Kinematics, maximal metabolic rate, sprint and endurance for a slow-moving lizard, the thorny devil (*Moloch horridus*)

Christofer J. Clemente[A], *Graham G. Thompson*[B,D], *Philip C. Withers*[A] *and David Lloyd*[C]

[A]Zoology, School of Animal Biology M092, University of Western Australia,
Stirling Highway, Crawley, WA 6009, Australia.
[B]Centre for Ecosystem Management, Edith Cowan University, Joondalup,
WA 6027, Australia.
[C]School of Human Movement and Exercise Science, University of
Western Australia, Stirling Highway, Crawley, WA 6009, Australia.
[D]Corresponding author. Email: g.thompson@ecu.edu.au

Abstract

Metabolic physiology, morphology, activity patterns, performance traits and movement kinematics are thought to have coevolved in lizards. We examined links between these parameters for the thorny devil (*Moloch horridus*), a morphologically and ecologically specialised agamid lizard (body mass ~30 g). It has a maximum sustainable metabolic rate ($V\text{O}_{2max}$) of 0.99 mL O_2 g^{-1} h^{-1} while running at a velocity of 0.11 m s^{-1} at 35°C. This $V\text{O}_{2max}$ is typical of that for other lizards (except varanids), but its burst speed (1.21 m s^{-1}) is slower than for a typical agamid (e.g. *Ctenophorus ornatus* at 3.59 m s^{-1}) and its endurance is appreciably higher. The kinematic pattern of hind-limb movement for *M. horridus* is different to that of a 'typical' similar-sized agamid, *Ctenophorus ornatus*, which is a fast-moving lizard that shelters in rock crevices. It is also different to the ecologically equivalent *Phrynosoma platyrhinos*. The slow and erratic ventilation of *M. horridus* (2.3 breaths min^{-1}) at its maximum sustainable aerobic running speed occurs when it stops running. This might be a consequence of the hypaxial muscles being used for both lung ventilation and locomotion, which might be impairing pulmonary ventilation when running, but might also contribute to its high endurance. *M. horridus* is metabolically typical of agamids, but its body shape, movement patterns and locomotory performance traits are different, and might have coevolved with its specialisation for eating ants.

Introduction

The metabolic physiology, morphology and activity patterns of some lizards might have coevolved, such that one variable can often be used to predict either of the other two (Garland and Losos 1994). For example, Beck and Lowe (1994) reported that slow-moving helodermatid lizards had lower resting metabolic rates than other lizards. Similarly, Thompson and Withers (1997) reported that the comparatively high standard metabolic rate ($V\text{O}_{2std}$) of small varanids is associated with high aerobic activity, and Garland (1999) reported a positive correlation for several lizard species between endurance, as measured on a treadmill, and the time spent moving while active in the field. It is also apparent that lizards differ in their foraging strategies (Perry 1999), and that these strategies are correlated with locomotory attributes such as speed and frequency of movement, and size of activity area (Magnusson *et al*. 1985). Because relative limb length is correlated with speed of movement (Huey 1982; Huey and Hertz 1982; Losos and Sinervo 1989) and body morphology is related to gait and kinematics of movement (Farley and Ko 1997; Irschick and Jayne 1999), it is likely that performance traits and kinematics of movement are also inter-related with metabolic physiology, morphology, activity patterns and foraging strategy.

Australian dragon lizards (Agamidae) are typically fast-moving, sit-and-wait predators with a catholic diet consisting mostly of small invertebrates (Pianka 1986). In contrast, the

thorny devil (*Moloch horridus*) is a highly specialised, slow-moving predator of small ants, primarily *Iridomyrmex* and *Crematogaster* spp. (Greer 1989; Cogger 1992; Witten 1993; Withers and Dickman 1995). It is exceptionally slow moving, and often rocks backwards and forwards while moving slowly or when stationary (Greer 1989; Cogger 1992; Witten 1993). Unlike most other dragon lizards, during undisturbed locomotion its tail and head are often raised above the body, forming an arc, and its locomotion appears to be almost mechanical (White 1947; Fig. 1). When threatened, *M. horridus* usually remains motionless and adopts a defensive posture, and if it 'runs' then it is generally over a short distance. Despite its unusual locomotory pattern, no detailed analysis has been made of the thorny devil's locomotor kinematics, although it might be expected to differ substantially from other Western Australian agamids because of its specialised ecology (myrmecophagous diet), unusual shape and slowness. Thompson and Withers (in press) reported that the body shape of *M. horridus* was the most different of 43 Western Australian agamid species that they examined. If metabolism is linked with locomotory behaviour, then the slow-moving *M. horridus* might be expected to have a lower locomotory capacity than other much faster agamids. However, its resting metabolic rate (VO_{2rest}) of 0.114 mL O_2 g^{-1} h^{-1} at 35°C is typical of agamids, and the field metabolic rate (0.134 mL CO_2 g^{-1} h^{-1}, FMR) of *M. horridus* is also typical of other semi-arid lizards (Withers and Bradshaw 1995).
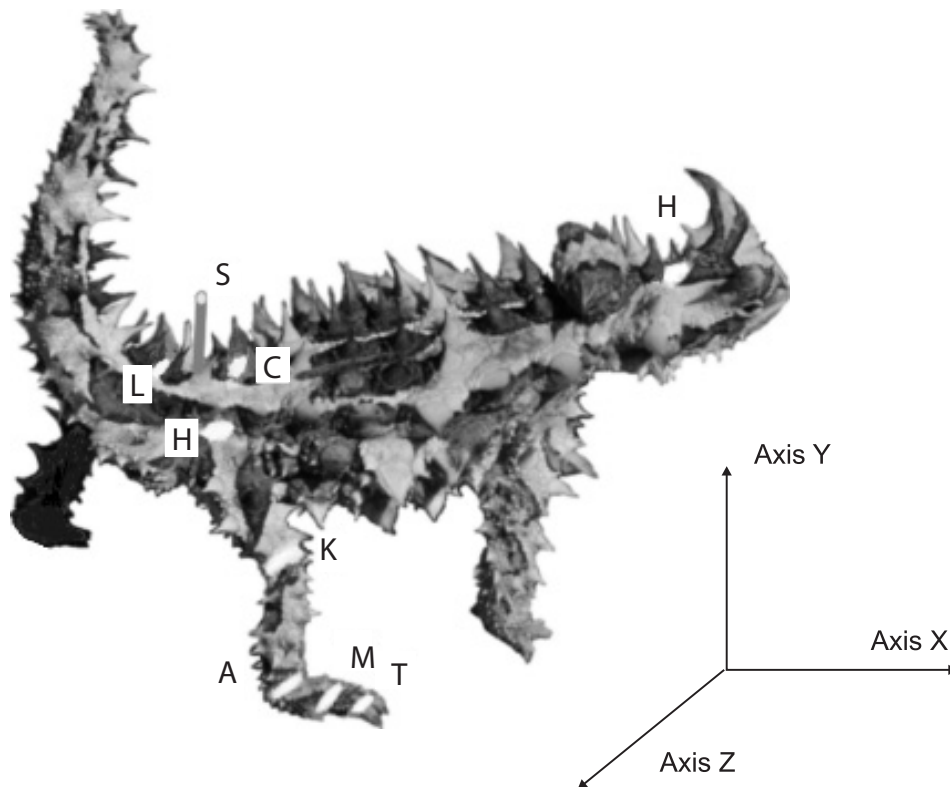

Fig. 1. *M. horridus* has an upright walking posture. Kinematic landmarks are: H, head/neck; Cv, above the caudal vertebra, anterior of the pelvis; S, top of stick positioned perpendicular to the caudal lumbar vertebrae; L, above the lumbar vertebra, posterior of the pelvis; H, hip above the acetabulum; K, the knee joint; A, the ankle joint; M, metatarsals; T, tip of the fourth toe.

This study examines the endurance, kinematics of movement and locomotory energetics of *M. horridus* at maximal sustainable speed and burst speed, to determine whether *M. horridus* differs from other agamids because of its highly specialised shape and foraging behaviour. To determine the extent to which *M. horridus* differs from other Western Australian agamids, we also examined a 'typical' fast-moving, similar-sized, insectivorous, rock-dwelling agamid, the ornate rock dragon (*Ctenophorus ornatus*). Adult *C. ornatus* are found exclusively on smooth granite outcrops in the south-west of Western Australia. They move widely over the open expanses on these rocks and retreat to narrow crevices under exfoliating sheets of granite (Bradshaw 1965). Like most Western Australian agamid lizards, ornate dragons will run bipedally at high speed (personal observation). They are not closely related to *M. horridus* (Melville *et al*. 2001). Burst speed, endurance and movement patterns of *C. ornatus* are within the range of other Western Australian agamid species (Clemente 2001, unpublished data), and Thompson and Withers (in press) reported that its 'body-plan' is similar to that of other agamids, particularly those that retreat to rocks. Therefore, we used *C. ornatus* as a 'generalised' agamid for comparison with the specialised *M. horridus*.

Materials and methods

Shape

Limb and body dimensions of 10 male and 10 female adult *M. horridus* and *C. ornatus* from the Western Australian Museum collection were measured. For each specimen, its museum acquisition number, sex (by examination of gonads), snout-to-vent length (SVL), tail length (tip of the tail to the vent; Tail), upper fore-limb length (UFL), lower fore-limb length (LFL), fore-foot length (Ffoot), upper hind-limb length (UHL), lower hind-limb length (LHL) and hind-foot length (Hfoot) were recorded. SVL and Tail length were measured with a ruler (±1 mm); all other measurements were taken with vernier callipers (±0.01 mm).

Maximal metabolic rate

Six *M. horridus* were collected on sand plain habitat of Western Australia (five at 30°24′S, 119°38′E and one at 31°31′S, 119°32′E) during 14–16 February 2000. These lizards were returned to Perth where they were housed in an outdoor enclosure, and fed on small black *Iridomyrmex* sp. ants under normal photoperiod. Metabolic experiments were undertaken during April 2000.

Each lizard was weighed and held at 35°C for at least 3 h before being exercised on a treadmill. Cloacal temperature (T_b) ranged between 35 and 38°C before each experiment. All lizards were given a single 'trial run' on a motorised treadmill, before measuring oxygen consumption (VO_2) and carbon dioxide production (VCO_2) at the highest sustainable treadmill speed. VO_2 and VCO_2 were measured using a flow-through respirometry system. A vacuum drew ambient air through a lightweight, transparent acetate mask placed over the lizard's head and neck. An airflow rate (Brooks mass-flow controller) of 200 mL min^{-1} maintained the excurrent O_2 content of air between 18 and 20.7%. A higher airflow rate of 500 mL min^{-1} was used during the 'trial run', but a more stable recording was obtained at 200 mL min^{-1} because of the periodic breathing pattern of the lizards. Excurrent air had water vapour removed by a Drierite column before passing through a CO_2 analyser (Hereus–Leybold Binos) and one channel of a paramagnetic O_2 analyser (Servomex OA184). Excurrent air temperature (T_a; °C) was measured with a Vaisala (HMP 35b) humidity/temperature probe. A PC monitored ambient temperature, excurrent O_2 and CO_2 content, and calculated VO_2 and VCO_2 (standard temperature and pressure, dry) after Withers (2001), every 6 s for 8–15 min; data were stored on disk for subsequent analysis. The O_2 analyser was calibrated using dry nitrogen and room air, and the CO_2 analyser was calibrated with dry ambient air and from the ratio of CO_2 produced to O_2 consumed (0.615) when burning a small butane flame in the metabolic system (Withers 2001).

Moloch horridus were placed on the stationary treadmill at 35°C with their mask in place to measure resting VO_2 and VCO_2. The treadmill speed was then adjusted progressively to the maximum speed that each lizard could sustain for the duration of the experiment. Lizards were encouraged to run by being touched or prodded at the base of their tail or on their hind limbs. The mean of the highest consecutive VO_2 recordings averaged over ~3 min was used as the measure of maximal aerobic oxygen consumption (VO_{2max}). Most often, VO_{2max} was achieved within 5 min of commencing to run on the treadmill. The

treadmill speed was determined from the time taken for a complete revolution of the treadmill belt and converted to m s^{-1}. VO_{2max} values were measured on two consecutive days, with the highest VO_{2max} used in analyses. We corrected for mixing of air in the out-flow current using the instantaneous correction of Bartholomew *et al.* (1981). Spikes in VO_2 were apparent in the computer-generated trace after applying the instantaneous correction, and visual observations indicated that these spikes corresponded with breaths; therefore, respiration rate while running on the treadmill was estimated by counting the number of spikes in VO_2 over a given period (7.3–10.85 min; see Fig. 2). Means are reported with ±1 s.e., and $\log_{10}$ transformations are used for comparative purposes.

Burst speed and endurance

Burst speed was measured by taking serial digital video pictures of each lizard as it ran down a racetrack. The shade cloth floor of the racetrack was 3.6 × 0.75 m with markings every 10 cm. Lizards often spontaneously ran away from the handler once released on the racetrack. If lizards did not run immediately, then they were encouraged to do so by tapping their tails. Each lizard was given 4–5 trials, then the process was repeated on two more occasions after the lizard had had a minimum of 24 h to recover. Digital images were recorded with a Sony Handycam (Model CCD-TR303e PAL) and subsequently digitised, and velocity calculated from the *x* and *y* coordinates of the snout using a Visual Basic program written for this purpose. Burst speed was taken as the fastest average velocity for five consecutive frames (video recorded at 25 frames s^{-1}). All lizards had a cloacal temperature between 35 and 38°C before each trial; this body temperature range coincides with the preferred body temperature and the range of enhanced performance traits for agamids (Licht *et al.* 1966; Pianka and Pianka 1970; Roberts 1998).

Endurance was determined as the time that a lizard would walk/run on a treadmill (in a controlled temperature room at 35°C) at 0.40 m s^{-1} before it refused or was unable to continue. Lizards had a cloacal temperature of 35–38°C before each trial. Each lizard was exercised for a total of three trials, with a minimum of 24 h between each trial. The longest time for continuous movement for each lizard was interpreted as the endurance time.

Kinematics

The hind limbs generally provide the major propulsive force for lizard locomotion (Reilly and Delancey 1997) and, for this reason, were the focus of kinematic analysis. Before each trial cloacal temperature was 35–38°C. Eight landmarks (Fig. 1) were painted on each lizard using white liquid paper. Markers were placed above the lumbar vertebra to mark the pelvis; hind-limb markings were placed on the hip joint, knee
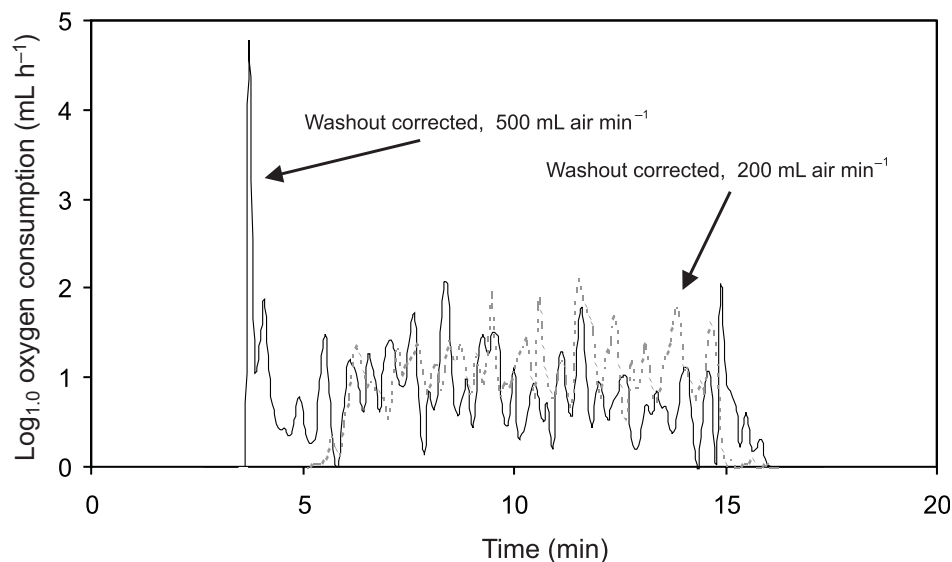

Fig. 2. Metabolic rate for *M. horridus* when running, showing ventilation patterns at two flow rates (500 and 200 mL air min^{-1}).

joint, ankle joint, the metatarsals at the base of the toe, and the tip of the toe excluding the claw. The joint of the head and neck was also used as a marker. A piece of matchstick (1-cm long) was glued upright from the midpoint between the caudal and lumbar vertebra, along the pelvis. This allowed a horizontal plane to be calculated, relative to the lizard, and facilitated the creation of a 3-D model.

Lizards were encouraged to run on a motor-driven treadmill while being video recorded for at least three consecutive strides of quadrupedal locomotion. Simultaneous dorsal and lateral views of each lizard were obtained using a two-camera (Peak HSC-200PM), high-speed video system operating at 200 images s^{-1}. A 2000 W light source, located ~1 m above the treadmill, provided illumination.

Peak Motus (V 2000) software was used to digitise marker points for each video frame of *M. horridus* and *C. ornatus* moving on the treadmill, and convert them to 3-D coordinates. The digitised coordinates were then imported into Body Builder software (V 3.55-Build 133, Oxford Metrics). Model files calculated kinematic variables for the lizard, including linear movements of each point along horizontal, vertical and lateral axes, 3-D angles between segments, and roll, yaw and pitch of single segments. The position and movement of each lizard was described by three axes; *X*, *Y* and *Z*. The *X*-axis ran horizontally from the posterior of the lizard to the anterior; the *Y*-axis ran vertically from the ventral surface of the lizard to the dorsal surface, and the *Z*-axis ran laterally, perpendicular to the longitudinal axis of the lizard (Fig. 1). Positive values of *X*, *Y* and *Z* indicated anterior, dorsal and right lateral positions respectively.

The kinematic analysis was undertaken at the fastest running speed recorded for each individual. Digitised points were examined for a single complete stride, with each stride beginning at hind-limb foot-fall (ff) and ending at ff of the subsequent step. Measured kinematic variables are similar to those recorded in previous studies (Fielder and Jayne 1998; Irschick and Jayne 1999; Jayne and Irschick 1999; Irschick and Jayne 2000). Six variables described aspects of the whole-limb stride-length; distance traveled along the *X*-axis, step length, stride width, stride duration, duty factor and average forwards velocity. Three linear variables described the height of the hip relative to the treadmill; hip height at time of ff (Y_{hip}(ff)), hip height at ff minus the minimum hip height during stance phase (ΔY_{hip}, stance), and maximum vertical oscillation of the hip for the entire stride cycle (ΔY_{hip}, total). Each stride has a stance phase (when the foot is in contact with the surface) and a swing phase (when the foot is not in contact with the surface and is being moved forwards ready for the next stride). Three-dimensional angles of the knee, ankle and the metatarsals were measured at ff and at the end of the stance phase; knee angle, ankle angle, and metatarsal joint angle. For the knee and ankle joints, the maximum distance moved along the flexion-extension axis during the stride cycle (Δjoint angle) was also measured.

The 2-D angle of the trunk to the treadmill surface was measured for a straight line connecting the *X–Y* coordinates of the caudal vertebrae and the head/neck point. Positive trunk values indicate that the chest and pelvis are elevated above the horizontal. A trunk angle was calculated for each frame in the stride, and averaged for each stride. From the dorsal perspective, 2-D angles were also used to calculate the angle between the pelvis and the foot, to measure foot orientation at ff. The 2-D angle between the straight line connecting the *X–Z* coordinates of the caudal and lumbar vertebrae, and the straight line connecting *X–Z* coordinates of the ankle and the toe tip were calculated. Angles of 0° and 90° indicate that the foot was orientated forwards and laterally, respectively. Negative angles indicate that the foot was oriented towards the body. Three angles described the movement of the femur; retraction, rotation and depression. Maximum and minimum values were determined during each stride cycle for each of these angles. To measure these angles a coordinate system was applied to the femur, but transformed making the femur segment of the *Z* axis. The *X–Z* plane is calculated using the pelvis as the *X*-axis, which can be used to calculate the *Y*-axis (Fig. 1). Hence, once the *Y* and *Z* axes are known the *X*-axis can be calculated relative to the femur. All values are given as mean ± 1 s.e. (n).

Differences between body dimensions were examined using ANCOVA, with SVL as a covariate. As angular variables are largely independent of speed (Irschick and Jayne 1999), a discriminant function analysis was performed on these variables to distinguish differences between the strides of the two species. Differences between other linear variables were examined by comparing mean values for the two species. Statistical analyses were undertaken using StatistiXL ver. 1.3 (www.statistiXL.com).

Results

Limb lengths

Snout-to-vent length (SVL) was slightly longer for *M. horridus* than *C. ornatus* (Table 1). Forelimbs of *M. horridus* are significant longer (ANCOVA: $F_{2,37}$ = 524.8, $P < 0.001$) than

those of the *C. ornatus*, but the hind limbs (ANCOVA: $F_{2,37} = 46.5$, $P < 0.001$), forefeet (ANCOVA: $F_{2,37} = 56.6$, $P < 0.001$), hind feet (ANCOVA: $F_{2,37} = 225.3$, $P < 0.001$) and tail (ANCOVA: $F_{2,37} = 429.3$, $P < 0.001$) of *M. horridus* are significantly shorter than those of *C. ornatus*.

General description of a stride

A single stride of the right hind limb is shown for *M. horridus* and *C. ornatus* in Fig. 3*A*–*C*, and stride and gait data are summarised in Table 2. The speed of movement at which we measured differences in limb kinematics on the treadmill was appreciably different for these two species (0.3 m $^{-1}$ for *M. horridus v.* 2.0 m s^{-1} for *C. ornatus*), which possibly accounts for some of the observed differences in the kinematics of movement. Using the presented method of measurement, maximum burst speed (3.59 ± 0.208 m^{-1} for *C. ornatus* and 1.21 ± 0.117 m^{-1} for *M. horridus*) is always much faster than the speed that lizards can attain on a treadmill, while being videoed for several strides. Over a distance in the laboratory, running speeds used for kinematic analysis approximate sprinting speeds for these lizards, although we have not been able to validate this in a field situation. Some of the kinematic variables might also vary with body size; however, SVL is similar for both species (*M. horridus*, SVL = 95.5 (s.e. $\pm$ 1.79) mm; *C. ornatus*, SVL = 80.3 (s.e. $\pm$ 2.25) mm). We believe that the large differences observed between species are more likely to reflect real differences rather than size effects.

Each stride is divided into two phases; the stance phase when the hind foot is on the ground (between ff and toe-off), and the swing phase when the foot is off the ground, swinging forwards (between toe-off and subsequent ff). The period of the stance phase (or duty factor) is much greater for *M. horridus* (67.9%) than *C. ornatus* (34.7%; Table 2). Multivariate analysis of kinematic variables revealed that the strides of the two species were quite difference. A discriminant analysis of all the angular variables was highly significant (Wilks' Lambda = 0.013, d.f. = 11, $P < 0.013$). The canonical correlations for the analysis of all angular variables was 0.99 and correctly classified 100% of the strides to species. Loading on the discriminant functions for minimum femur retraction (3.88), the change in femur retraction (3.72), minimum femur rotation (3.25) and the change in femur rotation (3.06) were the most important kinematic variables in separating the species. Variables that had low loading values in the discriminant analysis were ankle angle at ff (0.93), ankle angle at toe-off (1.32), metatarsals angle at ff (0.24), minimum femur depression (1.06), change of angle in femur depression (0.35) and torso angle (0.92).

Table 1.   Comparison of limb lengths for *M. horridus* and *C. ornatus*
Values are displayed as mean $\pm$ 1 s.e.; n = 10 for males and females of both species

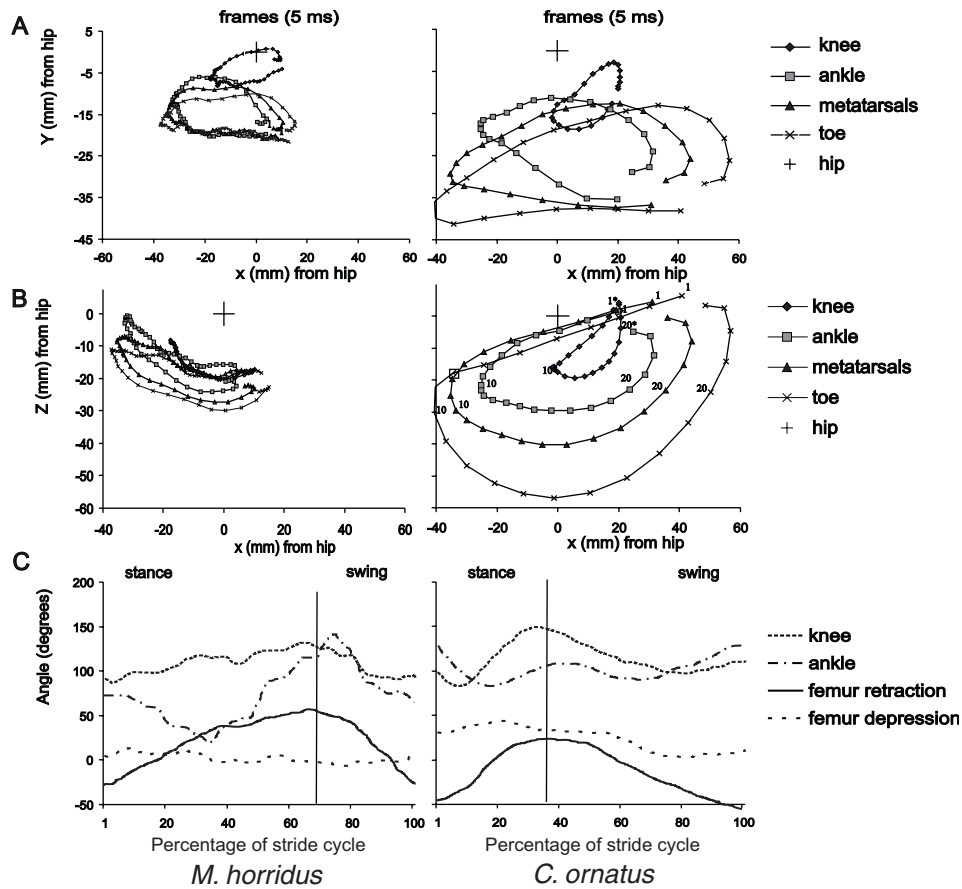|	*M. horridus*		*C. ornatus*	
	Males	Females	Males	Females
Snout-to-vent length (mm)	90.9 ± 1.22	100.1 ± 2.71	85.4 ± 0.28	75.2 ± 0.28
Upper forelimb length (% of SVL)	19.4 ± 0.33	19.1 ± 0.32	15.6 ± 0.28	15.1 ± 0.25
Lower forelimb length (% of SVL)	16.8 ± 0.45	16.6 ± 0.14	11.9 ± 0.42	11.9 ± 0.32
Fore-foot length (% of SVL)	9.6 ± 0.28	9.2 ± 0.43	14.7 ± 0.42	15.1 ± 0.55
Upper hind-limb length (% of SVL)	23.1 ± 0.66	22.2 ± 0.35	25.4 ± 0.26	24.5 ± 0.67
Lower hind-limb length (% of SVL)	19.6 ± 0.20	18.8 ± 0.34	25.3 ± 0.38	25.1 ± 0.52
Hind-foot length (% of SVL)	13.1 ± 0.32	12.9 ± 0.39	32.1 ± 0.13	33.3 ± 0.81
Tail length (% of SVL)	74.8 ± 0.18	71.4 ± 0.15	191.5 ± 0.59	200.0 ± 0.11

Fig. 3. Comparison of hind-limb movements for *M. horridus* (left) relative to a 'typical' agamid, *C. ornatus* (right). (*A*) Lateral view of the paths made by the right knee, ankle, metatarsal and toe-tip markers during a single stride. The hip is located at 0,0 and is marked by a cross. Positive values of *X* and *Y* axes indicate a position forwards and dorsal of the hip. Numbers in figures indicate marker positions in representative frames. (*B*) Dorsal view of the path made by the right knee, ankle, metatarsal and toe-tip markers during a single stride. The hip is located at 0,0 and is marked by a cross. Positive values of *X* and *Y* axes indicate a position forwards and dorsal of the hip. Numbers in figures indicate marker positions in representative frames. Numbers marked (*) indicate position of the knee. (*C*) Values of the angles of femur retraction, femur rotation, femur depression and of the knee and ankle joints versus time (% of stride cycle). Footfall occurs at 0% of the cycle.

For *M. horridus*, the hip moves forwards in a continuous manner, but the knee and ankle only move forward in the latter half of the stance phase. In comparison, although the knee of *C. ornatus* also moves forwards continuously, the speed is slower in the first half of the stance phase than the second half. The ankle of *C. ornatus* is stationary for the first half of the stance phase, commences to move forwards in the latter half of the stance phase as the heel rises but toes remain on the ground, then once the foot is off the ground it moves faster than the hip and knee to be positioned forwards of the knee just before ff. In comparison, the ankle of *M. horridus* is never in front of the knee.

Vertical oscillations of all markers (lumbar, hip, knee, ankle, metatarsal and toe) are appreciably greater for *C. ornatus* than *M. horridus* (Fig. 3*A*). Vertical displacement of the

Table 2. Gait and kinematic variables for *M. horridus* (*n* = 2) and
***C. ornatus* (*n* = 6)**

Values are displayed as mean ± 1 s.e. A description of variables is given in
the text. Abbreviations: es, end of stance phase; ff, footfall; max.,
maximum; min., minimum. All angular variables are in degrees

Linear variables	*M. horridus*	*C. ornatus*
Speed (m s^{-1})	0.3 ± 0.01	2.0 ± 0.1
Stride length (mm)	73.3 ± 2.7	224.3 ± 8.8
Step length (mm)	54.9 ± 1.6	85.2 ± 3.7
Stride width (mm)	61.5 ± 1.7	57.7 ± 2.5
Stride duration (s)	0.3 ± 0.0	0.1 ± 0.0
Relative phase	0.9 ± 0.03	0.8 ± 0.03
Duty factor (%)	67.9 ± 1.9	34.7 ± 4.3
Y_{hip}(ff) (mm)	20.8 ± 0.5	27.6 ± 2.7
ΔY_{hip}, stance (mm)	3.4 ± 1.4	2.7 ± 0.6
ΔY_{hip}, total (mm)	4.9 ± 0.6	9.9 ± 1.4
Angular variables		
Knee angle (ff)	91.0 ± 2.3	114.0 ± 2.8
Knee angle (es)	129.7 ± 1.9	112.8 ± 4.3
ΔKnee angle	48.2 ± 1.6	55.0 ± 5.5
Ankle angle (ff)	76.2 ± 1.7	94.3 ± 4.3
Ankle angle (es)	109.9 ± 8.4	125.8 ± 4.6
ΔAnkle angle	106.5 ± 7.7	86.2 ± 5.6
Meta-angle (ff)	177.0 ± 3.0	179.2 ± 3.8
Meta-angle (es)	174.9 ± 7.3	148.0 ± 6.3
Toe orientation (ff)	17.7 ± 6.6	18.1 ± 5.0
Max. femur retraction	59.2 ± 0.9	54.3 ± 2.0
Min. femur retraction	−28.4 ± 0.6	−25.9 ± 4.2
Max. femur depression	15.1 ± 0.7	23.0 ± 3.8
Min. femur depression	−8.9 ± 1.5	−4.8 ± 4.5
Max. femur rotation	62.1 ± 4.0	14.8 ± 3.7
Min. femur rotation	4.7 ± 1.3	−52.0 ± 4.1
Torso angle	0.2 ± 0.8	3.7 ± 1.1

hip of *C. ornatus* is approximately twice that of *M. horridus* (Table 2). The displacement of
the lower hind-limb segments for *C. ornatus* is ~10 times that of *M. horridus* (Fig. 3*A*). The
ankle and metatarsals commence to rise soon after ff for *C. ornatus*, which contrasts with
M. horridus, where they remain at a constant elevation for two-thirds of the period the foot
is in contact with the surface. The proportionally longer hind limbs of *C. ornatus* (Table 1)
possibly account for much of the anterior–posterior displacement of the distal hind-limb
segments. The knee, ankle and foot of *C. ornatus* are generally displaced in a more anterior
position relative to the hip than for *M. horridus*. Segments of the hind limbs are more
laterally displaced in the propulsive phase for *C. ornatus* than for *M. horridus*, as seen in
the dorsal view (Fig. 3*B*). For *M. horridus*, the knee joint moves back and forwards in an
arc with the centre point being the hip (Fig. 3*B*), suggesting that femur retraction
contributes substantially to movement of the hind limb, although femur depression is
reduced. In contrast, for *C. ornatus* the knee movement is more ellipsoidal, suggesting that
both femur retraction and depression contribute to the stride.

For both agamids, the angle of the ankle joint decreases after ff (76.2° and 94.3°, for *M.
horridus* and *C. ornatus*, respectively) then increases as the hip moves past the hind foot

and the heel of the foot commences to rise off the ground, increasing the angle at the ankle (Fig. 3*C*). The largest angle is approximately at toe-off for the thorny devil but at ff for *C. ornatus*. Femur retraction, both forwards and behind, is similar for both agamids (Table 2). The mean torso angle is greater for *C. ornatus* than for *M. horridus*; *C. ornatus* at high speed can run bipedally, but the torso is not very erect.

Figure 4 shows that *C. ornatus* lifts its hind knee, ankle and toes higher, and its feet are out of contact with the ground for longer than *M. horridus*. The knee of *M. horridus* is much less vertically displaced than in *C. ornatus*, with the consequence that the lower hind limb swings through in a pendulum fashion, compared with the lateral lift of the lower hind limb for *C. ornatus* during the recovery phase of the stride.

Maximal sustainable metabolic rate

Six *M. horridus* (27.7 ± 2.0 g) had a $V\text{O}_2$ of 0.99 (± 0.053) mL O_2 g^{-1} h^{-1} and a $V\text{CO}_2$ of 1.164 (± 0.099) mL CO_2 g^{-1} h^{-1} while running at their maximal sustainable speed of 0.11 (± 0.04) m s^{-1}. Fluctuations in $V\text{O}_2$ (taken to indicate periodic breathing) were clearly evident after instantaneous correction of $V\text{O}_2$ and $V\text{CO}_2$ (Fig. 2). These fluctuations were more evident during the trial runs when air-flow rate was 500 mL min^{-1}, but were still apparent when the air-flow rate was reduced to 200 mL min^{-1} during $V\text{O}_2$ and $V\text{CO}_2$ measurement. Mixing of excurrent air in the air line, the Drierite column and in the O_2 and CO_2 analysers diminished the magnitude of fluctuations at the lower flow rate, but did not alter the calculated average $V\text{O}_2$ and $V\text{CO}_2$. The mean frequency of breaths while running at maximum sustainable speed on the treadmill was 2.15 (± 0.026) min^{-1}.

Burst speed and endurance

Ctenophorus ornatus had a significantly faster burst speed (3.59 ± 0.208 m s^{-1}, *n* = 5) than *M. horridus* (1.21 ± 0.117 m s^{-1}, *n* = 6; *t* = 10.43, *P* < 0.010). *C. ornatus* walked/ran for a maximum of 178 s at a belt speed of 0.4 m s^{-1}. Two *M. horridus* walked for 1800 and 2100 s; they were obviously able to continue, but had exceeded the endurance time of any other species of agamid that we had measured, by at least 900 s (unpublished data). These two endurance times were included in the calculation of the species mean. The mean endurance
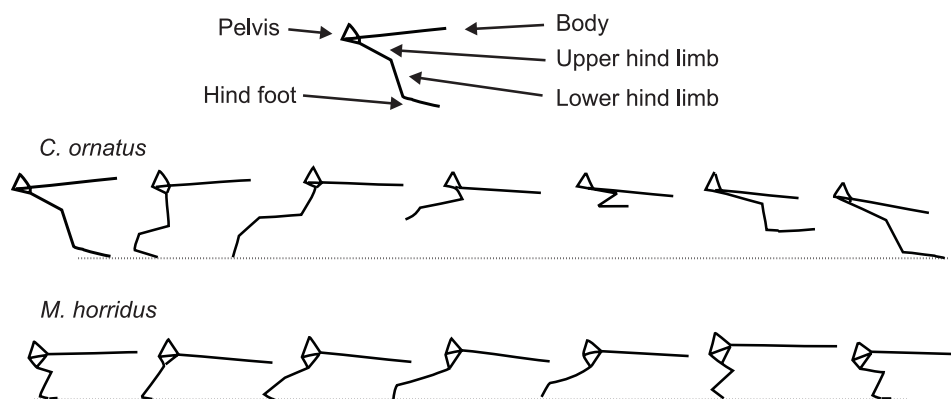

Fig. 4. Comparison of the sequence of lateral movements of the right hind-limb segments of *M. horridus* and *C. ornatus* for one complete stride from footfall to footfall. The triangle is the hip, with the near horizontal line forwards of the hip indicating body angle; upper and lower limbs and foot are shown as single lines.

period of 1233 ± 207 s (*n* = 7) for *M. horridus* is clearly an under-estimate; nevertheless, it is still much longer than that of *C. ornatus* (88.0 ± 25.23 s, *n* = 5; *t* = 5.48, *P* < 0.01).

Discussion

The body shape of *M. horridus* (Fig. 1) is appreciably different to all other Western Australian agamids, whereas *C. ornatus* is clustered in morphometric space with other *Ctenophorus* spp, in particular those that retreat to rock crevices (Thompson and Withers, in press). *M. horridus* has the shortest tail and neck, the narrowest and shortest head and the shortest forefeet of 43 Western Australian agamids. Morphological differences between *C. ornatus* and *M. horridus* that we measured in this study (Table 1) are typical of the magnitude of difference between *M. horridus* and 42 other agamids (Thompson and Withers, in press).

The hind-limb movement pattern of *M. horridus* is appreciably different to that of the rock-scampering *C. ornatus*. The femur of *M. horridus* remains more parallel with the ground than for *C. ornatus,* whereas the lower limbs and feet swing slowly in a pendulum-like fashion that forms a laterally compressed ellipsoid compared with the more open ellipsoid of *C. ornatus* (Fig. 4). The lower-limb segments are much more elevated and laterally displaced in the recovery phase of the stride cycle for *C. ornatus* (and *Sceloporus clarkii*; see Reilly and Delancey 1997) than for *M. horridus* (Fig. 3), and the hind limb is in contact with the substrate for a higher proportion of the stride cycle in *M. horridus* than *C. ornatus* (Fig. 4; also see *Sceloporus clarkii*, which is similar to *C. ornatus*; Reilly and Delancey 1997).

Numerous authors have commented that *Phrynosoma* and *Moloch* are ecological equivalents (Pianka and Pianka 1970; Pianka and Parker 1975; Pianka 1966, 1997; Sherbrooke 1999). Pianka (1997) reported that a multivariate morphometric analysis demonstrated that *Moloch* and *Phrynosoma* were anatomically closer to each other than other members of their own lizard fauna. If this is the case, then it is likely that the kinematics of locomotion for *M. horridus* would be more like that of *Phrynosoma* than other dragon lizards, because body shape and ecology have been shown to be associated with locomotory traits. We compared the lateral movement of the knee, ankle, metatarsal and toe-tip landmarks of *M. horridus* and *Phrynosoma platyrhinos*; we also made this comparison with more typical lizards, including *Callisaurus draconoides*, *Uma scoparia*, *Dipsosaurus dorsalis*, *Cnemidophorus tigris* (information provided by Irschick and taken from Irschick and Jayne, 1999). We also used a principal component analysis (PCA) of the angular kinematic variables during quadrupedal strides, comparing the same five American species (data from Irschick and Jayne 1999; their table 4) with data for *M. horridus* and *C. ornatus*; results of this PCA show the extent of the difference between *M. horridus* and the other species (Table 3, Fig. 5). Based on the differences between these seven species, in terms of the angular kinematic variables of quadrupedal locomotion, PCA 1 (eigenvalue = 5.12) accounts for 39.4% of the variance and PCA 2 (eigenvalue = 3.13) accounts for 24.1% of the variance. *M. horridus* is separated from the other species on PCA 1 (Fig. 5). It is placed at the negative end of PCA 1 that has high positive component loadings on knee angle (ff), ankle angle (ff), ankle angle (es) and maximum femur depression, and is negatively loaded on toe angle (es) and minimum femur rotation (Table 3). These data indicate that both the horizontal and vertical movement of the hind-limb joints of *M. horridus* are more constrained than those of the other lizards. Figure 6 shows that the vertical and horizontal displacement of the hind-limb landmarks for *M. horridus* are much less than those of the other five lizards, yet the SVL for the six species are similar (mean

Table 3. Component loadings and component score coefficients (eigenvectors) from a PC analysis of angular variables during quadrupedal locomotion for *Callisaurus draconoides*, *Uma scoparia*, *Phrynosoma platyrhinos*, *Dipsosaurus dorsalis*, *Cnemidophorus tigris* (taken from Irschick and Jayne 1999), and *Moloch horridus* and *Ctenophorus ornatus* (this study)
Variables are arranged according to their absolute component loading. PCA 1 and 2 are plotted in
Fig. 6. Abbreviations: es, end of stance phase; ff, footfall

| Variables	Component loadings		Component score coefficients (Eigenvectors)	
	PC 1	PC 2	PC 1	PC 2
Knee angle (ff)	0.96	–0.11	0.42	–0.06
Ankle angle (ff)	0.91	0.25	0.4	0.14
Max. femur depression	0.86	–0.28	0.38	–0.16
Ankle angle (es)	0.82	0.37	0.36	0.21
Toe angle (es)	–0.81	0.55	–0.36	0.31
Min. femur rotation	–0.73	–0.48	–0.32	–0.27
Max. femur rotation	0.58	–0.66	0.26	–0.37
Min. femur depression	–0.46	–0.6	–0.2	–0.34
Trunk angle	0.36	0.59	0.16	0.33
Max. femur retraction	0.25	–0.11	0.11	–0.06
Knee angle (ff)	–0.14	0.92	–0.06	0.52
Toe angle (ff)	–0.09	0.44	–0.04	0.25
Min. femur retraction	–0.02	–0.34	–0.01	–0.19
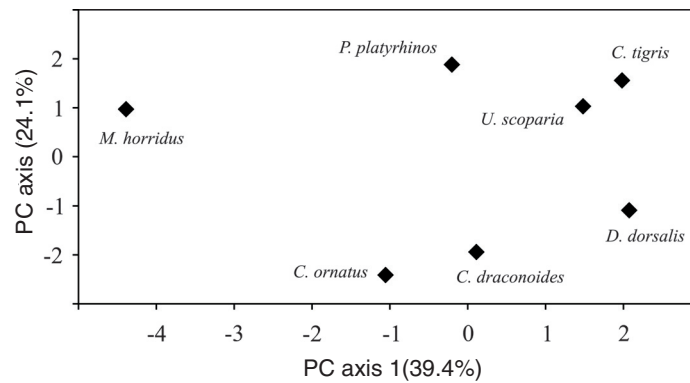
Fig. 5. PCA Axes 1 and 2 for angular variables during quadrupedal locomotion for
Callisaurus draconoides, *Uma scoparia*, *Phrynosoma platyrhinos*, *Dipsosaurus
dorsalis*, *Cnemidophorus tigris* (Irschick and Jayne 1999; their table 5), and *M.
horridus* and *C. ornatus*.

SVL: *C. draconoides*, 7.6 cm; *U. scoparia*, 8.0 cm; *D. dorsalis*, 8.7 cm; *P. platyrhinos*, 7.9
cm; *C. tigris*, 8.5 cm; *M. horridus*, 9.55 cm). These data show that although *M. horridus*
might be an ecological equivalent of *Phrynosoma* spp. and its body shape might be more
similar to this genus than to other Australian agamids, its locomotory kinematics are
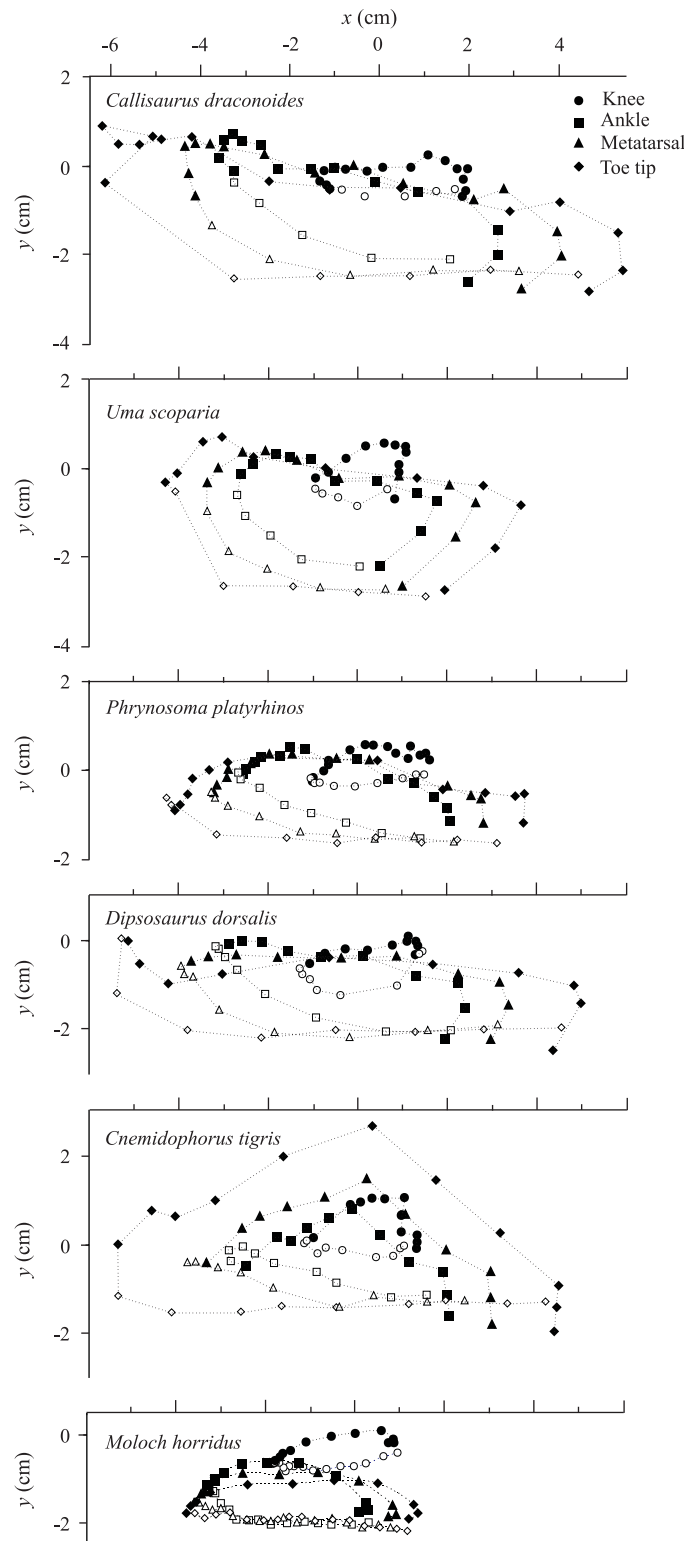appreciably different from *P. platyrhinos*.

Fig. 6. Lateral views of paths (*y v. x*) of the right knee, ankle, metatarsal and toe-tip landmarks during quadrupedal locomotion for *Callisaurus draconoides*, *Uma scoparia*, *Phrynosoma platyrhinos*, *Dipsosaurus dorsalis*, *Cnemidophorus tigris* (Irschick and Jayne (1999); their fig. 7) and *M. horridus*.

If the locomotory kinematics of *C. ornatus* are representative of 'typical' agamids, then it might be expected that the net cost of transport for the thorny devil would have been lower than for other faster-moving agamids, because limb displacement during running was relatively low (and hence more economical). We were unable to get *M. horridus* to move at various constant speeds on the treadmill so that we could measure $V\text{O}_2$ at incremental speeds to calculate the net cost of transport. Therefore, we could only report $V\text{O}_2$ at the single maximal sustainable running speed. The $V\text{O}_{2\text{max}}$ of *M. horridus* that we obtained does not differ from what would be predicted from other (non-varanid) lizards at 35°C (Fig. 7). The factorial aerobic scope of *M. horridus* was 11.9 at 35°C, which is within the normal range for most lizards (Cragg 1978; Bennett 1982; Garland 1984; Al-Sadoon 1986; Thompson and Withers 1997). Weinstein and Full (1999) reported that the distance travelled before fatigue (endurance) for the frog-eyed gecko (*Teratoscincus przewalskii*) was significantly increased by periodic pauses when exercising on a treadmill at 0.9 km h^{-1}, although the average cost of the intermittent exercise was not significantly different from $V\text{O}_{2\text{max}}$. The same may also apply to *M. horridus*, which has intermittent breathing and a very high endurance.

The burst speed of *M. horridus* was significantly slower than that of *C. ornatus*, suggesting that it would be very slow in escaping from predators, and unable to pursue and catch fast-moving prey. Withers and Dickman (1995) and Pianka *et al*. (1998) reported that thorny devils moved relatively short distances over several days, and that their foraging strategy does not require a high sprint speed to capture ants. Rather, the thorny devil remains relatively motionless at an ant trail to feed over a considerable period of time, often in an exposed position. Its 'horrific' (spiny) body form and cryptic colouration probably reduces predation while feeding in these exposed locations.
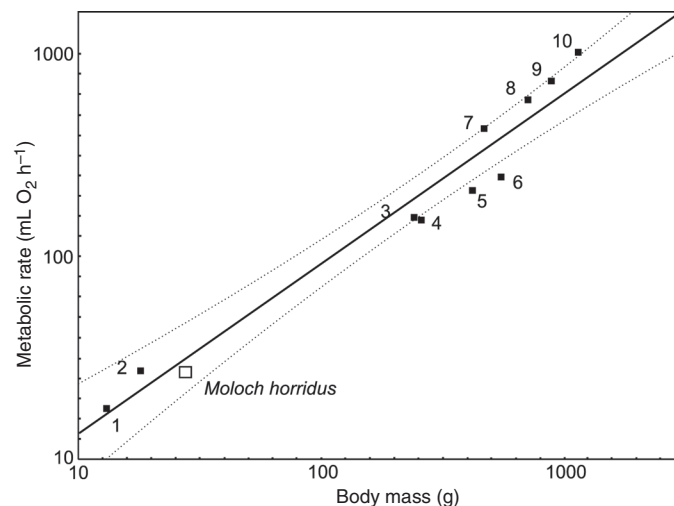

Fig. 7. Comparison of the maximal locomotory metabolic rate, at 35°C, between *M. horridus* and a selection of other lizard species. The 95% confidence limits around the regression lines for the other lizards are shown. Values are for (1) *S. occidentalis* (Gleeson 1979), (2) *C. tigris* (Asplund 1970), (6) *P. lesueuri*, (4) *E. cunninghami*, (5) *T. rugosa*, (3) *P. barbatus* (Wilson 1974), (9) *T. nigropunctatus* (Bennett and John-Alder 1984), (8) *I. iguana* (Gleeson *et al*. 1980), (7) *H. suspectum* (Bennett 1983) and (10) *C. nubila* (Christian and Conley 1994).

The reduction in the vertical movement of the femur during locomotion by *M. horridus* suggests that the femur is used for another purpose, most likely to hold its body off the ground while moving or stationary. This need for an elevated abdomen has influenced the stride of *M. horridus*. Conversely, *C. ornatus* extends the entire hind limb during each stride and has greater vertical movement in the femur during each stride. Therefore, it appears that the kinematics of its locomotory stride, lack of burst speed, and high endurance of *M. horridus* are suited to its myrmecophagous habit and its occasional long distance but slow movements, presumably to new foraging sites. We are unsure why *M. horridus* adopts such an erect posture even when standing, given that most other agamids have a much lower lateral profile.

There is a potential negative interaction between locomotion and breathing. Bennett (1973) reported that ventilation rates for active *Sauromalus hispidus* (17.3 breaths min^{-1}) and *Varanus gouldii rosenbergi* (13.5 breaths min^{-1}) at 35°C were approximately the same as at rest; ventilation rates were not increased above rest in proportion to their metabolic increment. In contrast, Carrier (1987) reported diminished lung ventilation with increased locomotion for *Iguana iguana*, *Ctenosaura similis*, *Varanus exanthematicus* and *V. salvator*. These results prompted Wang *et al.* (1997) to further examine the impact of activity on breathing rate. *I. iguana* and *V. exanthematicus* were found to ventilate their lungs during a locomotor stride, although their breathing pattern was adversely affected by locomotion. Wang *et al.* (1997) concluded that both *I. iguana* and *V. exanthematicus* use their hypaxial muscles for locomotion and ventilation, and that this adversely affected breathing rate, minute volume, airflow velocity and inspiration duration between breaths. More recently, Owerkowicz *et al.* (1999) reported that gular pumping to ventilate the lungs of *V. exanthematicus* largely circumvented the constraint imposed by intercostal muscles being used for ventilation and lateral body movement while running. Frappell and Daniels (1991) reported resting ventilation rates of 11–37 breaths min^{-1} for 10 species of agamids at 37°C (body mass range, 5–518 g). *M. horridus* had a mean breathing rate of 2.2 breaths min^{-1} while moving at its maximum aerobic sustainable running speed. This is appreciably lower than that for resting agamids (Frappell and Daniels 1991). We have no data on the resting ventilation rate for *M. horridus*. Based on the hypaxial constraint hypothesis (Carrier 1987; Wang *et al.* 1997), we assume that hypaxial muscles being used for both lung ventilation and limb movement compromise the ventilation rate of *M. horridus*. Our observations of *M. horridus* running on the treadmill indicated that they periodically paused, during which time there was substantial ventilation of the lungs, as observed by the lateral movement of the rib cage behind the forelimbs and a peak in $V\text{O}_2$.

Metabolic physiology, morphology and activity patterns may have coevolved in some lizards (Garland and Losos 1994). Foraging modes can be correlated with attributes like speed and frequency of movement (Magnusson *et al.* 1985), activity area size and relative limb length can be correlated with speed of movement (Huey 1982; Huey and Hertz 1982; Losos and Sinervo 1989), and body morphology is often related to gait and kinematics of movement (Farley and Ko 1997; Irschick and Jayne 1999). We commenced this investigation with the hypothesis that locomotory metabolism ($V\text{O}_{2\text{max}}$), morphology (limb lengths), activity patterns and kinematics of movement were interrelated for *M. horridus*. Body shape and foraging behaviour of *M. horridus* are atypical of that for most agamids and are obviously linked. The very different kinematic pattern of hind-limb movement is no doubt linked with its unusual body shape, slow burst speed and possibly high endurance. However, its metabolic physiology ($V\text{O}_{2\text{max}}$, $V\text{O}_{2\text{std}}$ and FMR) is within the expected range for agamids. If its $V\text{O}_{2\text{max}}$ and $V\text{O}_{2\text{rest}}$ are similar to that of other lizards, but its maximum

aerobic speed is much slower, then this would suggest that it is inefficient or has a high net cost of transport. Because we were unable to have these lizards run at various speed on the treadmill to measure the corresponding $V\text{O}_2$, we were unable to verify this.

Our results suggest that *M. horridus* has the metabolic physiology of a typical agamid, but appreciable specialisation of its body shape, movement patterns and performance traits might have coevolved with its specialisation for myrmecophagy. Because of the limitations of two-species comparative studies (Garland and Adolph 1994), we suggest that further studies of the links between metabolic physiology, morphology, activity patterns, kinematics and performance traits for specialised agamids in a phylogenetic context are needed to enhance our understanding of possible relationships and adaptations among these attributes. However, given that *M. horridus* is a monospecific genus that separated early from other Australian agamids (Melville *et al*. 2001), and is morphologically very distinct, it is difficult to separate phylogenetic effects from physiological and morphological adaptations to habitat and life history traits for this species.

Acknowledgments

References

Al-Sadoon, M. (1986). Contribution of aerobic and anaerobic scope to the total metabolic scope of the desert skink, *Chalcides ocellatus* (Forskäl). *Comparative Biochemistry and Physiology* **83A**, 745–749.

Asplund, K. K. (1970). Metabolic scope and body temperatures of whiptail lizards (*Cnemidophorus*). *Herpetologica* **26**, 403–411.

Bartholomew, G. A., Vleck, D., and Vleck, C. M. (1981). Instantaneous measurements of oxygen consumption during pre-flight warm-up and post-flight cooling in sphingid and saturniid moths. *The Journal of Experimental Biology* **90**, 17–32.

Beck, D. D., and Lowe, C. H. (1994). Resting metabolism of helodermatid lizards: allometric and ecological relationships. *Journal of Comparative Physiology* **164**, 124–129.

Bennett, A. F. (1973). Ventilation in two species of lizards during rest and activity. *Comparative Biochemistry and Physiology* **46A**, 653–671.

Bennett, A. F. (1982). The energetics of reptilian activity. In 'Biology of the Reptilia. Vol. 13'. (Eds C. Gans and F. H. Pough.) pp. 155–199. (Academic Press: London.)

Bennett, A. F. (1983). Ecological consequences of activity metabolism. In 'Lizard Ecology: Studies of a Model Organism'. (Eds R. B. Huey, E. R. Pianka and T. W. Schoener.) pp. 11–23. (Harvard University Press: Cambridge.)

Bennett, A. F., and John-Alder, H. B. (1984). The effect of body temperature on the locomotory energetics of lizards. *Journal of Comparative Physiology* **155**, 21–27.

Bradshaw, S. D. (1965). The comparative ecology of lizards of the genus *Amphibolurus*. Ph.D. Thesis, Department of Zoology, University of Western Australia, Perth.

Carrier, D. R. (1987). Lung ventilation during walking and running in four species of lizards. *Experimental Biology* **47**, 33–42.

Christian, K. A., and Conley, K. E. (1994). Activity and resting metabolism of varanid lizards compared with 'typical' lizards. *Australian Journal of Zoology* **42**, 185–193.

Clemente, C. J. (2001). Locomotion in Australian Agamidae: How does morphology and kinematics affect performance? B.Sc.(Honours) Thesis, School of Animal Biology, University of Western Australia, Perth.

Cogger, H. G. (1992). 'Reptiles and Amphibians of Australia.' (Reed: Sydney.)

Cragg, P. A. (1978). Oxygen consumption in the lizard genus *Lacerta* in relation to diel variation, maximum activity and body weight. *The Journal of Experimental Biology* **77**, 33–56.

Farley, C. T., and Ko, T. C. (1997). Mechanics of locomotion in lizards. *The Journal of Experimental Biology* **200**, 2177–2188.

Fielder, C. L., and Jayne, B. C. (1998). Effects of speed on the hind limb kinematics of the lizard *Dipsosaurus dorsalis. The Journal of Experimental Biology* **201**, 609–622.

Frappell, P. B., and Daniels, C. B. (1991). Ventilation and oxygen consumption in agamid lizards. *Physiological Zoology* **64**, 985–911.

Garland, T. (1984). Physiological correlates of locomotory performance in a lizard: an allometric approach. *The American Journal of Physiology* **247**, R806–R815.

Garland, T. (1999). Laboratory endurance capacity predicts variation in field locomotor behaviour among lizard species. *Animal Behaviour* **58**, 77–83. doi:10.1006/ANBE.1999.1132

Garland, T., and Adolph, S. C. (1994). Why not to do two-species comparative studies: Limitations on inferring adaptation. *Physiological Zoology* **67**, 797–828.

Garland, T., and Losos, J. B. (1994). Ecological morphology of locomotor performance in squamate reptiles. In 'Ecological Morphology: Integrative Organismal Biology'. (Eds P. C. Wainwright and S. M. Reilly.) pp. 240–302. (University Chicago Press: Chicago.)

Gleeson, T. T. (1979). The effects of training and captivity on the metabolic capacity of the lizard *Sceloporus occidentalis. Journal of Comparative Physiology* **129**, 123–129.

Gleeson, T. T., Mitchell, G. S., and Bennett, A. F. (1980). Cardiovascular responses to graded activity in the lizards *Varanus* and *Iguana. The American Journal of Physiology* **239**, R174–R179.

Greer, A. E. (1989). 'The Biology and Evolution of Australian Lizards.' (Surrey Beatty: Sydney.)

Huey, R. B. (1982). Phylogenetic and ontogenetic determinants of sprint performance in some diurnal Kalahari lizards. *Koedoe* **25**, 43–48.

Huey, R. B., and Hertz, P. E. (1982). Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *The Journal of Experimental Biology* **97**, 41–49.

Irschick, D. J., and Jayne, B. C. (1999). Comparative three-dimensional kinematics of the hindlimb for high-speed bipedal and quadrupedal locomotion of lizards. *The Journal of Experimental Biology* **202**, 1047–1065.

Irschick, D. I., and Jayne, B. C. (2000). Size matters: ontogenetic variation in the three dimensional kinematics of steady-speed locomotion in the lizard *Dipsosaurus dorsalis. The Journal of Experimental Biology* **203**, 2133–2148.

Jayne, B. C., and Irschick, D. J. (1999). Effects of incline and speed on the three-dimensional hind-limb kinematics of a general iguanian lizard (*Dipsosaurus doralis*). *The Journal of Experimental Biology* **202**, 143–159.

Licht, P., Dawson, W. R., Shoemaker, V. H., and Main, A. R. (1966). Observations on the thermal relations of Western Australian lizards. *Copeia* **1966**, 97–110.

Losos, J. B., and Sinervo, B. (1989). The effects or morphology and perch diameter on sprint performance of *Anolis* lizards. *The Journal of Experimental Biology* **145**, 23–30.

Magnusson, W. E., Junqueira de Paiva, L., Moreira da Rocha, R., Franke, C. R., Kasper, L. A., and Lima, A. P. (1985). The correlates of foraging mode in a community of Brazilian lizards. *Herpetologica* **41**, 324–332.

Melville, J., Schulte, J. A., and Larson, A. (2001). A molecular phylogenetic study of ecological diversification in the Australian lizard genus *Ctenophorus. The Journal of Experimental Zoology* **291**, 339–353. doi:10.1002/JEZ.1133

Owerkowicz, T., Farmer, C. G., Hicks, J. W., and Brainerd, E. L. (1999). Contribution of gular pumping to lung ventilation in monitor lizards. *Science* **284**, 1661–1663. doi:10.1126/SCIENCE.284.5420.1661

Perry, G. (1999). The evolution of search modes: ecological versus phylogenetic perspectives. *American Naturalist* **153**, 98–109. doi:10.1086/303145

Pianka, E. R. (1966). Convexity, desert lizards, and spatial heterogeneity. *Ecology* **47**, 1055–1059.

Pianka, E. R. (1986). 'Ecology and natural history of desert lizards: Analyses of the ecological niche and community structure.' (Princeton University Press: Princeton.)

Pianka, E. R. (1997). Australia's thorny devil. *Reptiles* **5**, 15–21.

Pianka, E. R., and Parker, W. S. (1975). Ecology of horned lizards: A review with special reference to *Phrynosoma platyrhinos. Copeia* **1975**, 141–162.

Pianka, E. R., and Pianka, H. D. (1970). The ecology of *Moloch horridus* (Lacertilia: Agamidae) in Western Australia. *Copeia* **1970**, 90–103.

Pianka, G. A., Pianka, E. R., and Thompson, G. G. (1998). Natural history of thorny devils *Moloch horridus* (Lacertilia: Agamidae) in the Great Victoria Desert. *Journal of the Royal Society of Western Australia* **81**, 183–190.

Reilly, S. M., and Delancey, M. J. (1997). Sprawling locomotion in the lizard *Sceloporus clarkii*; the effects of speed on gait, hindlimb kinematics, and axial bending during walking. *Journal of Zoology* **243**, 417–433.

Roberts, A. R. (1998). Ecophysiology of semi-arid geckos. Relationships between ecology and physiology in sympatric nocturnal geckos from a semi-arid sandplain habitat with particular emphasis on locomotion and thermal biology. Ph.D. Thesis, The University of Western Australia, Perth.

Sherbrooke, W. (1999). Why should these lizards look and act so alike? Thorny devils and horny toads. *Nature Australia* **Spring**, 54–63.

Thompson, G. G., and Withers, P. C. (1997). Standard and maximal metabolic rates of goannas (Squamata : Varanidae). *Physiological Zoology* **70**, 307–323.

Thompson, G. G., and Withers, P. C. (2004). Shape of Western Australian dragon lizards (Agamidae). *Amphibia-Reptilia*, In press.

Wang, T., Carrier, D. R., and Hicks, J. W. (1997). Ventilation and gas exchange in lizards during treadmill exercise. *The Journal of Experimental Biology* **200**, 2629–2639.

Weinstein, R. B., and Full, R. J. (1999). Intermittent locomotion increase endurance in a gecko. *Physiological and Biochemical Zoology* **72**, 732–739. doi:10.1086/316710

White, S. R. (1947). Observations on the mountain devil. *Western Australian Naturalist* **1**, 78–81.

Wilson, K. J. (1974). The relationship of oxygen supply for activity to body temperature in four species of lizards. *Copeia* **1974**, 920–934.

Withers, P. C. (2001). Design, calibration and calculation for flow-through respirometry systems. *Australian Journal of Zoology* **49**, 445–461. doi:10.1071/ZO00057

Withers, P. C., and Bradshaw, S. D. (1995). Water and energy balance of the thorny devil *Moloch horridus*: is the devil a sloth? *Amphibia-Reptilia* **16**, 47–54.

Withers, P. C., and Dickman, C. R. (1995). The role of diet in determining water, energy and salt intake in the thorny devil *Moloch horridus* (Lacertilia : Agamidae). *Journal of the Royal Society of Western Australia* **78**, 3–11.

Witten, G. J. (1993). Family Agamidae. In 'Fauna of Australia, Vol. 2A, Amphibia and Reptilia'. (Eds C. J. Glasby, G. J. B. Ross and P. L. Beesley.) pp. 240–252. (AGPS: Canberra.)