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Optimal Body Size with Respect to Maximal Speed for the Yellow-Spotted Monitor Lizard (*Varanus panoptes*; Varanidae)

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ABSTRACT

Studies of locomotor performance often link variation in morphology with ecology. While maximum sprint speed is a commonly used performance variable, the absolute limits for this performance trait are not completely understood. Absolute maximal speed has often been shown to increase linearly with body size, but several comparative studies covering a large range of body sizes suggest that maximal speed does not increase indefinitely with body mass but rather reaches an optimum after which speed declines. Because of the comparative nature of these studies, it is difficult to determine whether this decrease is due to biomechanical constraints on maximal speed or is a consequence of phylogenetic inertia or perhaps relaxed selection for lower maximal speed at large body size. To explore this issue, we have examined intraspecific variations in morphology, maximal sprint speed, and kinematics for the yellow-spotted monitor lizard *Varanus panoptes*, which varied in body mass from 0.09 to 5.75 kg. We show a curvilinear relationship between body size and absolute maximal sprint speed with an optimal body mass with respect to speed of 1.245 kg. This excludes the phylogenetic inertia hypothesis, because this effect should be absent intraspecifically, while supporting the biomechanical constraints hypothesis. The relaxed selection hypothesis cannot be excluded if there is a size-based behavioral shift intraspecifically, but the biomechanical constraints hypothesis is better supported from kinematic analyses. Kinematic measurements of hind limb movement suggest that the distance moved by the body during the stance phase may limit maxi-

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mum speed. This limit is thought to be imposed by a decreased ability of the bones and muscles to support body mass for larger lizards.

Introduction

In ecomorphological studies, locomotion is often used as a link between relevant aspects of the ecology of a species and the morphological characteristics it displays (Arnold 1983; Irschick and Garland 2001). Maximal sprint speed is the most commonly measured locomotor performance trait in such studies because it is often considered to be relevant for catching prey and evading predators (see Garland and Losos 1994 for review).

For most animal groups, absolute speed tends to scale positively with body size (Schmidt-Nielsen 1972; Heglund et al. 1974; Garland 1983; Van Damme and Vanhooydonck 2001). Originally, it was thought that maximum speed should be independent of mass (M) because the length of the leg (and hence stride length [S_L]) should scale in inverse proportion to stride frequency (f; $S_L \propto M^{0.33}$; $f \propto M^{-0.33}$; Hill 1950). However, it was later shown that with increasing body size, S_L increases more rapidly than stride frequency decreases, and the consequence of this is that larger animals are able to attain higher speeds (Heglund and Taylor 1988; Strang and Steudel 1990; White and Anderson 1994; Irschick and Jayne 1999). However, this explanation does not seem to hold at the largest of body sizes (Garland 1983; Van Damme and Vanhooydonck 2001; Clemente et al. 2009).

It has long been known that when a large enough body size range is examined, larger animals do not run faster than intermediate-sized animals (Currey 1977; Coombs 1978). The few studies that have examined this across several mammalian families (Garland 1983), several lizard families (Van Damme and Vanhooydonck 2001), and within a single lizard genus (Clemente et al. 2009) have reported that speed may not increase linearly with body size but instead is best described by a curvilinear fit (Jones and Lindstedt 1993; Iriarte-Díaz 2002). This suggests there is an optimal size with respect to speed above which further increases in M are associated with a decrease in speed.

Most studies that have examined speeds over a large body size range have pooled data from multiple sources; therefore, differences in accuracy of measuring maximal speed at different masses are difficult to avoid. Further, as body size tends to be conserved within lineages of mammals (Garland 1983) and lizards (Van Damme and Vanhooydonck 2001; Clemente et al.

2009), it is difficult to exclude the possible influence of phylogenetic patterns on the relationship between speed and body size. For example, within the mammals included in Garland's (1983) study, most large-bodied species tended to be from the Proboscidea or Perissodactyla, whereas most small-bodied mammals were members of the Rodentia; in Van Damme and Vanhooydonck's (2001) study, most large-bodied lizards were from the family Agamidae, and in the study of Clemente et al. (2009) from the genus *Varanus*, all large-bodied species were clustered in the *gouldi* clade.

There are three possible explanations for the curvilinear relationship between maximal sprint speed and M. (1) Phylogenetic inertia: given that traits are influenced by their evolutionary history and that as shown above, large-bodied species tend to be clustered phylogenetically, then the reduced speed at large size may be a consequence of this clustering, an artifact of phylogenetic history (Blomberg and Garland 2002). (2) Relaxed selection: reduced selective pressure for speed in large-bodied species may be expected as the number of predators for large animals will decrease. This may result in lower than expected sprint speeds (from M) for larger-body species. Convergent evolution of this reduced selection for large-bodied phylogenetic lineages may then explain the repetition of this pattern in different phylogenetic groups. Or, (3) biomechanical constraint: biomechanical limitations for maximal speed at larger body sizes causes maximal speed to decline above some optimal M (Jones and Lindstedt 1993). This may be caused by a decreased ability of muscles and bones to support the increased M in larger animals, and speed must be decreased in order to maintain similar safety factors (Iriarte-Díaz 2002; Biewener 2003; Clemente et al. 2011).

One possible way to differentiate between these competing hypotheses is to examine these traits in a single species, removing phylogenetic bias. While several studies have investigated speed and body size intraspecifically, none has yet examined maximal sprinting speed for a species with a broad M range comparable with those investigated via interspecific studies.

Because size has been documented to have a large effect on running speed, a body length–dependent scale (relative running speed) might be more appropriate when characterizing the performance of animals (Jones and Lindstedt 1993; Van Damme and Van Dooren 1999; Iriarte-Díaz 2002). Analysis of maximum relative speeds rather than maximum absolute speeds may be advantageous for several reasons. In a computer simulation, objects with higher relative speeds were less likely to be caught, suggesting an advantage for animals with higher relative speeds (Van Damme and Van Dooren 1999). Further, when maximum relative speeds of terrestrial mammals were analyzed, differential scaling was observed. Small-bodied mammals showed a nearly independent relationship between maximum relative running speed and body mass, while large-bodied mammals showed a strong negative relationship (Iriarte-Díaz 2002). These measures of maximal relative and absolute running speed can then provide information about mechanical constraints for each group.

In this study, we measured morphology and maximal and relative sprint speed for individuals of a single lizard species to determine whether there is an intraspecific optimal body size for maximizing sprint speed. The yellow-spotted monitor (*Varanus panoptes*) is the third largest monitor in Australia, with a large range in body size, measuring from 0.025 kg (120 mm snout-vent length [SVL]) in juveniles to 6.56 kg (740 mm SVL) in adults (Christian et al. 1995; Christian 2004). It is terrestrial and an active forager, covering as much as 6 km in a day (Christian et al. 1995; Christian and Weavers 1996; Christian 2004), so there is likely to be high selection for locomotor performance. The active-foraging habit, large variation in body size, and the relative abundance of the yellow-spotted monitor in the wild make it ideal for studying the scaling of maximal speeds. Further, we measured the locomotor kinematics of this monitor lizard's stride to determine which, if any, stride parameters might limit maximal speed.

Methods

Morphology

We measured various morphological dimensions for 38 specimens of *Varanus panoptes* from the Western Australian Museum and the Queensland Museum collections. SVL, tail length (Tail), head length (HL), upper forelimb length (UFL), lower forelimb length (LFL), upper hind limb length (UHL), and lower hind limb length (LHL) were measured as shown in figure 1 using digital calipers (± 0.1 mm) or flexible measuring tape (± 1 mm). Additionally, we analyzed total forelimb length (FLL) and total hind limb length (HLL), the sum of the upper and lower limb segments, respectively. Because preservation is known to produce shrinkage in soft tissues, body mass was not measured for museum specimens. However, body mass and the same morphological measurements as above were made for an additional 23 individual *V. panoptes* taken from the field. M was measured for large lizards ($>2,000 \pm 25$ g), medium-sized lizards ($<2,000$ g; $>1,000 \pm 0.5$ g), and small lizards ($<1,000 \pm 0.05$ g). Each lizard was measured and weighed within 2 wk of capture; individuals ranged in M from 0.09 to 5.75 kg.

The extent of geometric similarity was determined by examining slopes of regression lines for logarithmically transformed body dimensions with logarithmically transformed M or SVL. Scaling exponents were determined using model II reduced major axis (RMA) regression. For each regression, the slope was tested against the expectation of isometric growth (McMahon 1984; Schmidt-Nielsen 1984). RMA slope estimates, confidence intervals (CIs), and comparisons between the RMA slopes and expectations (using the likelihood ratio test) were implemented using the program SMATR (Falster et al. 2006).

Maximal Sprint Speed

Maximum sprint speeds were measured for 19 individual *V. panoptes* (a subset of the 23 individuals taken from the field— M range, 0.09–5.10 kg) by taking serial digital pictures at 25
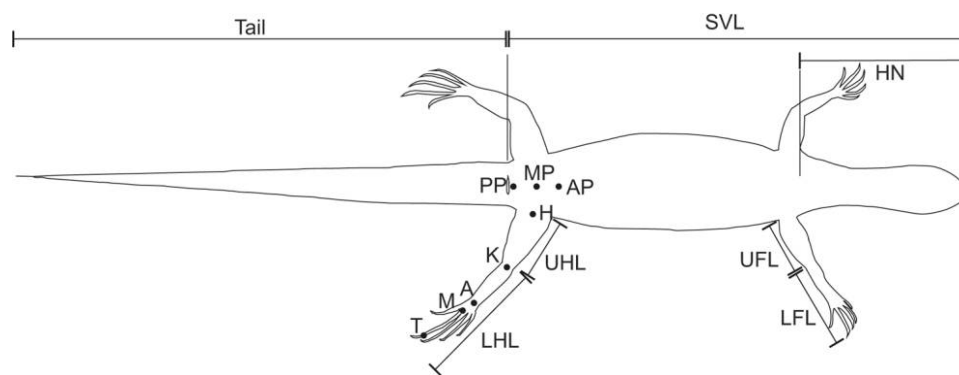
Figure 1. Morphological measurements and kinematic markers for varanids used in this study. Morphological measurements: SVL = snout-vent length; Tail = tail length; HN = head and neck length; UFL = upper forelimb length; LFL = lower forelimb length; UHL = upper hind limb length; LHL = lower hind limb length. Kinematic markers: AP = anterior pelvis; MP = midpelvis; PP = posterior pelvis; H = hip over the acetabulum; K = knee; A = ankle; M = metatarsophalangeal; T = toe tip, excluding claw.

Hz of each lizard as it ran along a "racetrack." Clear plastic or metal sheeting formed the sides of a sand-based racetrack 13.6 m long by 0.75 m wide. A canvas chute was placed at the end of the racetrack to catch running lizards. A Sony MiniDV digital Handycam (model DCR-TRV27 PAL) at the end of the racetrack was directed down at 45° to the center. Lizards were run four or five times during each trial with a total of three trials for each individual. Twenty-four hours rest was allowed between subsequent trials. Multiple runs for each individual were compared, and the maximal speed for each individual was used in subsequent analyses. Body temperature (measured cloacally) was 35°–38°C in all experiments. Each lizard's run was filmed, and the images were analyzed frame by frame using custom-written video analysis software (Visual Basic, ver. 6; Philip Withers, University of Western Australia). The field of view was calibrated to remove the parallax effect, and speed between frames was calculated by digitizing the tip of the lizard's snout for each frame and dividing the distance moved between frames by frame rate (25 s^{-1}). Speed was smoothed using a three-point moving average. This reduced digitizing standard error to 0.06 m s^{-1} as calculated by repeated digitization of the same sprint sequence. Relative speed was calculated in body lengths (SVL) covered per second.

Kinematics

We measured kinematic variables for 32 strides of 9 individual *V. panoptes* (a subset of the 23 individuals taken from the field—$M = 0.1$–5.10 kg) using a Vicon Motion Analysis system (Vicon, Oxford Metric Group). This consisted of 12 infrared cameras mounted on tripods or the wall around a runway. The infrared cameras operated at 250 frames s^{-1} and captured only the three-dimensional position of retroreflective spherical markers (5-mm diameter). Markers were placed on the pelvis, hip, knee, and ankle joints; the metatarsals at the base of the toe; and the tip of the toe excluding the claw (fig. 1). Lizards

were then encouraged to run down the center of the room on a carpet substrate.

The three-dimensional coordinates of the markers were then imported into BodyBuilder software (Vicon, Oxford Metric Group). The position and movement of each lizard were described relative to three axes: X, Y, and Z. Positive values of x, y, and z indicated greater-anterior, right-lateral, and dorsal positions relative to a global coordinate system superimposed on the racetrack. Each stride began at footfall of the right hind limb and ended at the next footfall of the same limb. The measured variables and the terminology used to describe these variables were similar to those used by previous studies (Irschick and Jayne 1999, 2000; Jayne and Irschick 1999). Average forward velocity was taken as distance moved (m) along the X-axis by the anterior pelvis marker during a stride divided by stride duration (s). S_L was the distance traveled by the body along the X-axis between successive footfalls. This was further divided into step length, the distance traveled by the body during the stance phase of the trial, and float length, the distance moved by the body during the swing phase. Similarly, stride duration was divided into stance duration and swing duration for analysis.

Three angles described the movement of the femur relative to the hip. Femur retraction was the angle between the femur and a line perpendicular to the long axis of the pelvis, passing through the hip, such that values of 0° indicated the femur was perpendicular to the long axis of the pelvis and positive and negative values indicated greater amounts of retraction and protraction, respectively. Femur adduction described the angle between the femur and a horizontal plane passing though the hip, with positive and negative values indicating the knee was below or above the hip, respectively. Femur rotation is the angle between the plane containing the femur and the tibia (assuming dorsiflexion of the knee) with a vertical reference plane passing through the hip and knee such that greater positive values indicate greater clockwise rotation of the knee joint.

Statistics

Maximum speed and kinematic variables were regressed against M using both linear and curvilinear (second-order polynomial) models. Akaike Information Criterion (AIC), implemented in Prism (ver. 4.03, Graphpad Software), was used to determine whether a linear model (lm) or a curvilinear model (clm) best fit the relationship between the variables. The model with the lowest corrected AIC (AICc) score was selected as the best model. AICc scores are rescaled to $\Delta_{\text{model}} = \text{AICc}_{\text{model}} - \text{AICc}_{\text{min}}$, where AICc_{min} is minimum of the two AICc values (Burnham and Anderson 2002). This transformation forces the best model to have $\Delta = 0$ and the other model to have a positive score. In addition, Akaike weights are presented for the best model, which can be regarded as the probability that the selected model is correct.

Because of restrictions in size of our kinematic gait laboratory, we were unable to measure all kinematic strides at maximal speed, most strides being less than 70% of maximal speed (as recorded during sprint speed trials). Each individual was measured at various speeds. We excluded strides that were <20% of maximal speed. There was no significant relationship between the percentage of maximum speed for kinematic strides with either body mass ($r^2 < 0.01$, $P = 0.977$) or SVL ($r^2 < 0.01$, $P = 0.870$). The mean percentage of maximal speed for strides was 38.9% ± 13.9% (mean ± SD). This suggests that lizards of different masses were running at or near equivalent speeds.

Results

Morphology

The relationship between M and morphological dimensions is shown in table 1. The increase of SVL with M does not differ from the predictions of geometric scaling with increasing body size. There was some variation in linear morphometric scaling of body parts when compared with SVL. Tail length did not appear to differ from the expectations under geometric growth,

but head and neck length (HN) showed lower than expected scaling, suggesting that larger lizards had relatively shorter heads/necks for a given body size. Total hind limb length had a scaling exponent above 1.0, suggesting larger lizards have relatively longer hind limbs relative to body length. This appeared to be due to the contribution of the upper hind limb, which showed a higher scaling exponent than expected under geometric growth, while the lower hind limb did not appear to differ from expectations. Similarly, the UFL had a higher than expected scaling, while the LFL did not scale differently from 1.0.

Maximum Sprint Speed

The fastest speed recorded for *Varanus panoptes* in laboratory sprint speed trials was 8.32 m s^{-1} for an individual with $M = 1.05$ kg. Maximum sprint speed varied with M, with larger lizards tending to have a higher speed. However, the relationship between speed and M was best described not by a linear relationship but rather by a second-order polynomial ($r^2 = 0.65$ vs. 0.30; $\Delta_{\text{clm}} = 0$, $\Delta_{\text{lm}} = 9.99$, 99.33%). The equation relating maximum sprint speed to M was $\log_{10}$ speed (m s^{-1}) $= -0.2779 \log_{10} M^2$ (g) $+ 1.72 \log_{10} M$ (g) $- 1.863$. This indicated an optimal M of 1.243 kg at a speed of 6.3 m s^{-1} (fig. 2*a*). If the optimal M from speed is used to separate large-bodied and small-bodied lizards, similar to Iriarte-Díaz (2002), then the linear regression of maximal speed for smaller lizards (<1.2 kg) scales with a slope of $M^{0.422}$ (95% CI, 0.243–0.735) using RMA ($r^2 = 0.66$, $P = 0.014$, $n = 8$). The slope for larger-bodied lizards was not significantly different from 0 ($M^{-0.423}$; $r^2 = 0.06$, $P = 0.456$, $n = 11$).

Similar results were obtained when SVL was examined in relation to maximal speed. A curvilinear regression had a better fit to maximal speed than linear regression ($r^2 = 0.74$ vs. 0.34; $\Delta_{\text{clm}} = 0$, $\Delta_{\text{lm}} = 14.45$, 99.93%). The equation relating SVL to maximum speed was $\log_{10}$ speed (m s^{-1}) $= -2.515 \log_{10}$ SVL^2 (m) $- 1.952 \log_{10}$ SVL (m) $+ 0.423$; indicating a maximal sprint

Table 1: Morphology measurements for *Varanus panoptes*

Parameters	n	a	b	r^2	P	Lower CI	Upper CI	Ho	$F_{2, n}$	P
M vs. SVL	23	.335	.370	.953	<.001	.304	.370	.33	.115	.738
SVL vs. Tail	61	.949	.225	.916	<.001	.916	1.034	1.0	.820	.369
SVL vs. HN	61	.871	−.105	.975	<.001	.836	.908	1.0	44.95	<.001
SVL vs HLL	61	1.055	−.515	.977	<.001	1.014	1.098	1.0	7.249	.009
SVL vs. UHL	61	1.106	−1.143	.962	<.001	1.052	1.164	1.0	16.16	<.001
SVL vs. LHL	61	1.012	−.547	.982	<.001	.977	1.048	1.0	.432	.514
SVL vs. FLL	61	1.016	−.577	.983	<.001	.982	1.051	1.0	.895	.348
SVL vs. UFL	61	1.074	−1.221	.966	<.001	1.024	1.127	1.0	8.962	.004
SVL vs. LFL	61	.973	−.602	.982	<.001	.939	1.007	1.0	2.516	.118

Note. For each pair of parameters, the fit of linear reduced major axis regression ($ax + b$) is shown along with the 95% upper and lower confidence intervals (CIs). The slope of the regression (a) is then compared with the predictions from geometric scaling (Ho). Where $n = 23$, live specimens were measured; where $n = 61$, a combination of live and museum specimens were used. M = mass; SVL = snout-vent length; Tail = tail length; HN = head and neck length; HLL = hind limb length; UHL = upper hind limb length; LHL = lower hind limb length; FLL = forelimb length; UFL = upper forelimb length; LFL = lower forelimb length.
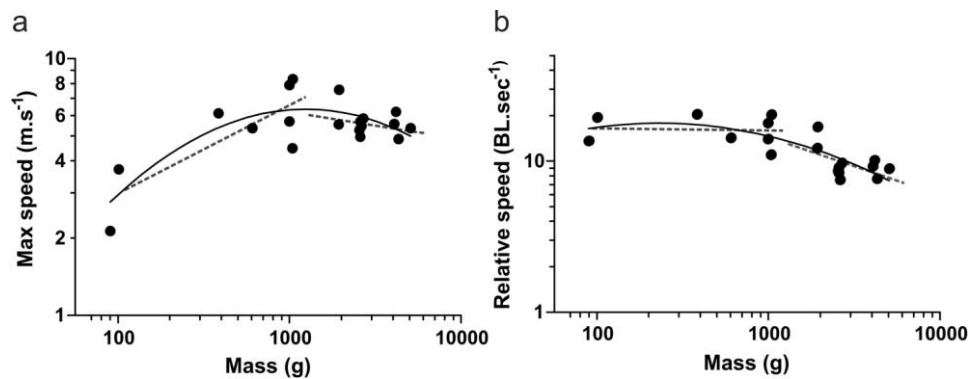
Figure 2. *a*, Curvilinear relationship between body mass and maximal sprint speed for *Varanus panoptes* sprinting down a laboratory racetrack. The curvilinear relationship predicts a maximal speed of 6.3 m s^{-1} at a body mass of 1.243 kg. Regression lines are shown for smaller-bodied lizards (as defined by lizards with body mass below the optimal mass for speed) and large-bodied lizards. *b*, Curvilinear relationship between body mass and relative sprint speed in body lengths per second (BL s^{-1}) for the same lizards shown in *a*. As in *a*, regression is shown for larger- and smaller-bodied lizards.

speed of 6.3 m s^{-1} at an optimal SVL of 0.41 m. When the optimum is again used to separate small- and large-bodied lizards, small-bodied lizards scale with $M^{1.117}$ (95% CI, 0.682–1.264) using RMA ($r^2 = 0.73$, $P = 0.006$, $n = 8$), while large-bodied lizards showed a negative trend ($M^{-1.144}$ RMA) but did not scale significantly different from 0 ($r^2 = 0.28$, $P = 0.093$, $n = 11$).

Relative Sprint Speed

We also compared the relative sprint speed, in body lengths per second, with body mass (fig. 2*b*). This relationship was also best described by a second-order polynomial ($r^2 = 0.64$ vs. 0.49; $\Delta_{clm} = 0$, $\Delta_{lm} = 3.37$, 84.38%; $\log_{10}$ speed [body lengths s^{-1}] $= -0.212 \log_{10} M^2$ [g] $+ 1.004 \log_{10} M$ [g] $+ 0.064$). This indicates an optimum M of 0.233 kg for relative speed, which is much lower than the optimal M for absolute speed shown above. If the optimal M from absolute speed is used to separate small-bodied and large-bodied lizards as above, then the relative speed for small lizards appeared largely independent of M ($M^{-0.218}$ RMA, $r^2 = 0.02$, $P = 0.740$, $n = 8$), while relative speed for larger lizards appeared to decline with increasing M, though statistical support for this was weak ($M^{-0.694}$ RMA, $r^2 = 0.26$, $P = 0.107$, $n = 11$).

Kinematics

The relationships between the kinematic stride parameters and body mass are shown in table 2. For the linear kinematic variables, all variables showed a linear relationship with body size (fig. 3) with the exception of step length (the distance traveled by the body during the stance phase). AIC supported a curvilinear relationship between step length and body mass, reaching a maximal step length at a body mass of 3.5 kg (table 2; fig. 3*b*) when all strides were included ($r^2 = 0.85$ vs. 0.78). When step length is reanalyzed using individual means rather

than strides, the r^2 value for a curvilinear trend was still higher ($r^2 = 0.86$ vs. 0.79); however, AIC support for the curvilinear model is decreased, and the linear model is preferred ($n = 9$, $\Delta_{clm} = 3.79$, $\Delta_{lm} = 0$, 86.94%). Therefore, a larger sample size may be required before a curvilinear relationship between step length and M can be confirmed.

For angular kinematic variables, only the retraction of the femur showed a significant linear relationship with body mass (table 2); all other angular variables showed a nonsignificant relationship with body mass. Femur rotation at midstance showed a weak negative relationship with M, which became significant when regressed with SVL ($r^2 = 0.13$, $P = 0.043$). This suggests larger lizards rotate the femur less at midstance when compared with small-bodied lizards.

Discussion

The measurement of sprint speed of organisms is often central to ecomorphological studies (Arnold 1983; Irschick and Garland 2001). We have confirmed, within a species, that there is an optimal body size in relation to speed. While several studies have shown this effect interspecifically in mammals (Garland 1983), across multiple families of lizards (Van Damme and Vanhooydonck 2001), and within the monitor lizards (Clemente et al. 2009), no previous study has shown this relationship intraspecifically.

By finding this curvilinear relationship within a species, we have shown that this scaling effect occurs where phylogenetic history is not a confounding influence and that an alternative model explaining this result may have broader implications. An alternative model, the biomechanical constraints hypothesis, is consistent with the intraspecific results presented in this study and previous results from interspecific studies. However, the relaxed selection hypothesis may still be significant intraspecifically if there is a size-related shift in behavior. Some lizards have been shown to have considerable behavioral plasticity

Table 2: Relationship between stride parameters and body size

Parameter	AIC preferred model	r^2	P	Δ_{lm}	Δ_{clm}	Probability correct (%)	Best-fit coefficients		
							a	b	c
Stride duration	$ax + b$	.30	.001	0	2.61	78.7	.101	−.887	...
Swing duration	$ax + b$	.15	.029	0	2.37	76.6	.065	−1.061	...
Stance duration	$ax + b$	.19	.011	0	2.34	76.3	.142	−1.348	...
Stride length	$ax + b$	.68	<.001	0	.94	61.6	.222	−1.007	...
Float length	$ax + b$	.30	.001	0	2.61	78.6	.191	−1.181	...
Step length	$ax^2 + bx + c$	.85	<.001	8.75	0	98.8	−.174	1.237	−2.753
Duty factor	...	.08	.126	...	...	...	...	...	...
Femur rotation FF	...	.01	.845	...	...	...	...	...	...
Femur rotation mid	...	.12	.056	...	...	...	...	...	...
Femur rotation ES	...	.01	.822	...	...	...	...	...	...
Femur depression FF	...	.08	.116	...	...	...	...	...	...
Femur depression mid	...	.05	.249	...	...	...	...	...	...
Femur depression ES	$ax + b$	.13	.040	0	2.44	77.2	−.159	1.926	...
Femur retraction FF	...	.01	.692	...	...	...	...	...	...
Femur retraction mid	...	.05	.198	...	...	...	...	...	...
Femur retraction ES	...	.01	.618	...	...	...	...	...	...

Note. For each stride parameter, corrected Akaike Information Criterion (AICc) was used to compare the fit between a linear model ($ax + b$) and a curvilinear model ($ax^2 + bx + c$). All values were log transformed before regression; $n = 32$ strides from nine individuals. AICc scores are expressed as $\Delta_{model} = AICc_{model} - AICc_{min}$, where model is either the linear model (lm) or a curvilinear model (clm). For cases where the fit for linear or curvilinear regression was not significant, AIC analysis was not performed. FF = footfall; mid = midstance; ES = endstance.

within a species, which can affect performance (Moermond 1979; Huey et al. 1990; Garland and Losos 1994; Martín and López 1995; Lailvaux et al. 2003; Asbury and Adolph 2007). Therefore, we cannot exclude the possibility that intraspecific size-related behavior differences are driving this curvilinear speed response to body size. Instead, stronger support for the biomechanical constraints hypothesis could be achieved if the mechanism by which speed is constrained could be described.

Given the largely geometrical scaling of body length and M for the yellow-spotted monitor, it is an ideal species to determine whether biomechanical constraints do exist. While there are numerous hypotheses concerning the positive linear scaling of speed with body size (McMahon 1973, 1975; Gunther 1975; Bejan and Marden 2006), fewer biomechanical explanations have been proposed for curvilinear scaling of speed with body size or why an optimal M in relation to speed could and does occur (but see Iriarte-Díaz 2002).

By comparing both the absolute and relative speeds in these lizards, there is evidence that the initial increase in speed (up to the optimal speed) is based on an increase in body size. When the optimum M for absolute speed is used to separate smaller- and large-bodied lizards, small-bodied lizards appear to scale independently of M when relative maximal speeds are considered and scale close to the predictions for increases in hind limb length with absolute maximum speed. For example, the scaling of absolute speed with body length, $SVL^{1.117}$ (using RMA), is very similar to the allometric scaling of hind limb length with body length, $SVL^{1.055}$ (table 1).

For large-bodied lizards, however, scaling of relative and absolute speed appears to be independent of body size and may even show a negative (but nonsignificant) trend similar to that reported for mammals (Iriarte-Díaz 2002). This suggests a constraint on speed above the optimal M. This constraint did not appear to be related to the morphometric scaling of limb lengths, because linear rather than curvilinear scaling of HLL with SVL was supported by AIC ($\Delta_{clm} = 1.413$, $\Delta_{lm} = 0$, 66.96%). Instead, the decrease in speed above the optimal M may be related to biomechanical properties of the lizard's stride.

As speed is simply S_L divided by stride duration, a runner may obtain a faster top speed by taking steps more frequently or by increasing S_L, thus traveling farther with each step (Biewener 2003). Weyland et al. (2000) suggested that S_L is also determined by the product of the average mass-specific force applied to oppose gravity during foot contact and the forward distance that the body moves during this period (step length). Therefore, speed may be increased by changes in stride duration, step length, or the amount of force applied to the running surface.

Previous reports suggest that speed increases linearly with both S_L and stride frequency (1/stride duration) in mammals (Heglund and Taylor 1988; Strang and Steudel 1990) and several lizard families (White and Anderson 1994; Van Damme et al. 1998; Irschick and Jayne 1999). However, a linear increase with size of both S_L and stride frequency suggests that speed should also scale linearly, which is not the case. For nonlinear scaling of speed to occur, stride duration, S_L, or force applied must also scale nonlinearly and therefore impose an upper limit to sprint speed in relation to body mass.

Both stride duration and S_L can be further divided into a stance phase (when the limb is in contact with the ground)
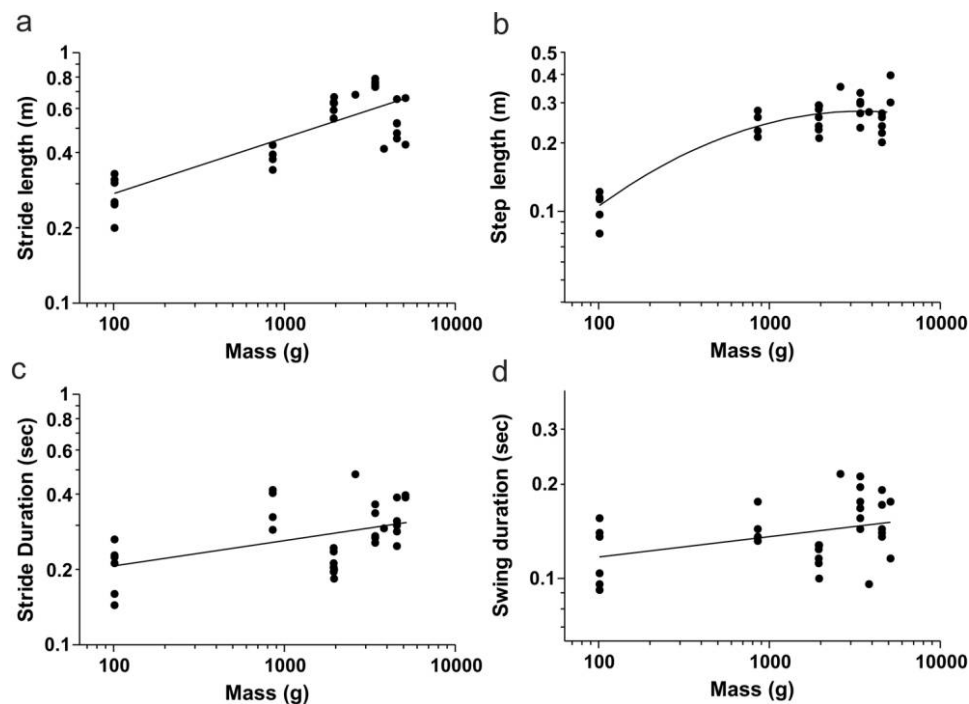
Figure 3. Relationships between kinematic variables for strides and body mass for *Varanus panoptes*. *a*, Stride length with mass (*M*), linear relationship. *b*, Step length with *M*, curvilinear relationship. *c*, Stride duration (log$_{10}$) with *M*, linear relationship. *d*, Swing duration (log$_{10}$) with *M*, linear relationship. $n = 32$ strides from nine individuals.

and a swing phase (when the limb is in the air), each of which could be theoretically altered to modulate running speed. Within *Varanus panoptes*, we were unable to find strong statistical support for nonlinear scaling in either swing duration or stride duration or a curvilinear relationship between float length and body mass. This suggests that the ability to retract the limbs or propel the body forward during the swing phase does not limit maximum speed. However, AIC did support a curvilinear relationship for step length with body mass (fig. 3*b*), at least when all strides were considered. Though a larger sample size would be required to confirm this, these results suggest some support for a stance phase limitation to S_L and therefore speed.

A stance phase limitation to maximum speed was also previously reported for lizards (Higham et al. 2011) and humans (Weyland et al. 2000, 2010). For lizards, attributes of stance phase muscle (gastrocnemius) were better correlated with maximum performance than swing phase muscles (iliofibularis) for *Sceloporus woodi*, a small semiarboreal lizard (Higham et al. 2011). It was then predicted that increased rates of force generation (and increased power) from stance phase muscle decreased stance time, thus increasing S_L and therefore speed. However, this prediction was not supported for *V. panoptes* because the decreased stance time at the largest body sizes was associated with a decrease in the absolute speed achievable.

Instead, previous studies that have examined locomotion across a large range of body sizes for mammals and lizards have shown that maximum speed may be limited by the ability of

bones and muscles to cope with size-related increases in stress rather than a muscular power limitation (Biewener 2003; Clemente et al. 2011). Because locomotor forces exerted on the ground should be some constant multiple of body mass but cross-sectional area of bones and muscles scales with $M^{0.66}$, then stress (force per unit area) should increase with $M^{0.33}$ for geometric animals. This means that larger animals may have an increased risk of limb bone failure (Biewener 1982, 1983*a*).

Mammals appear to reduce this size-related increase in stress by adopting a more upright posture, decreasing the moment arm of the ground reaction force relative to the muscle moment arm, which reduces the muscular effort required to prevent limbs from collapsing and reduces bending forces on long limb bones (Biewener, 1983*a*, 1983*b*, 1989, 1990). However, this strategy was not apparent for lizards; in a large comparative study of varanids, body posture was independent of body size (Clemente et al. 2011). The lack of a trend toward upright posture with body size for lizards was also supported within this study; femur depression did not increase with increasing body size—there even appeared to be a significant decrease (i.e., a change to less upright posture with increased size) at the end of the stance phase for *V. panoptes*. The likely reason that posture does not become more upright with size in lizards is that an upright posture in animals with a sprawling posture may actually lead to an increase in muscle and bone stress as has been reported for iguanas and alligators (Blob and Biewener 1999, 2001; Reilly and Blob 2003). Instead, it was hypothesized

by Clemente et al. (2011) that lizards may reduce size-related stress by decreasing both duty factor and femur rotation.

In reptiles, step length is determined by a combination of both femur protraction and retraction and femur rotation (Brinkman 1981; Reilly and DeLancey 1997). Therefore, it is possible that the magnitude of movement for these kinematic features may be reduced in large lizards. Of these, femur rotation is probably most significant because safety factors for limb bone torsion are approximately half those for bending in the femur and tibia in iguanas and alligators (Blob and Biewener 1999, 2001). As limb length increases, both the torsional moment acting on the femur and the force due to body mass will increase, eventually reaching stresses that the limb bones can no longer support. To reduce this moment arm, larger lizards may reduce femur rotation as has been shown previously for varanids (Clemente et al. 2011). In *V. panoptes* there is some support for a reduction in femur rotation with increasing body size. This reduction in femur rotation will result in a decrease in the step length traveled because the body can travel only a shorter distance before that maximum rotation of the femur is reached. However, an increased sample size would be required to determine that the decrease in femur rotation is greater for large-bodied lizards when compared with small-bodied lizards.

These findings provide a preliminary exploration of limits to sprint speed for monitor lizards. The primary purpose of this study was to demonstrate that there is a limit to sprint speed in a single species as size increases. Several factors could limit maximum locomotor performance, such as muscle energetics, neuromuscular coordination, dynamic constraints, and efficiency (Jones and Lindstedt 1993). Our data suggest that speed initially increases with body size, but limitations to step length appear to constrain maximum speed, and this limitation may be imposed by a decreased ability of the bones and muscles to support body mass for larger lizards. However, these results need to be verified across many species with a larger range in body mass before the details for limits to sprint speed can be fully determined.

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