

Why go bipedal? Locomotion and morphology in Australian agamid lizards

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SUMMARY

Bipedal locomotion by lizards has previously been considered to provide a locomotory advantage. We examined this premise for a group of quadrupedal Australian agamid lizards, which vary in the extent to which they will become bipedal. The percentage of strides that each species ran bipedally, recorded using high speed video cameras, was positively related to body size and the proximity of the body centre of mass to the hip, and negatively related to running endurance. Speed was not higher for bipedal strides, compared with quadrupedal strides, in any of the four species, but acceleration during bipedal strides was significantly higher in three of four species. Furthermore, a distinct threshold between quadrupedal and bipedal strides, was more evident for acceleration than speed, with a threshold in acceleration above which strides became bipedal. We calculated these thresholds using probit analysis, and compared these to the predicted threshold based on the model of Aerts et al. Although there was a general agreement in order, the acceleration thresholds for lizards were often lower than that predicted by the model. We suggest that bipedalism, in Australian agamid lizards, may have evolved as a simple consequence of acceleration, and does not confer any locomotory advantage for increasing speed or endurance. However, both behavioural and threshold data suggest that some lizards actively attempt to run bipedally, implying some unknown advantage to bipedal locomotion.

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Key words: bipedal, sprint speed, acceleration, endurance, locomotion, agamids, dragon lizards.

INTRODUCTION

Bipedalism has been suggested to have risen independently at least six times over the course of vertebrate evolution (Snyder, 1962). Both the thecodont–dinosaur group and modern-day lizards are capable of a bipedal walking gait, as are birds and some primates (including humans). Hopping on two legs has risen independently in placental mammals, marsupials and birds (Snyder, 1962). Bipedalism in these groups may therefore convey some advantage over quadrupedal locomotion, or may be a consequence of the front limbs being used for a different purpose. In birds, the forelimbs have been modified for flight, requiring bipedal terrestrial movement, whereas hopping in mammals may provide an energetic advantage (Bennett, 1985). In some primates, the forelimb may be used for tool making, food handling and carrying articles when standing or walking (Howell, 1944). For lizards, the front limbs are not adapted for a function other than quadrupedal locomotion, thus the advantages of bipedalism for these taxa are not clear.

In extant lizards the bauplan with potential for bipedalism seems to have arisen only once (Fig. 1). Based on the literature (e.g. Irschick and Jayne, 1999; Aerts et al., 2003), personal communications (J. B. Losos, Harvard University) and personal observations (C.J.C.), bipedal locomotion has not been observed in Sphenodontida, Gekkonidae, Scincidae, Cordylidae or Xantusiidae, with quadrupedal locomotion almost certainly being ancestral for these groups. Bipedal locomotion first appears in some Teiioidea and in some Lacertidae (Irschick and Jayne, 1999; Aerts et al., 2003). It is retained in some members of the lineage leading to Iguanidae and Acrodonta, although it is reduced or lost in some groups within these families (e.g. Chamaeleonidae, Phrynosomatidae). The lineage

leading to Anguimorpha, however, seems to have lost the ability to run bipedally (e.g. *Shinisaurus*, *Lanthanotus*) only to reappear within the Varanidae. To our knowledge, the re-emergence of facultative bipedalism within varanids is limited to three species within the gouldii group of the Indo-Australian clade of *Varanus* (*V. gouldii*, *V. panoptes* and *V. giganteus*; C.J.C., personal observation). Therefore, bipedalism seems to have emerged to be lost and regained in subsequent groups, which suggests it is an adaptive trait. So what are the advantages (or disadvantages) of bipedal locomotion. In other words, why do lizards go bipedal?

Snyder was one of the first authors to attempt to answer this question (Snyder, 1949; Snyder, 1952; Snyder, 1954; Snyder, 1962). He argued that bipedal lizards differed from their quadrupedal counterparts in morphology, speed and economy of movement. Of the morphological features cited, long hindlimbs, short forelimbs, a narrow pelvis and a long tail were thought to aid bipedalism mostly through increased stride length. If stride rate remains constant, then increased stride length leads to an increase in a second trait associated with bipedalism, increased speed. Differences in speed between bipedal and quadrupedal lizards were noted, but analysis was difficult since Snyder (Snyder, 1962) was forced to compare lizards that ran only quadrupedally with those that ran only (or seemingly so) bipedally. Moreover, it was often difficult to differentiate between morphological adaptations that were for speed rather than bipedalism *per se*.

Snyder also suggested that bipedalism would increase the economy of movement as no internal work was done to move the front limbs (Snyder, 1949; Snyder, 1952; Snyder, 1954; Snyder, 1962), although he did not test this idea. This issue was examined

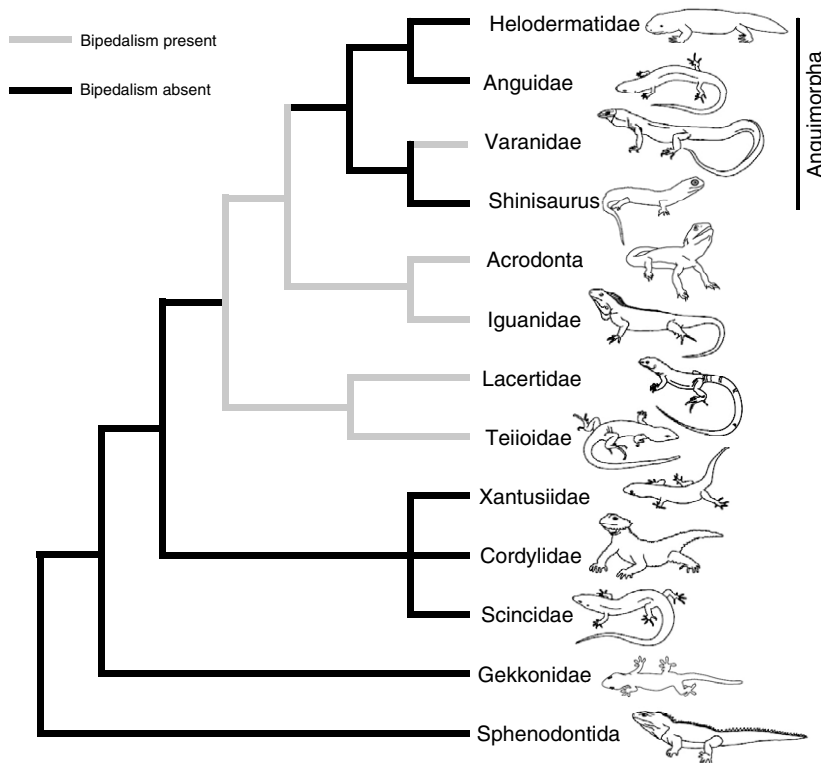


Fig. 1. Evolution of bipedalism within extant lizards. Phylogeny and cartoons from Fry et al. (Fry et al., 2006) and Townsend et al. (Townsend et al., 2004) with permission.

by Fedak and Seeherman (Fedak and Seeherman, 1979) who showed similar costs of transport for ponies and ostriches (of similar size), and further by Roberts et al. (Roberts et al., 1998) who found similar economy for similar-sized dogs and turkeys. Thus bipedalism does not seem to convey any economic advantage in species studied so far. However, these studies were often forced to compare animals that differed greatly, both anatomically and phylogenetically.

Recently, Aerts et al. proposed a more radical explanation for the cause of bipedalism (Aerts et al., 2003). Manoeuvrability, they suggested, benefits from a caudal shift of the body centre of mass (body-COM). They modelled a small lacertid lizard (*Acanthodactylus erythrurus*), to show that acceleration combined with this caudal shift in the body-COM would cause the front legs of the lizard to lose traction with the ground, resulting in bipedal locomotion. Thus, Aerts et al. (Aerts et al., 2003) proposed that bipedalism may just be a consequence of acceleration and a caudal shift of the body-COM. For their theory to be supported, there would be a maximum threshold of acceleration for quadrupedal movement beyond which the lizard would have no choice but to run bipedally, with the front limbs losing contact with the ground. Aerts et al. predicted that this acceleration threshold would be influenced by the relationship between the horizontal body-COM and the vertical body-COM (Aerts et al., 2003).

We used high-speed cinematography to analyse quadrupedal and bipedal locomotion in Australian agamid lizards, in the light of the hypothesis of Aerts et al. (Aerts et al., 2003). The comparative method was used to test these ideas and explore this evolutionary puzzle in a phylogenetic context. The fundamental question that we addressed was whether bipedalism is dependent on phylogeny, morphology, energetic cost of locomotion, speed and/or acceleration.

MATERIALS AND METHODS

Sixteen species of Western Australian agamid lizard were collected from the field; *Chlamydosaurus kingii* Gray 1825 ($N=6$),

Ctenophorus caudicinctus Gunther 1875 ($N=14$), *C. cristatus* Gray 1841 ($N=4$), *C. femoralis* Storr 1965 ($N=11$), *C. isolepis* Fischer 1881 ($N=8$), *C. maculatus* Gray 1831 ($N=3$), *C. nuchalis* De Vis 1884 ($N=14$), *C. ornatus* Gray 1875 ($N=14$), *C. reticulatus* Gray 1845 ($N=7$), *C. rubens* Storr 1965 ($N=3$), *C. scutulatus* Stirling and Zietz 1893 ($N=5$), *Lophognathus gilberti* Gray 1842 ($N=2$), *L. longirostris* Boutenger 1883 ($N=6$), *Pogona minor* Sternfeld 1919 ($N=6$), *Rankinia adelaidensis* Gray 1841 ($N=6$) and *Tympanocryptis cephalo* Gunther 1867 ($N=3$). Each lizard ran on a motorised treadmill 180 cm long by 56 cm wide, with a Plexiglas side, 28 cm high. The treadmill was kept at a constant speed of 1000 mm s^{-1} ; no attempt was made to run the lizards at a steady-state pace, since changes in velocity over the stride were of interest in this analysis. Each lizard was encouraged to run until exhaustion, past two synchronised high-speed video cameras (Peak HSC-200 PM, Peak Performance Technologies, Inc., Oxford, UK), capturing data at $200 \text{ frames s}^{-1}$ from both a dorsal and lateral view. The videos were examined frame-by-frame to categorise each stride as bipedal, quadrupedal or a transitional stride. A stride was only analysed if the video sequence included three sequential strides or completely crossed the field of view. Strides that stopped halfway across the field of view were not considered. For each lizard, the percentage of bipedal strides (%bipedal) was calculated. Species means were then used in all statistical analyses.

Various morphological dimensions were measured for each lizard. These were, snout-to-vent length (SVL), tail length (TAIL), head-neck length (HN), thorax-abdomen length (TA), upper forelimb length (UFL), lower forelimb length (LFL), forefoot length (FFOOT), upper hindlimb length (UHL), lower hindlimb length (LHL), hindfoot (HFOOT) and body mass. These linear measurements were made to $\pm 0.05 \text{ mm}$ using digital callipers; body mass was measured using electronic scales to $\pm 0.05 \text{ g}$. Species means were used in all analyses. For morphological dimensions, the effects of size were removed using a variation of Somers' size free analysis

(Sommers, 1986) developed by Thompson and Withers (Thompson and Withers, 2005) for *Ctenophorus*. %Bipedal data were corrected for size dependence by computing residuals from logSVL.

The horizontal body-COM was measured for each species on a subset of the lizards (either live or dead). Each lizard was placed in a 'natural' position with its hindlimbs under the hips, and the forelimbs under the shoulder. Lizards were placed on a ruler that was suspended by string, in perfect balance. The lizard was moved forward or backwards until the balance of the ruler was restored. The body-COM was recorded as the anterior distance from the body-COM to the vent of each lizard.

We were unable to train lizards to run at various constant speeds on a treadmill to calculate the net cost of transport and efficiency of locomotion. Instead we used endurance as a surrogate for locomotor efficiency. Endurance was determined in a separate trial on the motorised treadmill at 280 mm s⁻¹ in a controlled-temperature room at 35°C. Time to exhaustion for each lizard was recorded with a stopwatch. Exhaustion was indicated by a lack of righting response, once turned on its back. Since mass is thought to have a significant effect on endurance (Garland, 1994), residuals from a log-log plot of mass and endurance were regressed against %bipedal.

Speed and acceleration of both bipedal and quadrupedal strides was measured for four species; *C. caudicinctus* (N=5, 66 strides), *C. femoralis* (N=4, 16 strides), *C. nuchalis* (N=4, 25 strides) and *R. adalaidensis* (N=4, 12 strides). These species were chosen for speed and acceleration studies because they were representative of the overall %bipedal range. Speed and acceleration were determined by digitizing a mark on the lizard over the pelvis and a mark on the treadmill, at 200 frames s⁻¹, using Peak Motus software (V2000; Peak Performance Technologies, Inc.). The position of the pelvis was calculated relative to the treadmill to remove the effect of speed of the treadmill. The resulting three-dimensional coordinates were smoothed using a mean square error algorithm in Matlab (ver. 7.1, Mathworks, Inc., Natick, MA, USA) since this approach was least biased and error prone, and outperformed other available methods (Walker, 1998).

Since bipedalism may be the result of sustained speed or acceleration (as opposed to maximal speed and acceleration that may occur for very short periods of time), both maximal and average values for speed and acceleration were analysed. The highest recorded speeds and accelerations for each stride were used for maximum speeds and accelerations. Average speed was calculated as the mean value for speed scores over the entire stride. The derivative of the regression for speed over time was used to calculate average acceleration.

The log-likelihood statistic was used to calculate the presence and strength of a threshold between bipedal and quadrupedal for speed and acceleration. This statistic describes the probability that the observed values of the dependent variable (speed or acceleration) may be predicted from the observed values of the independent variables (bipedal or quadrupedal). This statistic ranges from 0 to minus infinity, where for this test values closer to zero indicate a tighter threshold. This statistic was calculated using the probit analysis in Minitab (ver. 15, Minitab, Inc., State College, PA, USA).

The acceleration thresholds for bipedalism were calculated for each species from acceleration data. The 50th percentile from the probit analysis was used as an estimate of the acceleration threshold. All strides from each individual in a species were grouped together for analysis.

Lizard acceleration thresholds were compared to those predicted by the model of Aerts et al. (Aerts et al., 2003), which relates

bipedalism to both the position of the horizontal body-COM and vertical body-COM by the equation

$$a_x = (a_y - g) (x_{bc} - x_{fh}) / (y_{bc}),$$

where a_x is the instantaneous fore-aft acceleration of the body-COM, a_y is the instantaneous up-down acceleration of the body-COM (assumed to be approximately zero), g is -9.81 m s^{-2} , x_{bc} is the horizontal position of the body-COM forward of the hip, x_{fh} is the point of application of the ground reaction force (GRF) of the hindlimb and y_{bc} is the vertical position of the body-COM. To determine x_{fh} and y_{bc} , the hip and toe were digitized using Peak Motus software (Peak Performance technologies, Inc. V2000). The point of application of the ground reaction force (x_{fh}) was the distance along the x axis of the toetip and the hip. Since x_{fh} changes during the stride, the midpoint between the most forward and distal position of the toe relative to the hip was used. The vertical position of the body-COM (y_{bc}) was assumed to approximate the hip height at footfall. Lizard acceleration thresholds predicted by the model of Aerts et al. (Aerts et al., 2003) were calculated from the midpoint of strides that showed obvious bipedal behaviour.

Statistical analysis

All statistical analyses were carried out using StatistixL (ver. 1.5, Statistix.com, Perth, WA, Australia), unless otherwise stated. All data were tested for the presence of a normal distribution using Lilliefors test implemented in Matlab. If this condition was met,

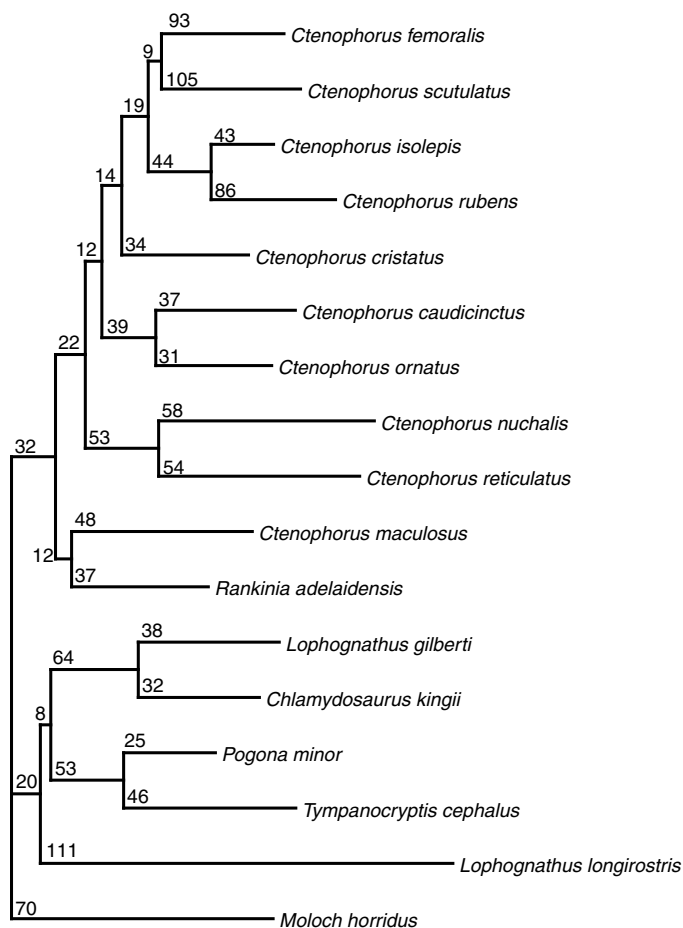


Fig. 2. Maximum likelihood hypothesis for Australian agamids using 1748 bp from mitochondrial gene sequences (Melville et al., 2001). Branch lengths are in substitutions per site \times 1000.

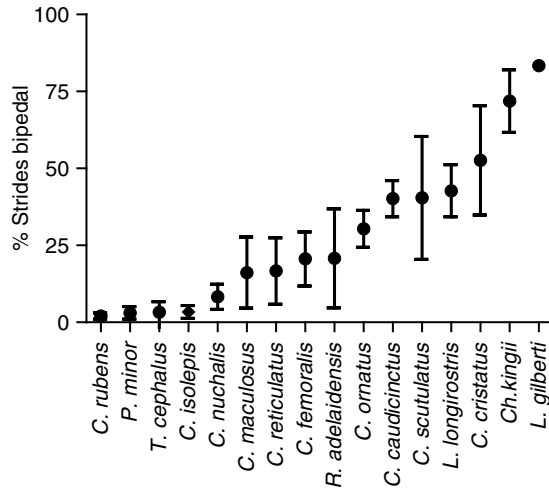


Fig. 3. Percentage of strides that were bipedal for each of the lizards used in the study. Species means and standard errors are shown.

then parametric tests were performed; otherwise their non-parametric equivalent was used. The relationship between morphological traits and %bipedal was tested using Pearson's correlations. To test the effect of bipedalism on speed and acceleration, one-tailed *t*-tests were used. In each case, quadrupedal strides were assumed to have a lower speed and acceleration than bipedal strides. Strides from all individuals from each species were grouped for analysis.

The effects of phylogenetic inertia on %bipedal were tested using independent contrasts (I-C PCW) using custom-written software (P.C.W.). The independent contrasts analysis is based on documentation for PDAP (Garland et al., 1993), and k^* calculation is based on (Blomberg et al., 2003) for a Brownian motion model ($d=1$).

The phylogenetic relationships among Australian agamids has been largely resolved (Melville et al., 2001; Hugall et al., 2008), but no single tree is available with branch lengths for all species included in this study. A distance matrix was calculated from a maximum likelihood tree using 1748 bp of mitochondrial gene sequences (ND1, ND2 and COI) for the species published in GenBank from Melville et al. (Melville et al., 2001). *Moloch horridus* was used as an outgroup based on Hugall et al. (Hugall et al., 2008). Sequences were aligned using ClustalX (Thompson et

al., 1997). The phylogenetic tree was constructed using the maximum likelihood algorithm by the computer program PAUP* [Sinauer Associates, Inc., Sunderland, MA, USA, ver. 4.0b2a (Swofford, 2000)]. The appropriate model of molecular evolution for the maximum likelihood analysis was evaluated by the likelihood ratio test implemented by the computer program MrModeltest 3.7 (Posada and Crandall, 1998).

RESULTS

Phylogeny

The maximum likelihood phylogeny for the lizards in this study is given in Fig. 2. The tree was similar to previous relationships published for Australian agamids (Melville et al., 2001; Hugall et al., 2008). The *Ctenophorus* clade was retained by this tree, as was the nesting of *Rankina* within this clade. The close association between *Typanocryptis* and *Pogona* was also apparent. Therefore this tree is useful in phylogenetic analysis.

%Bipedal

All species measured were capable of bipedal running, but differed in their proportion of bipedal strides. Variation in bipedalism among species spanned the entire range in almost a continuum (Fig. 3). Some lizards would readily run bipedally, e.g. up to 85% of the strides for *L. gilberti*, whereas others rarely ran bipedally, e.g. *C. rubens*. The k^* value for %bipedal was 0.789 with a *P* value of 0.532 suggesting that bipedalism is not strongly associated with phylogeny within this group of agamids.

Morphology

Morphological data for the 16 species of Australian agamid (Table 1) showed a significant relationship to %bipedal. %Bipedal was significantly correlated with log snout-vent length ($r^2=0.44$, $P=0.005$, $N=16$; Fig. 4A), with the larger lizard species running bipedally more frequently. When phylogenetically independent data were examined, contrasts for bipedalism were still significantly correlated with contrasts for logSVL ($r^2=0.46$, $P=0.004$, $N=15$).

Few of the relative body dimensions (after the effect of size was removed using Somers' size-free analysis) were significantly correlated with %bipedal (Table 2). Size-free features such as a relatively long tail or short forelimbs were not correlated with size-corrected %bipedal in these lizards. Only size-free UHL, size-free HN length and size-free TA had a significant correlation with %bipedal (Table 2). Both HN and TA were negatively related to

Table 1. Morphological, endurance and %bipedal species means \pm standard error for 15 species of Australian agamid

Species	<i>N</i> (strides)	%bipedal \pm s.e.m.	SVL \pm s.e.m. (mm)	B-COM \pm s.e.m. (in mm) (<i>N</i>)	Endurance \pm s.e.m. (in sec) (<i>N</i>)
<i>Ch. kingii</i>	6 (65)	71.90 \pm 10.18	196.46 \pm 11.21	41.21 \pm 8.05 (2)	
<i>C. caudicinctus</i>	13 (248)	40.20 \pm 5.88	64.30 \pm 2.99	17.84 \pm 1.78 (6)	132.75 \pm 21.70 (12)
<i>C. cristatus</i>	4 (77)	52.59 \pm 17.75	90.30 \pm 10.36	16.27 \pm 2.41 (2)	80.00 \pm 18.01 (3)
<i>C. femoralis</i>	5 (66)	20.59 \pm 8.76	49.36 \pm 0.62	12.65 \pm 0.15 (2)	
<i>C. isolepis</i>	9 (126)	3.37 \pm 2.06	46.98 \pm 2.98	13.6 \pm 0.00 (1)	133.67 \pm 29.29 (6)
<i>C. maculosus</i>	3 (36)	16.15 \pm 11.52	53.78 \pm 1.41		86.33 \pm 6.64 (3)
<i>C. nuchalis</i>	14 (319)	8.29 \pm 4.11	84.76 \pm 5.24	34.72 \pm 4.08 (3)	311.67 \pm 88.86 (9)
<i>C. ornatus</i>	19 (341)	30.35 \pm 5.98	84.19 \pm 0.87	21.12 \pm 0.00 (1)	155.83 \pm 13.41 (6)
<i>C. reticulatus</i>	7 (128)	16.67 \pm 10.80	69.05 \pm 4.31	22.30 \pm 1.99 (2)	102.57 \pm 29.89 (5)
<i>C. rubens</i>	3 (146)	2.05 \pm 1.03	68.22 \pm 0.25	15.90 \pm 0.00 (1)	
<i>C. scutulatus</i>	4 (46)	40.43 \pm 19.94	74.73 \pm 16.59	15.79 \pm 4.71 (2)	90.33 \pm 13.92 (3)
<i>L. gilberti</i>	2 (18)	83.33 \pm 0.00	100.50 \pm 14.50	19.20 \pm 0.00 (1)	125.50 \pm 10.19 (15)
<i>L. longirostris</i>	7 (89)	42.72 \pm 8.45	89.91 \pm 6.10	14.70 \pm 2.33 (2)	104.67 \pm 16.07 (6)
<i>P. minor</i>	6 (208)	3.06 \pm 2.05	89.48 \pm 9.49	32.08 \pm 4.38 (8)	200.67 \pm 8.76 (2)
<i>R. adelaidensis</i>	6 (77)	20.81 \pm 16.10	43.55 \pm 1.70	15.22 \pm 1.82 (2)	67.09 \pm 10.51 (3)
<i>T. cephalala</i>	3 (37)	3.33 \pm 3.33	45.62 \pm 2.17	18.78 \pm 0.68 (3)	87.00 \pm 0.00 (1)

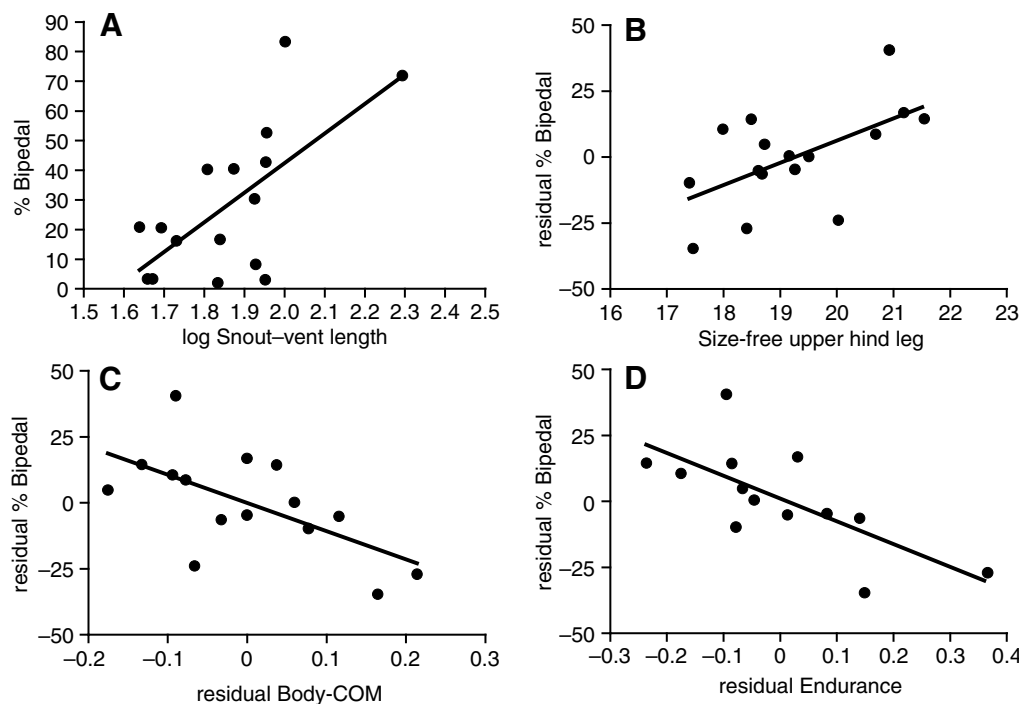


Fig. 4. Relationship between the percentage of strides run bipedally with morphological and performance variables. Residual %bipedal and residual body centre of mass (body-COM) scores are from snout-vent length. Residual endurance scores are from mass.

%bipedal, whereas UHL was positively related to %bipedal (Fig. 4B). However, these were not significant after Šidák-Bonferonni correction for multiple tests was applied.

The horizontal body-COM position was significantly and positively correlated with size (log body-COM vs logSVL, $r^2=0.47$, $P=0.004$, $N=15$). After the effect of size was removed by computing residuals, differences in body-COM were significantly related to %bipedal ($r^2=0.38$, $P=0.015$, $N=15$; Fig. 4C). Lizards for which body-COM was relatively closer to the hip were bipedal more frequently than lizards with the body-COM located more anteriorly. This result was still significant when analysed in a phylogenetic context, using independent contrasts for size-corrected body-COM and size-corrected %bipedal ($r^2=0.40$, $P=0.012$, $N=14$).

Endurance

Size-corrected endurance was negatively correlated with %bipedal ($r^2=0.49$, $P=0.008$, $N=13$; Fig. 4D). This was also true for phylogenetically corrected data ($r^2=0.40$, $P=0.012$, $N=12$). Lizards

that were more bipedal generally had a lower endurance, whereas those running predominantly quadrupedally could do so for longer. Endurance was also positively related to body-COM. Lizards with relatively higher endurance tended to show an anterior shift in the body-COM ($r^2=0.53$, $P=0.007$, $N=12$).

Speed and acceleration

Average speed of bipedal strides was not significantly higher than average speed for quadrupedal strides for any of the four species tested (Table 3). However, for average acceleration there was a significant difference between quadrupedal strides and bipedal strides for three of the four species tested (Table 3). Average acceleration for bipedal strides was significantly higher than for quadrupedal strides, except for *C. femoralis*, which had no significant difference between average acceleration of bipedal and quadrupedal strides. This suggests that acceleration rather than speed is important for bipedalism.

To determine the presence of a threshold between quadrupedal and bipedal strides logistic regression was used. Here results of the log-likelihood statistic close to zero suggest a more distinct threshold. For each of the four species tested, average acceleration had a more distinct threshold between quadrupedal and bipedal strides, than did average speed (Table 3).

Maximal speed of bipedal strides was not significantly different from the maximal speed of quadrupedal strides for three of the four species tested (Table 4). The exception was *R. adelaidensis*, which had a higher speed for bipedal strides. Similarly, maximal acceleration of bipedal strides was not significantly different from maximal acceleration of quadrupedal strides for three of the four species examined (Table 4). The exception was *C. nuchalis*, which had significantly higher acceleration for bipedal strides compared with quadrupedal strides.

Acceleration thresholds differed for each species (Table 5, Fig. 5). For both maximum and average accelerations, *C. femoralis* showed the lowest acceleration threshold (i.e. ran bipedally at lower accelerations), whereas *R. adelaidensis* showed the highest

Table 2. Correlations between %bipedal and size-free dimensions

Size-free dimension	r^2	P
Head-neck length	0.35	0.016
Thorax-abdomen length	0.26	0.043
Tail length	0.05	0.389
Fore-foot length	0.05	0.411
Upper-forelimb length	-0.21*	0.429
Lower-forelimb length	0.08	0.285
Hind-foot length	0.39*	0.133
Upper-hindlimb length	0.09	0.255
Lower-hindlimb length	0.34	0.018

Parametric tests used Pearson correlations, non-parametric tests used Spearman rank correlation. *Spearman's rank correlation (r_s).

Significant values ($P<0.05$) are in bold type. After Šidák-Bonferonni corrections for multiple tests, significance levels for parametric and non-parametric tests are 0.007 and 0.025, respectively.

Table 3. Results of one-way *t*-tests and log-likelihood statistics for bipedal vs quadrupedal speeds and accelerations, using average speed and acceleration (over entire stride)

Species	Speed			Acceleration		
	<i>t</i> _{d.f.}	<i>P</i>	Log likelihood	<i>t</i> _{d.f.}	<i>P</i>	Log likelihood
<i>C. caudicinctus</i>	-1.24 ₍₆₎	0.131	-32.6	-3.45 ₍₆₎	0.007	-12.6
<i>C. femoralis</i>	-0.32 ₍₅₎	0.381	-9.7	-1.02 ₍₅₎	0.178	-9.0
<i>C. nuchalis</i>	-1.29 ₍₇₎	0.119	-11.4	-3.70 ₍₇₎	0.004	-4.8
<i>R. adelaidensis</i>	-0.72 ₍₅₎	0.252	-8.0	-2.52 ₍₅₎	0.027	-3.5

Significant values (*P*<0.05) are in bold type. Log-likelihood statistic shows the strength of the threshold; values closer to 0 denote less overlap.

Table 4. Results of one-way *t*-tests and log-likelihood statistics for bipedal vs quadrupedal speeds and accelerations, using maximum speed and acceleration (over entire stride)

Species	Speed			Acceleration		
	<i>t</i> _{d.f.}	<i>P</i>	Log likelihood	<i>t</i> _{d.f.}	<i>P</i>	Log likelihood
<i>C. caudicinctus</i>	-1.84 ₍₆₎	0.058	-31.1	-2.13 _(4.01)	0.050	-29.8
<i>C. femoralis</i>	-0.41 ₍₅₎	0.350	-9.5	-0.33 ₍₅₎	0.377	-10.0
<i>C. nuchalis</i>	-1.77 ₍₇₎	0.060	-9.4	-4.59 _(3.58)	0.010	-1.6
<i>R. adelaidensis</i>	-2.90 ₍₅₎	0.017	-5.6	-1.34 ₍₅₎	0.119	-6.2

Significant values (*P*<0.05) are in bold type. Log-likelihood statistic shows the strength of the threshold; values closer to 0 denote less overlap.

Table 5. Predicted threshold values from four species of Australian agamids

Species	Maximum acceleration threshold (mm s ⁻²)	Average acceleration threshold (mm s ⁻²)*	<i>x</i> _{th} (mm)	<i>x</i> _{bc} (mm)	<i>y</i> _{bc} (mm)	Threshold (mm s ⁻²)*
<i>C. caudicinctus</i>	3394±2513	722±491	-5.23	14.95	26.06	7391
<i>C. femoralis</i>	3294±7176	-154±3507	-6.23	7.44	26.76	5011
<i>C. nuchalis</i>	4027±358	1116±789	-9.17	32.09	31.41	8023
<i>R. adelaidensis</i>	12093±10744	3076±1734	-3.84	11.35	14.04	9991

*Based on Aertz et al. (Aertz et al., 2001).

*x*_{th} is the point of application of the GRF of the hindlimb; *x*_{bc} is the horizontal position of the body-COM forward of the hip; *y*_{bc} is the vertical position of the body-COM. Values for acceleration show mean ± s.e.m.

acceleration threshold (i.e. higher accelerations for bipedal strides). Acceleration thresholds were not significantly related to %bipedal, nor any morphological trait.

The acceleration threshold predicted from the model of Aerts et al. (Aerts et al., 2003) also differed for each species (Table 5). The order for threshold values was the same as those calculated from acceleration scores above, with *C. femoralis* and *C. caudicinctus* showing lower thresholds and *C. nuchalis* and *R. adelaidensis* showing higher thresholds. For *R. adelaidensis* the model closely agreed with the maximum acceleration threshold, however, for the three remaining species, the thresholds predicted from the model of Aerts et al. (Aerts et al., 2003) were higher when compared to the maximum acceleration thresholds calculated from acceleration data (Table 5).

DISCUSSION

Is bipedalism adaptive or just a consequence of acceleration?

Snyder suggested that changes in morphology, speed and endurance were associated with bipedalism (Snyder, 1962). The latter were thought to be advantageous and hence bipedalism was considered an adaptation. We have shown that some of these morphological features are related to bipedalism, but most are related to a caudal shift of the body-COM. Snyder suggested that long hindlimbs, short forelimbs, long tails and a narrow pelvis were adaptations to bipedalism (Snyder, 1962). Of these, only upper hind limb length was related to %bipedal for Australian dragons. Body size was also

strongly related to %bipedal, complicating the issue, since both size and long hindlimbs are also widely associated with sprint speed (Garland and Losos, 1994), thus as Snyder (Snyder, 1962) noted it is often difficult to separate whether these features have developed as an adaptation to bipedalism or speed.

Snyder also suggested that running bipedally may provide a significant economic advantage over running quadrupedally since no work needs to be done to move the front limbs (Snyder, 1962). Endurance data from the current study do not support this notion. Lizards that ran bipedally did not run for as long, which suggests, (1) lizards that run bipedally are not doing so to conserve energy, and (2) lizards that run bipedally may incur an energetic cost. The latter point suggests that bipedalism may provide some other benefit(s) to balance this cost. Whether endurance is a useful proxy for estimating the energetic cost of transport is still unclear. However, previous studies have shown that while endurance capacity generally *increases* with mass (Garland, 1994), the energetic cost of transport usually *decreases* with mass (John-Alder et al., 1986). Thus, what little evidence exists suggests that low costs of transport are associated with higher endurance capacities.

Since %bipedal and body-COM are related, it is possible that body-COM may influence endurance. For instance, a quadruped may benefit from an anterior shift of the body-COM since both the fore and hindlimb can contribute to forward propulsion, and may reduce the role of fatigue for the hind limbs. A posterior shift in

the body-COM may result in the hindlimbs contributing most of the propulsive force, and thus fatiguing earlier.

Snyder also proposed that bipedalism would allow an increase in speed, since the hindlimbs were able to move through a larger stride without being interrupted by the forelimbs (Snyder, 1962),

however the current data do not support consistently higher speeds for bipedal strides.

The conclusion of Aerts et al. (Aerts et al., 2003), that lizards run bipedal because forward acceleration creates a lift on the front part of the body, receives stronger support. We show that

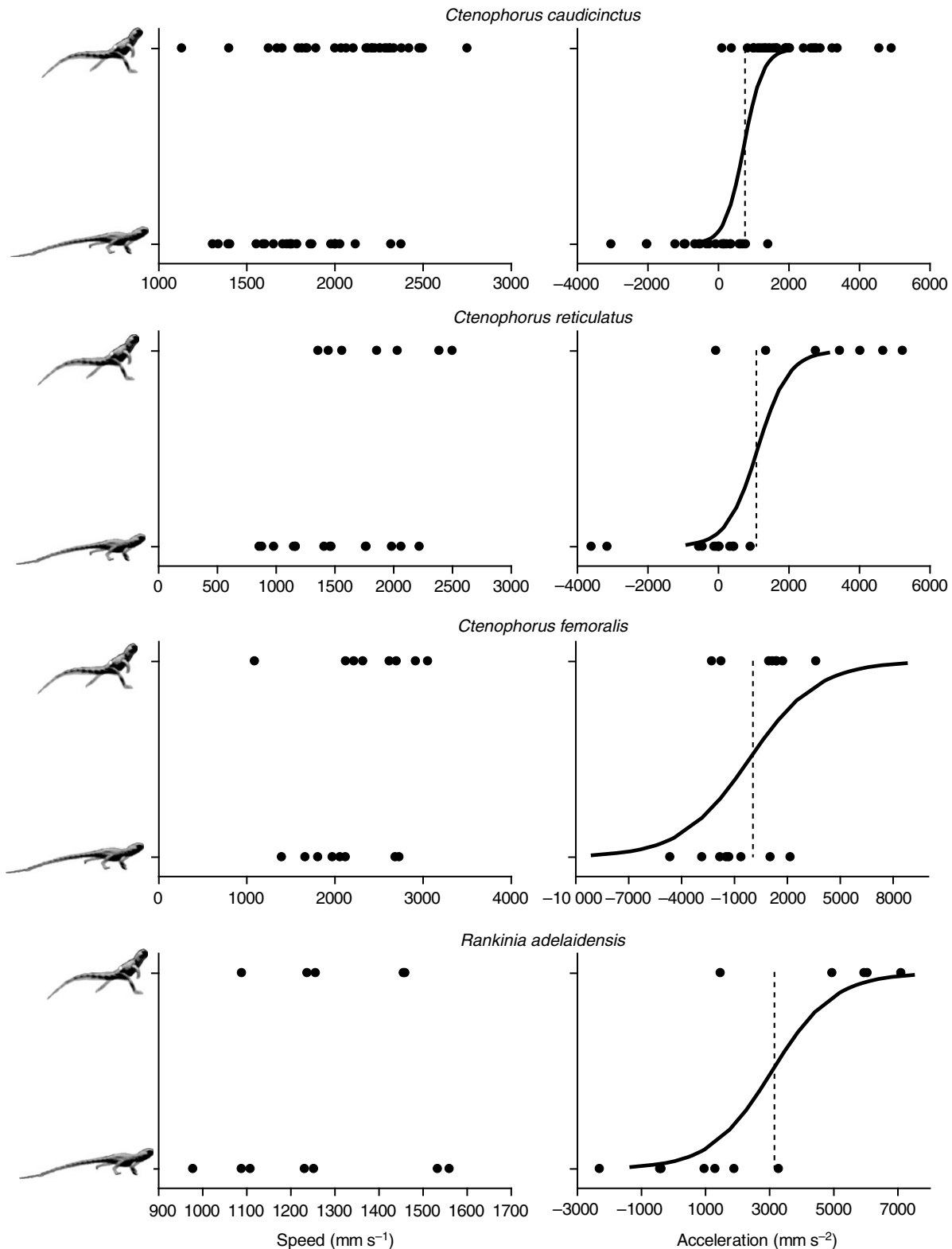


Fig. 5. Average speed and acceleration scores for all strides of four species of Australian agamid. For acceleration scores, the transitional point, indicated by the broken line, is predicted from probit analysis.

acceleration was a better indicator than speed of posture during the stride, at least for average acceleration. The cause of the disparity between maximal and average acceleration data is unknown. Perhaps this suggests that bipedalism is dependent on longer periods of constant acceleration, or it may reflect the higher error rate inherent in calculating maximum acceleration (Walker, 1998).

The models developed by Aerts et al. (Aerts et al., 2003) to predict acceleration thresholds matched the data order for our Australian agamids, i.e. it predicted species with low thresholds, from those with high thresholds. However, the absolute values for the threshold predicted by Aerts et al. (Aerts et al., 2003) were considerable higher. This shows that while the point of application of the hindlimb, and the horizontal and vertical positions of the body-COM may be important to bipedalism, there may be other factors which allow lizards to run bipedally at lower accelerations. One possibility is that lizards are able to modify these factors during a stride. Certainly the point of application of the hindlimb changes relative to the hip throughout the stride, but incorporating this into the model will only produce a predicted threshold higher than the ones presented here.

Another possibility is that lizards actively manipulate the body-COM which may cause bipedalism at lower than predicted accelerations. Aerts et al. (Aerts et al., 2003) noted that active tail lifting during the acceleratory phase will affect trunk rotation positively, causing the front limbs to lose contact with the ground earlier than predicted by the model. Furthermore, the forelimb position can change from one stride to the next. Some species actively tuck their fore limbs along the side of the body during some bipedal strides (compare *C. caudocinctus* Movie 1 in supplementary material, where arms are held away from body, with *L. gilberti* Movie 2 in supplementary material, where arms are tucked into the body). This may have the effect of moving the body-COM closer to the hip, allowing bipedal locomotion at lower accelerations, extending a bipedal stretch. These observations are important as they suggest that some lizards actively attempt to run bipedally, which implies an advantage; however the advantage does not appear to be speed or endurance.

In any case, the presence of an acceleration threshold seems likely, and the conclusions of Aerts et al. (Aerts et al., 2003), that bipedalism evolved as a consequence of acceleration, seems probable. However, the exact position of these thresholds, a model to predict them and any derived benefit of bipedalism requires further investigation.

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