  $\dot{V}O_2\text{max}$  (highest  $O_2$  consumption sustained for 2 min on either of two consecutive days). Long-term laboratory maintenance was associated with a decline in  $\dot{V}O_2\text{max}$  of approximately 15% in *Tupinambis nigropunctatus* (Bennett and John-Alder, 1984). This was not the case with *Heloderma* in our trials; in fact some captive *Heloderma* had aerobic capacities that exceeded those of the wild-caught lizards (Appendix). The iguanid lizard *Sceloporus occidentalis* showed no change in  $\dot{V}O_2\text{max}$  after several weeks of training or inactivity (Gleeson, 1979).

At 0.4 km/h, a 500 g *Heloderma* in this study had a sustained  $\dot{V}O_2$  of 229.7 ml  $O_2$ /h (equation 2), and a cost of locomotion of 0.46 ml  $O_2$   $g^{-1}$   $km^{-1}$ . This cost is midway between the 0.40 and 0.50 ml  $O_2$   $g^{-1}$   $km^{-1}$  predicted for *H. suspectum* at 0.4 km/h from equations 1 and 3 of John-Alder et al. (1983) at 25 and 35 C, respectively. These temperatures are near the upper and lower boundaries of *Heloderma*'s activity temperature range [24.1–36.8 C for *H. suspectum* (Beck, 1990) and 22.5–36.0 C for *H. horridum*, (Beck and Lowe, 1991)]. The mean activity tem-

perature for both species is near 30 C (Beck and Lowe, 1991).

Our values of  $\dot{V}O_2$ max for both *Heloderma* species at 31 C are slightly higher than those reported by John-Alder et al. (1983) for *H. suspectum* at 35 C, confirming that helodermatids have high aerobic capacities. At 25 C, *H. suspectum* has the highest  $\dot{V}O_2$ max of any lizard reported to date (John-Alder et al., 1983). At 31 C, *Heloderma* still has among the highest  $\dot{V}O_2$ max of any lizard measured (assuming a  $Q_{10}$  of 2.0 for other lizards; see comparative data in John-Alder et al., 1983; and Bickler and Anderson, 1986).

The high  $\dot{V}O_2$ max of helodermatids, in combination with a low standard metabolic rate (Beck and Lowe, 1994), results in a very high aerobic scope. At 30.8 C, a 500 g *Heloderma* has a predicted standard metabolic rate (SMR) of 17.46 ml  $O_2$ /h ( $Q_{10}$  of 3.0 and equation 7 of Beck and Lowe, 1994) and a  $\dot{V}O_2$ max of 530.68 ml  $O_2$ /h (equation 3, this study). Thus, *Heloderma* can sustain a rate of oxygen consumption that is 30.4 times its SMR. This is the highest factorial aerobic scope of any lizard reported to date.

*Behavioral and ecological correlates of aerobic capacities.*—Other lizards of the Varanoidea (i.e., most *Varanus*) have been shown to possess high  $\dot{V}O_2$ max (Bennett, 1972, 1983; Wood et al. 1978) but normal factorial aerobic scopes of 7–10 (Bickler and Anderson, 1986). Because many varanid lizards are active foragers, their high aerobic capacities might be interpreted as adaptations to high levels of activity (Bennett, 1972, 1983; but see Gleeson, 1981). However, some varanids are relatively sedentary (Pianka, 1969; Greene, 1986). For example, *Varanus gilleni* is an arboreal, secretive species found beneath the bark of trees in deserts of central Australia. It feeds on large arthropods and small arboreal gekkos (Pianka, 1969) and exhibits foraging behaviors that are not likely to require a high aerobic capacity (Bickler and Anderson, 1986).

As with *V. gilleni*, foraging behaviors of helodermatids seem unlikely to require a high aerobic capacity. *Heloderma* feeds on eggs and juvenile vertebrates encountered in nests. To find these widely distributed prey, a widely foraging strategy must be employed. High aerobic capacities may be adaptive for some lizards that forage widely or cover greater distances during their daily movements (Bennett, 1983; John-Alder et al., 1983; Garland, 1993). However, the relatively large body sizes (and consequent high fat storage capacities), low resting metabolic rates, and abilities to take large meals make

frequent foraging activity unnecessary for helodermatids (Beck, 1990; Beck and Lowe, 1991). In southwestern Utah, *H. suspectum* is active less than 10 days/month during its 90-day activity season and spends less than 1 h/day on the surface during those days active (Beck, 1990). *Heloderma horridum* exhibits peak seasonal activity of approximately 17 days/month in May and spends only 67 min, on average, on the surface per day abroad (Beck and Lowe, 1991). Both species exhibit less than 140 h/yr of surface activity (Lowe et al., 1986; Beck, 1990; Beck and Lowe, 1991). Finally, in nature, helodermatids normally forage at a pace less than half of that which they can sustain for prolonged periods on a treadmill (Beck 1990; Beck and Lowe, 1991; this study). Thus, the high aerobic capacities of these lizards are probably not a simple adaptation to foraging behavior and general activity levels.

A high  $\dot{V}O_2$ max in helodermatid lizards may be a plesiomorphy from their ancestral varanoid stock (Beck, 1990). Similarly, Christian and Weavers (1994) suggest this for *Varanus rosenbergi*. An alternative explanation for a high  $\dot{V}O_2$ max in helodermatid lizards lies in their intensive intraspecific agonistic interactions. Males of both *H. suspectum* (Demeter, 1986; Lowe et al. 1986; Beck, 1990) and *H. horridum* (Ramírez-Velazquez and Guichard-Romero, 1989; Beck and Ramírez-Bautista, 1991) perform strenuous fighting rituals that may last for several hours. The apparent objective of these fights is to force the opponent to the ground or remain atop the opponent throughout a series of ritualistic bouts until he retreats (Demeter, 1986; Beck, 1990; Beck and Ramírez-Bautista, 1991). Large size is a great asset, but a high  $\dot{V}O_2$ max and greater endurance may also be advantageous. Winners of these tests of dominance may increase their access to females and probability of mating (Beck and Ramírez-Bautista, 1991).

Other members of the Varanoidea also exhibit strenuous grappling behaviors during male fighting (Auffenberg 1981; Murphy and Mitchell, 1974; Carpenter et al., 1976). Interestingly, the relatively sedentary varanid *V. gilleni* performs fighting postures very similar to those of *H. horridum* (Murphy and Mitchell, 1974; Carpenter et al., 1976), and it too has a high  $\dot{V}O_2$ max and low SMR, resulting in a factorial scope of 27.5, which is comparable to that of *Heloderma* (Bickler and Anderson, 1986).

Winners of male-male combat interactions in other squamates may have greater access to females and a higher probability of mating (Carpenter and Ferguson, 1977; Gillingham, 1987). In *Sceloporus occidentalis* tested in laboratory are-

nas, winners of social dominance encounters for basking sites had significantly higher sprint speeds, but not higher stamina, than did losers (Garland et al., 1990b). Copulation after combat has been commonly observed in captive squamates (Gates, 1956; Carpenter and Ferguson, 1977).

The hypothesis that high aerobic capacities of helodermatids relate to their strenuous male-male combat behaviors is further supported by our discovery that males of *Heloderma* have significantly higher  $\dot{V}O_2$ max than do females. In garter snakes,  $\dot{V}O_2$ max is correlated with treadmill endurance, and both traits have high heritabilities, based on full sibling data (Garland and Bennett, 1990; Garland et al., 1990a). Locomotor performance is also highly heritable in *Sceloporus occidentalis* (Tsuji et al., 1989). Sexual selection within species of snakes that exhibit male-male aggression appears to favor large body size (Shine, 1978, 1994). We suggest that in *Heloderma*, and perhaps some *Varanus*, sexual selection may favor males with high aerobic capacities through male-male combat rituals.

Ritualized grappling postures are more pervasive in the Varanoidea than in other lizard taxa (Carpenter and Ferguson, 1977; Beck and Ramírez-Bautista, 1991). Future studies of aerobic capacities, and intersexual comparisons of activity energetics within the Varanoidea, might help to elucidate the behavioral, ecological, and evolutionary factors that influence various aspects of performance in lizards.

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APPENDIX. RESULTS OF TREADMILL PERFORMANCE OF 12 *Heloderma horridum* AND 10 *H. suspectum* (h = *H. horridum* and s = *H. suspectum*; c = captivity, w = wild;  $Tb_{init}$  = body temperature at beginning of trial,  $Tb_{final}$  = body temperature at end of trial).  $\dot{V}O_2$  at 0.4 km/h was calculated only on animals that ran >20 min; the lowest rates of  $O_2$  consumption over 5- and 10-min periods are shown.  $\dot{V}O_{2max}$  was interpreted as the highest  $O_2$  consumption over a 2-min interval at 0.8–1.0 km/h measured on either of two consecutive days.

ID	Species	Source	Mass (g)	Sex	Trial 1			Trial 2			Lowest $\dot{V}O_2$ (ml/ $O_2$ /h) @ 0.4 km/h		Max speed (km/h)	Endurance		
					$Tb_{init}$ (C)	$Tb_{final}$ (C)	$\dot{V}O_{2max}$ (ml $O_2$ /h)	$Tb_{init}$ (C)	$Tb_{final}$ (C)	$\dot{V}O_{2max}$ (ml $O_2$ /h)	5 contin- uous min	10 contin- uous min		Time (min) @ 1.0 km/h	Time (min) @ 0.8 km/h	Time (min) @ 0.6 km/h
ASDM-1	h	c	1215	♂	32.9	32.2	1179.0	—	—	—	646.9	745.1	1.44	—	—	—
ASDM-2	h	c	1146	♂	30.8	32.2	1048.9	30.6	32.5	1188.5	617.0	666.8	—	—	—	—
ASDM-3	h	c	949	♂	31.9	29.8	561.4	30.0	32.5	1018.5	187.7	256.5	1.41	5.07	—	—
BMHS-1	s	c	467	♀	31.1	32.2	526.0	30.0	31.6	427.4	287.7	312.0	—	—	—	—
BMHS-2	s	c	531	♂	29.5	32.1	476.2	31.5	31.3	570.0	292.0	297.4	—	—	—	—
BMHS-3	s	c	524	♀	31.2	32.1	393.2	—	—	—	206.1	232.0	—	—	—	—
CBL90-1	h	w	673	♂	31.2	29.0	579.5	32.1	32.1	545.9	329.0	345.0	1.80	15.90	61+	61+
CBL90-2	h	w	194	J	28.5	29.7	226.5	31.2	31.7	251.5	136.1	145.1	1.73	13.48	61+	61+
CBL90-3	h	w	1220	♂	29.6	32.7	1109.2	29.8	28.8	1126.3	—	—	1.41	45.25	220+	61+
CBL90-4	h	w	703	♀	30.2	31.7	543.4	30.5	32.8	505.0	409.5	409.5	1.86	23.87	61+	61+
HS90-2	s	w	32.5	J	30.5	30.3	47.5	32.0	30.6	54.2	46.0	30.7	1.38	3.10	25.27	61+
HS90-4	s	w	532	♀	29.1	33.2	395.0	31.0	—	429.8	229.8	239.9	1.53	17.37	32.25	61+
HS90-5	s	w	465	♂	31.2	32.9	559.0	—	—	—	409.8	384.7	1.51	16.85	29.68	61+
HS90-6	s	w	673	♀	31.4	31.2	591.7	31.6	31.8	597.0	94.2	108.2	1.50	9.10	28.08	61+
HS90-7	s	w	24.5	J	—	—	—	—	—	—	—	—	1.54	2.92	14.52	61+
HS90-12	s	w	55	J	—	—	—	—	—	—	—	—	—	16.28	40.93	61+
UAZH-1	h	c	717	♀	29.7	30.5	372.6	30.7	31.0	695.3	167.1	169.9	1.51	—	10.92	—
UAZH-2	h	c	641	♂	30.7	28.8	580.4	30.2	31.7	873.6	332.9	348.3	2.26	—	—	—
UAZH-3	h	c	701	♂	29.7	29.1	265.1	31.6	31.1	791.6	106.9	123.0	1.88	15.53	61+	61+
UAZH-4	h	c	832	♀	30.6	30.1	404.0	30.9	30.7	714.1	194.9	242.1	1.54	—	—	—
UAZH-5	h	c	649	♂	—	—	687.9	30.7	31.3	773.1	479.5	476.1	1.82	23.92	61+	61+
LF2RR2	s	c	650	♀	—	—	—	—	—	—	—	—	1.88	—	—	—