Limb segment contributions to the evolution of hind limb length in phrynosomatid lizards

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Longer hind limbs are often associated with faster maximum sprint speeds measured in the laboratory and sometimes with increased Darwinian fitness in studies of individual variation in natural populations. Limb length may be altered by changing the length of one or all segments, with different functional consequences. Segment length evolution can be influenced by both natural and sexual selection, and lineage-specific effects (multiple solutions) may also occur. We examined the evolution of total hind limb length, as well as thigh, crus, pes, and toe length, among 46 species of phrynosomatids and also investigated the role of habitat use and shared evolutionary history in shaping limb morphology. Because sexes are usually behaviourally and morphologically dimorphic, we examined them separately. In females, habitat was only an important predictor of crus (lower leg) length. In males, habitat was not an important predictor of any variable. Overall, clade-level differences were more important than habitat as predictors of segment or total hind limb length. Not all limb segments scaled isometrically with the combined length of other segments, and both sex and clade affected the scaling of some segments. These results suggest that clade-level differences are more important than habitat use for explaining differences in limb length and proportions, and sexual dimorphism may be an important consideration in morphology–performance–behaviour–fitness relationships. © 2015 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2016, **117**, 775–795.

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INTRODUCTION

Locomotion is used by many animals for avoiding predators (Foster *et al.*, 2015), obtaining resources, and interacting with conspecifics (Swingland & Greenwood, 1983), and so locomotor performance capacity can have important impacts on Darwinian fitness (Jayne & Bennett, 1990; Walker *et al.*, 2005; Husak, 2006; Husak *et al.*, 2006; Calsbeek & Irschick, 2007; Irschick & Meyers, 2007; Irschick *et al.*, 2008; Lailvaux & Husak, 2014). According to the morphology–performance–behaviour–fitness para-

digm, limb morphology may respond to selection for increased locomotor performance if (1) performance during locomotor behaviour is important for components of fitness such as survival or reproductive output and (2) limb morphology affects performance ability (Arnold, 1983; Garland & Losos, 1994; Careau & Garland, 2012).

The relationships between morphology, performance, and fitness are often examined in lizards because of the wide diversity in morphology, physiology, and behaviour among species (Garland & Losos, 1994). Links have been established between aspects of fitness, such as survival and reproductive output, and performance measures such as maximum sprint speed and endurance (Irschick *et al.*, 2008; Lailvaux

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& Husak, 2014). Similarly, locomotor performance has been linked to limb morphology both within and among species of lizard (Losos, 1990a, b; Sinervo, Hedges & Adolph, 1991; Sinervo & Losos, 1991; Garland & Losos, 1994; Bauwens *et al.*, 1995; Macrini & Irschick, 1998; Bonine & Garland, 1999; Melville & Swain, 2000; Zani, 2000; Vanhooydonck & Van Damme, 2001; Toro *et al.*, 2003; Toro, Herrel & Irschick, 2004; Irschick *et al.*, 2005a, b; Vanhooydonck *et al.*, 2006; Gifford, Herrel & Mahler, 2008; Goodman, Miles & Schwarzkopf, 2008; Tulli, Abdala & Cruz, 2012). Specifically, longer hind limbs have been associated with increased jump distances, as well as increased sprint speed, on both level and inclined surfaces in interspecific comparisons (Losos, 1990b; Bauwens *et al.*, 1995; Bonine & Garland, 1999; Vanhooydonck & Van Damme, 2001; Goodman *et al.*, 2008). Thus, understanding the evolutionary patterns of lizard hind limbs can help reveal how a diverse group of species may respond to selection for increased (or decreased) locomotor performance, as well as the likelihood of trade-offs between different aspects of performance (Vanhooydonck *et al.*, 2014; Albuquerque, Bonine & Garland, 2015).

As in many vertebrates, lizard hind limbs are complex structures made up of multiple segments. Although some studies have examined the evolution of individual segment lengths (Vanhooydonck & Van Damme, 1999, 2001; Melville & Swain, 2000; Kohlsdorf, Garland & Navas, 2001; Herrel, Meyers & Vanhooydonck, 2002; Schulte *et al.*, 2004; Gifford *et al.*, 2008; Goodman *et al.*, 2008; Grizante *et al.*, 2010; Tulli *et al.*, 2012), others relate performance, Darwinian fitness, and habitat using total hind limb length (Losos, 1990b; Bauwens *et al.*, 1995; Irschick *et al.*, 1997; Bonine & Garland, 1999; Calsbeek & Irschick, 2007; Bonino *et al.*, 2011). However, each segment of the hind limb is structurally and functionally distinct and changes to each segment could have different effects on locomotion. The elongation of any one or more segments in a limb could achieve increased hind limb length in response to selection for greater sprinting or jumping performance, although there are biomechanical reasons to expect elongation of certain segments over others, depending on which aspect of locomotor performance is under selection. Adding length to any segment will add mass to that segment, which can have important consequences for locomotion because it would require more work to overcome the momentum and inertia of the limb to decelerate or change the direction. In general, proximal limb segments tend to be more massive (per unit length) than distal segments, minimizing the inertial moments during locomotion. Thus, increasing the length of a proximal segment in response to selection for greater hind limb length

will result in a greater increase in mass of the limb than a similar lengthening of a distal segment (Coombs, 1978). An increase in length of the thigh could result in additional costs because it is positioned perpendicular to the direction of gravitational force when lizards move with a sprawling gait (Snyder, 1952; Brinkman, 1981; Rewcastle, 1981; Reilly & Delancey, 1997a). The length of the thigh is a moment arm about which the gravitational pull on the centre of mass is acting, and an increase in thigh length will increase the magnitude of the gravitational moment at the knee joint that must be resisted by muscles to support the body (Biewener, 1989). Thus, a long thigh could be both energetically costly and place high demand on the muscles of the hind limb (Biewener, 1989). In contrast to the thigh, the toes might be expected to elongate without as many associated costs. Toes are both the most distal segment and also the most slender, and so elongation would add the least amount of mass relative to the hind limb length (Coombs, 1978). However, a long slender toe would be less resistant to bending and more likely to fracture. Therefore, individual hind limb segments are expected to respond differently to selection on various aspects of locomotor performance (e.g. acceleration vs. speed vs. stamina).

The functional constraints imposed by habitat on morphology may differ among the segments of the same limb (Snyder, 1954, 1962; Vanhooydonck & Van Damme, 1999; Herrel *et al.*, 2002). Lizards living in open terrestrial habitats may be largely unconstrained in their locomotion, although more complex habitats, such as rocky areas or dense vegetation, may limit the length of certain hind limb segments. Reducing the lateral extent of the limbs when moving through complex habitats is likely beneficial with respect to limiting the obstruction of limb movements (Vanhooydonck & Van Damme, 1999; Vanhooydonck, Van Damme & Aerts, 2000). Arboreal animals moving on narrow branches are expected to have shorter limbs in general to reduce the distance of the body (centre of mass) from the substrate, and hence maintain stability (Cartmill, 1985; Pounds, 1988; Sinervo & Losos, 1991; Losos & Irschick, 1996; Kohlsdorf *et al.*, 2001). During slow movements on narrow branches, the toe may not contribute to the effective length of the limb (Spezzano & Jayne, 2004). Thus, a long toe may not increase the distance of the body from the branch but could still be beneficial during faster running behaviours or jumps. Differentially elongating one segment over the others may allow for a beneficial elongation of the hind limb at the same time as circumventing certain habitat-related constraints. Specific predictions for crus and pes length evolution are less obvious because the contributions of these segments depend largely on

the details of locomotor kinematics. In any case, if some segments shorten in response to selection whereas others lengthen, then lizards living in different habitats may have the same overall limb length but different relative segment lengths.

In addition to habitat, the evolution of locomotor morphology in lizards may be influenced by the effect of sexual dimorphism on locomotor performance (Garland & Else, 1987; Lailvaux, 2007; Kaliontzopoulou, Carretero & Llorente, 2010; Kaliontzopoulou, Bandeira & Carretero, 2013). For example, males of the lacertid species *Podarcis bocagei* and *Podarcis carbonelli* have longer hind limbs and forelimbs than females (Kaliontzopoulou *et al.*, 2010) and, for *P. bocagei*, males have higher sprint speeds compared to females, with the pattern extending to other measures of locomotor performance (Kaliontzopoulou *et al.*, 2013). Differences in behaviour and habitat use presumably reflect differences in selection that drive sexual dimorphism in morphology and locomotor performance (Kaliontzopoulou *et al.*, 2013), although they can also arise as a result of differences in the hormonal milieu acting across ontogeny (Cox, Butler & John-Alder, 2007; John-Alder & Cox, 2007). For example, male lizards often hold and defend a territory to secure mates, whereas females do not engage in this behaviour. In *Crotaphytus collaris*, sex-specific locomotor performance is related to Darwinian fitness (Husak *et al.*, 2006). The fastest sprinting speeds are observed in *C. collaris* that are defending territories, and faster males are more successful at defending territories and sire more offspring (Husak & Fox, 2006; Husak *et al.*, 2006; Husak, Fox & Van Den Bussche, 2008). Females of this species do not face the same type of territory-related selection for high sprint speeds (Husak & Fox, 2006). Intraspecific studies may reveal the causal links between sexual dimorphism in locomotor morphology, behaviour, and performance, although interspecific phylogenetic analyses can also provide indirect evidence for different selective regimes between the sex-specific patterns of morphological evolution.

In the present study, we examined patterns of limb segment variation by comparing possible explanatory hypotheses, including habitat use, (natural or sexual selection on) total limb length, and shared evolutionary history (differences among clades), as well as all their combinations. Because species share common evolutionary histories to varying degrees, phylogenetic statistical methods were used (Felsenstein, 1985; Blomberg, Garland & Ives, 2003; Garland, Bennett & Rezende, 2005; Rezende & Diniz-Filho, 2012; Garamszegi, 2014). The specific predictions for limb segments are that: (1) lizards with longer hind limbs relative to body length will have relatively shorter proximal limb segments and relatively longer distal limb segments, which would allow increased limb length at the same time as minimizing the addition of mass to the limb; (2) arboreal species will have shorter hind limbs overall to reduce the distance of the body from the locomotor surface; and (3) lizards living in terrestrial habitats with dense vegetation or rocky habitats will have shorter thighs to reduce contact of the limbs with vegetation, rocks, or other obstacles.

MATERIAL AND METHODS

Data were obtained for separate sexes for 28 species of phrynosomatid lizards from Herrel *et al.* (2002) and supplemented with data for an 18 additional species measured from museum specimens using a digital caliper (accuracy of 0.1 mm; Mitutoyo Corp.). Morphological measurements included the lengths of the thigh, crus, pes, and fourth toe, as well as snout–vent length (SVL) (see Appendix, Table A1). The total length of the hind limb (HL) was calculated as the sum of the individual segment lengths. Mean values were obtained for each sex in each species and were treated separately during analyses. The data from Herrel *et al.* (2002) represent a mix of measurements from live and preserved specimens and therefore may be influenced by the effects of preservation on body dimensions. We expect preservation to affect all limb segments equally and thus not alter the lengths relative to one another. Preservation may impact upon the relationship between each segment length and SVL, although this is unlikely because these measurements are dependent on the lengths of skeletal elements rather than soft tissue. Habitat classification was determined based on descriptions of habitat use and collection locations from the literature (Smith, 1936, 1939, 1996; Mittleman, 1942; Stebbins, 1985; Burquez, Flores-Villela & Hernandez, 1986; Ortega-Rubio & Arriaga, 1990; Conant & Collins, 1991; Ortega-Rubio *et al.*, 1992; Ballinger & Watts, 1995; Morrison *et al.*, 1995; Mink & Sites, 1996; Block & Morrison, 1998; Grismer, 2002; Herrel *et al.*, 2002; Lemos-Espinal, Smith & Ballinger, 2002; Sherbrooke, 2003).

To avoid part-whole correlations when examining the relationship between segment length and HL, each segment was compared with the length of the remaining hind limb when that segment was removed (HL – Segment) (Christians, 1999). Log (SVL) was highly correlated with all log-transformed morphometric measurements (see Appendix, Table A1), and so we corrected for SVL using the allometric exponent method from Blomberg *et al.* (2003). Specifically, the slope of the regression line

from a phylogenetic generalized least squares (PGLS) regression of log(variable) on log(SVL) was used as the exponent in the equation: log[variable/(SVL^b)] (Table 1).

To examine the patterns of hind limb morphology evolution within each sex, we selected the best regression model for each variable including simple regressions and analysis of covariance (ANCOVA), including habitat and clade as categorical variables, and two-way interactions between variables based on the Akaike information coefficient with correction for small sample size (AICc). To account for the shared evolutionary history between these species in regression models, we used a phylogeny modified from the combined mitochondrial DNA plus nuclear DNA phylogeny in Pyron, Burbrink & Wiens, 2013. Branches were removed to exclude taxa for which we did not have limb segment data using MESQUITE, version 2.75 (Maddison and Maddison, 2011) (Fig. 1). The branch lengths used in all analyses were from the original phylogeny based on molecular data. Additionally, the species were divided into five clade groupings for use in statistical analyses to determine whether the phylogenetic signal exists mainly in the

Table 1. Slopes of phylogenetic generalized least squares regressions of each morphometric trait [log(trait)] with body size [log(snout–vent length)] used to correct for body size for each sex

Variable	Sex	r^2	Parameter	Coefficient	Lower 95%	Upper 95%
HL	Male	0.87	Y_int	−0.09	−0.29	0.10
			Slope	0.98	0.87	1.08
	Female	0.82	Y_int	−0.09	−0.34	0.15
			Slope	0.97	0.84	1.11
Thigh	Male	0.81	Y_int	−0.69	−0.97	−0.43
			Slope	1.03	0.88	1.17
	Female	0.85	Y_int	−0.77	−1.01	−0.52
			Slope	1.06	0.93	1.19
Crus	Male	0.82	Y_int	−0.86	−1.13	−0.60
			Slope	1.10	0.96	1.25
	Female	0.76	Y_int	−0.82	−1.16	−0.53
			Slope	1.08	0.92	1.26
Pes	Male	0.79	Y_int	−0.91	−1.18	−0.63
			Slope	0.99	0.84	1.14
	Female	0.69	Y_int	−0.90	−1.26	−0.55
			Slope	0.99	0.79	1.18
Toe	Male	0.59	Y_int	−0.34	−0.68	0.00
			Slope	0.76	0.58	0.95
	Female	0.52	Y_int	−0.26	−0.61	0.12
			Slope	0.70	0.50	0.90
HL − Thigh	Male	0.84	Y_int	−0.22	−0.44	0.01
			Slope	0.95	0.83	1.08
	Female	0.75	Y_int	−0.18	−0.47	0.10
			Slope	0.93	0.78	1.09
HL − Crus	Male	0.86	Y_int	−0.16	−0.36	0.04
			Slope	0.93	0.82	1.03
	Female	0.80	Y_int	−0.17	−0.41	0.08
			Slope	0.93	0.79	1.06
HL − Pes	Male	0.86	Y_int	−0.17	−0.38	0.05
			Slope	0.97	0.85	1.09
	Female	0.83	Y_int	−0.16	−0.40	0.06
			Slope	0.97	0.84	1.09
HL − Toe	Male	0.88	Y_int	−0.33	−0.54	−0.14
			Slope	1.04	0.93	1.15
	Female	0.84	Y_int	−0.35	−0.60	−0.12
			Slope	1.05	0.92	1.19

Each segment length has a corresponding measure of remainder hind limb length that is the length of the hind limb minus the length of that segment. All regression slopes are statistically different from zero (all $P < 0.001$).
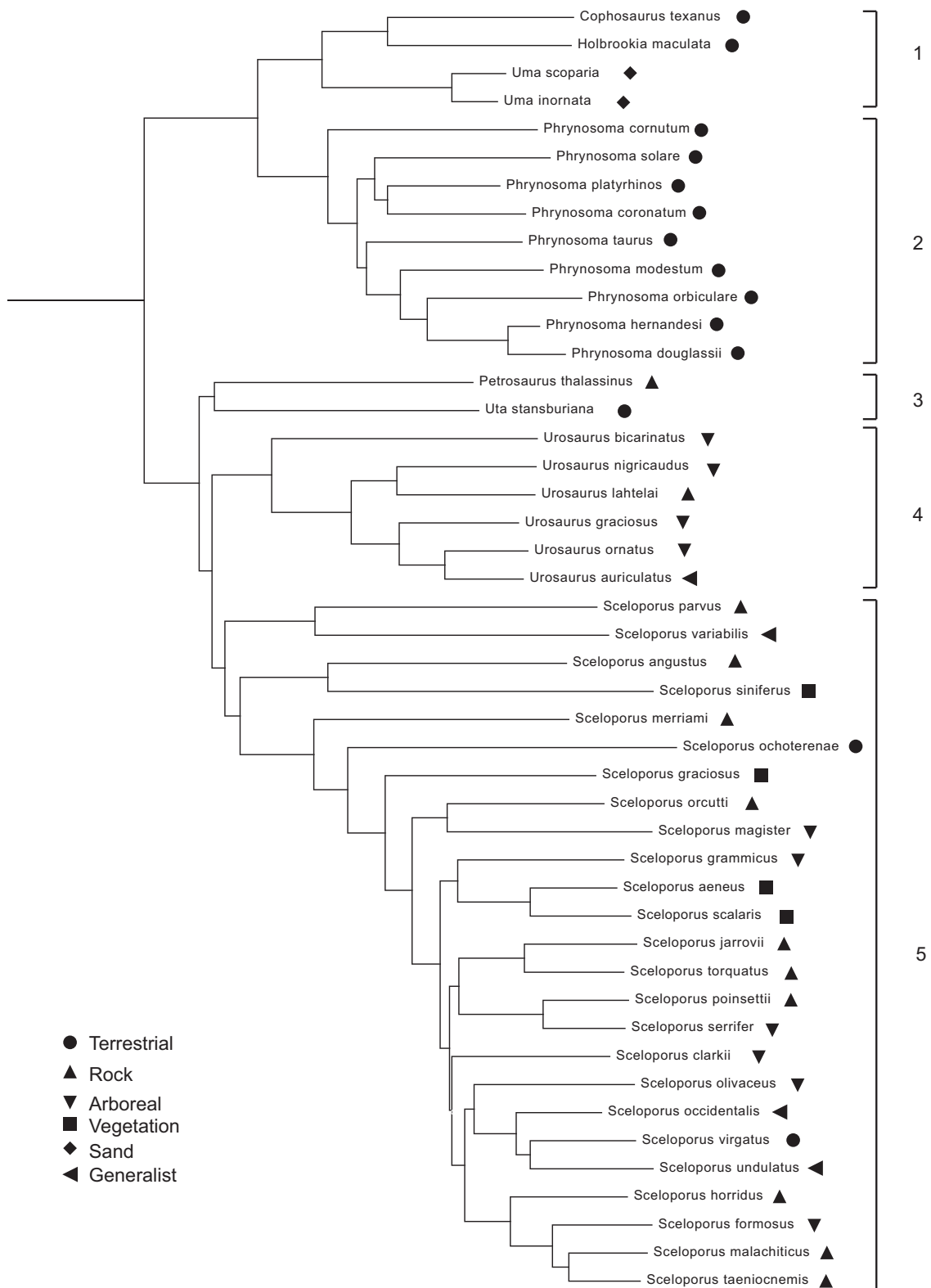
Figure 1. Phylogenetic tree showing the relationships for 46 species of phrynosomatid lizards (modified from Pyron *et al.*, 2013). Symbols indicate the habitat classification for each species into one of six categories: terrestrial, rocky habitats, arboreal, terrestrial living in dense vegetation, sand-dwelling, and generalist. The brackets indicate the five clades recognized for statistical analyses. Branch lengths are consistent with the original phylogeny (Pyron *et al.*, 2013).

major clade transitions or in the structure within the clades (Fig. 1) (Gartner *et al.*, 2010). The monophyletic groups used were sand lizards (Clade 1), *Phynosoma* species (Clade 2), *Petrosaurus thalassinus* and *Uta stansburiana* (Clade 3), *Urosaurus* species (Clade 4), and *Sceloporus species* (Clade 5). We tested for a phylogenetic signal in individual variables and assessed significance using 10 000 randomizations in PHYSIG_LL (Blomberg *et al.*, 2003) in MATLAB (R2012a; The MathWorks, Inc.).

Using REGRESSIONv2 in MATLAB (Lavin *et al.*, 2008), we assessed the fit of various models for each variable, including simple regressions, and ANCOVA, including habitat, clade, and habitat + clade as categorical variables (Gartner *et al.*, 2010). Evolution was represented in three different ways for each regression model: ordinary least squares (OLS) regression, which assumes a star phylogeny with contemporaneous tips, PGLS regression using the tree as shown in Figure 1, and regression with residuals modelled to have evolved via an Ornstein–Uhlenbeck process (RegOU). The RegOU models effectively compute the phylogenetic signal of the residual variation simultaneous with calculation of the regression coefficients. The internal nodes of the tree are pulled towards either the root or the tips, stretching or shrinking the branch lengths. The estimated parameter d takes a value of 1 when branch lengths are left unchanged; $d > 1$ results in a more hierarchical tree and indicates a stronger phylogenetic signal in the residuals than implied by the original tree, and $d < 1$ indicates the residuals match a phylogeny that is somewhat closer to a star phylogeny than the original tree (Blomberg *et al.*, 2003; Lavin *et al.*, 2008). An estimated d value of zero indicates that a star yields the best-fitting model.

The AICc was determined from the ln maximum likelihood for each model and used to compare the fit of each model. The relative fit of each model was assessed qualitatively using the Akaike weight, which is the probability of that model being selected as the best model if data were collected again under similar circumstances. The evidence ratio was calculated as another way to assess the relative strength of the models. A model with an evidence ratio of 4 means that the best model is four times better than the current model.

Models using OLS were confirmed using JMP, version 10.0.2 (SAS Institute Inc.) and Tukey–Kramer honestly significant difference (HSD) tests were used to determine pairwise differences for significant categorical variables in these OLS models. Pairwise comparisons for categorical variables in models using PGLS regression or RegOU were simple *t*-tests with α reduced to 0.001 to account for multiple comparisons. The (partial) regression slopes were compared

with the hypothesized null value of one for isometric scaling using a simple *t*-test [$T = $ (slope – null slope)/ SE of slope]. When interaction terms were significant, separate regression slopes were determined for each group and used to test for isometry. Note that the estimates of allometric regression slopes will generally underestimate the true functional relationships when measurement error exists in the independent variable(s), as is the case in all of our analyses. At present, however, methods to perform model selection via information-theoretic criteria in a phylogenetic context with measurement error models are not well developed.

RESULTS

For both male and female phrynosomatid lizards (Table 2), SVL and all size-adjusted traits had a statistically significant phylogenetic signal based on randomization tests, except for thigh length in both sexes and female crus length. Although almost all variables showed a strong phylogenetic signal when considered independently, this does not necessarily mean that phylogeny is an important predictor when considering the relationships between these variables. Additionally, the clade variable included in the possible models represented some phylogenetic signal that may be present in the data. Therefore, OLS models, both with and without clade, were considered in the model selection process. The top three (of 27 total) regression models for each trait are presented separately for males (Table 3) and females (Table 4).

For males, the best model of hind limb length was a PGLS regression with SVL (Fig. 2, Table 3). For females, the hind limb length was best explained by an OLS regression including SVL and clade (Fig. 2, Table 4). Both SVL and clade were statistically significant factors in that model, and females in clade 1 had significantly longer hind limbs than clade 2 (Tukey–Kramer HSD, $P = 0.0018$), clade 4 ($P = 0.0017$), and clade 5 (0.0248) (Table 5).

For both males and females, the best model of thigh length was an OLS regression with remainder length of the hind limb (Tables 3, 4, Fig. 3), and the relationship with remainder hind limb length was statistically significant for both sexes (Table 5). Crus length in males was best explained by a PGLS regression with remainder hind limb length (Table 3) and remainder hind limb length had a significant positive relationship with crus length (Fig. 4, Table 5). The length of the crus in females was best explained by an OLS model including remainder hind limb length, habitat, and the interaction

Table 2. Univariate tests for phylogenetic signal using PHYSIG_LL (Blomberg *et al.*, 2003) in MATLAB

Trait	Sex	Observed MSE_0/MSE	K	MSE_{tree}	MSE_{star}	P	LML
HL	Male	1.32	0.788	0.0016	0.0021	0.000	83.54
HL	Female	1.08	0.643	0.0026	0.0027	0.008	72.17
Thigh	Male	0.64	0.383	0.0028	0.0017	0.856	70.32
Thigh	Female	0.93	0.557	0.0025	0.0022	0.083	73.34
Crus	Male	1.45	0.865	0.0024	0.0029	0.000	74.08
Crus	Female	1.08	0.643	0.0044	0.0042	0.052	59.84
Pes	Male	1.07	0.640	0.0029	0.0031	0.006	69.37
Pes	Female	0.96	0.573	0.0055	0.0052	0.032	55.02
Toe	Male	2.45	1.465	0.0045	0.0109	0.000	59.72
Toe	Female	1.74	1.037	0.0057	0.0099	0.000	53.98
HL – Thigh	Male	1.67	0.998	0.0017	0.0027	0.000	81.79
HL – Thigh	Female	1.04	0.620	0.0035	0.0035	0.014	65.24
HL – Crus	Male	1.64	0.982	0.0016	0.0025	0.000	83.87
HL – Crus	Female	1.24	0.742	0.0027	0.0033	0.000	71.37
HL – Pes	Male	1.30	0.774	0.0017	0.0021	0.001	81.55
HL – Pes	Female	1.10	0.658	0.0024	0.0025	0.005	74.04
HL – Toe	Male	1.16	0.692	0.0016	0.0016	0.005	83.92
HL – Toe	Female	1.02	0.608	0.0026	0.0024	0.043	71.94
SVL	Male	1.32	0.790	0.0113	0.0148	0.000	38.31
SVL	Female	1.39	0.828	0.0123	0.0163	0.000	36.45

Snout–vent length (SVL) was log-transformed. All other variables were corrected for SVL using the allometric scaling procedure of Blomberg *et al.* (2003) (see text). K is a measure of phylogenetic signal. The P value is for randomization tests using the mean square error (MSE). The phylogenetic tree is shown in Fig. 1 (Expected MSE_0/MSE = 1.68). LML, log marginal likelihood.

Table 3. The top three regression models for each trait ranked based on Akaike information coefficient with correction for small sample size (AICc) for male lizards

Dependent variable	Independent variables	Model type	d	ln maximum likelihood	AICc	Cumulative Akaike weight	Evidence ratio
Thigh	HL – Thigh	OLS		89.336	−172.10	0.63	1.00
Thigh	HL – Thigh	RegOU	1.30E-17	89.336	−169.70	0.81	3.33
Thigh	Habitat + HL – Thigh	OLS		94.482	−169.07	0.95	4.54
Crus	HL – Crus	PGLS		85.929	−165.29	0.41	1.00
Crus	Clade + HL – Crus	OLS		90.737	−164.53	0.69	1.46
Crus	HL – Crus	RegOU	0.991	85.995	−163.02	0.82	3.11
Pes	Clade + HL – Pes	OLS		85.687	−154.43	0.37	1.00
Pes	HL – Pes	OLS		80.120	−153.67	0.63	1.46
Pes	HL – Pes, Clade, HL – Pes * Clade	OLS		91.245	−152.72	0.78	2.34
Toe	HL – Toe, Clade, HL – Toe * Clade	OLS		86.974	−144.18	0.70	1.00
Toe	Clade + HL – Toe	OLS		78.972	−141.00	0.84	4.92
Toe	HL – Toe, Clade, HL – Toe * Clade	RegOU	0.296	86.880	−140.30	0.94	6.96
HL	SVL	PGLS		85.279	−163.99	0.47	1.00
HL	SVL	RegOU	1.191	85.302	−161.63	0.62	3.25
HL	Clade + SVL	OLS		89.211	−161.48	0.76	3.51

Hind limb length (HL) and snout–vent length (SVL) were log-transformed. All other continuous variables were corrected for SVL using the allometric scaling procedure of Blomberg *et al.* (2003) (see text).

between remainder hind limb length and habitat (Fig. 4, Table 4). All of these factors were statistically significant for explaining crus length (Table 5).

Female lizards in open terrestrial habitat had significantly longer crura than females in arboreal habitats (Tukey–Kramer HSD, P = 0.0064) (Fig. 4).

Table 4. The top three regression models for each trait ranked based on Akaike information coefficient with correction for small sample size (AICc) for female lizards

Dependent variable	Independent variables	Model type	d	ln Maximum likelihood	AICc	Cumulative Akaike weight	Evidence ratio
Thigh	HL – Thigh	OLS		88.940	−171.31	0.68	1.00
Thigh	HL – Thigh	RegOU	1.30E-17	88.940	−168.90	0.89	3.33
Thigh	Clade + HL – Thigh	OLS		92.003	−167.06	0.97	8.37
Crus	HL – Crus, Habitat, HL – Crus * Habitat	OLS		90.793	−144.21	0.51	1.00
Crus	Clade + HL – Crus	OLS		79.794	−142.64	0.74	2.19
Crus	Clade + HL – Crus	RegOU	0.614	80.046	−140.20	0.81	7.43
Pes	HL – Pes	OLS		79.750	−152.93	0.38	1.00
Pes	Clade + HL – Pes	OLS		84.823	−152.70	0.72	1.12
Pes	HL – Pes	RegOU	0.266	79.949	−150.92	0.86	2.73
Toe	Clade + HL – Toe	OLS		72.739	−128.53	0.44	1.00
Toe	Clade + HL – Toe	RegOU	1.011	73.792	−127.69	0.73	1.52
Toe	Clade + HL – Toe	GLS		71.832	−126.72	0.90	2.48
HL	Clade + SVL	OLS		82.451	−147.96	0.62	1.00
HL	SVL, Habitat, SVL * Habitat	OLS		91.368	−145.36	0.79	3.66
HL	Clade + SVL	RegOU	0.315	82.451	−145.01	0.93	4.36

Hind limb length (HL) and snout–vent length (SVL) were log-transformed. All other continuous variables were corrected for SVL using the allometric scaling procedure of Blomberg *et al.* (2003) (see text).

The best model for pes length in male lizards included clade and remainder hind limb length (Fig. 5, Table 3), and both were statistically significant factors (Table 5), although there were no significant differences between clades in *post-hoc* analyses. For females, the best model of pes length was OLS regression with remainder hind limb length (Fig. 5, Table 4) and there was a significant positive relationship between the two (Table 5).

In males, the best model for toe length included clade, remainder hind limb length, and the interaction between the two (Fig. 6, Table 3), and clade and the interaction term were statistically significant (Table 5). Male lizards in clade 2 have significantly shorter toes than males in clade 1 (Tukey–Kramer HSD, $P < 0.0001$), clade 3 ($P < 0.001$), clade 4 ($P < 0.0001$), and clade 5 ($P < 0.0001$). For females, the best model of toe length was an OLS model including clade and remainder hind limb length (Fig. 6, Table 4) and both of these were statistically significant (Table 5). Female lizards in clade 2 have significantly shorter toes than females in clade 1 (Tukey–Kramer HSD, $P < 0.0001$), clade 3 ($P = 0.022$), clade 4 ($P < 0.0001$), and clade 5 ($P < 0.0001$).

Scaling relationships between segment lengths are presented separately for males (Table 6) and females (Table 7). The thighs of males and females had significant negative allometric relationship with remainder hind limb length. The crura of male lizards scaled isometrically with remainder hind limb length but, in females, the crura of lizards living in open terrestrial habitats had a negative allometric relationship with hind limb length and generalists had a positive allometry. For both males and females, pes length scaled isometrically with remainder hind limb length. Toe length had a negative allometric relationship with remainder hind limb length in both female and male lizards in clade 2.

DISCUSSION

The results of model selection do not support the overall hypothesis that limb segment evolution is principally the result of habitat use (Tables 2, 3). Habitat was only an important predictor of limb segment length in the crus of female lizards. The length of the limb as a whole was a better predictor of individual segment lengths, in combination with shared evolutionary history. However, patterns of segment length evolution differed between the sexes and among the individual segments of the limb. Overall, our results indicate a complex evolutionary history for the lengths of limb segments, as well as overall hind limb length in phrynosomatid lizards.
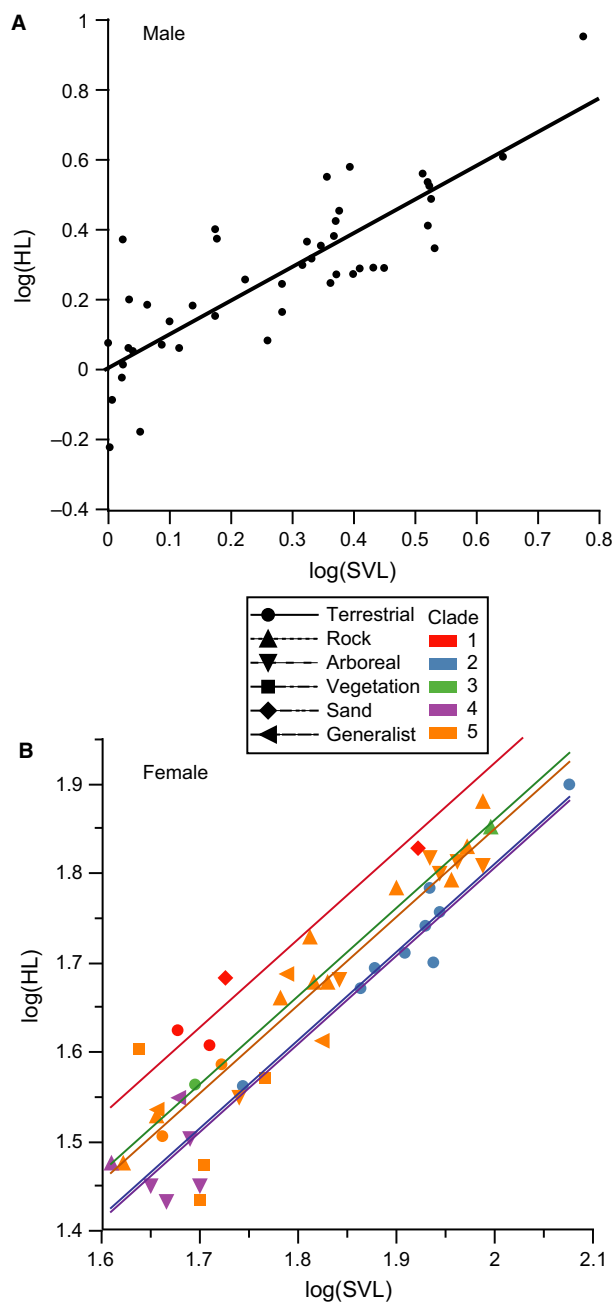
Figure 2. The relationship between hind limb length (HL) and snout–vent length (SVL). For males (A), the best model was a phylogenetic generalized least squares regression as represented by phylogenetic independent contrasts of log(HL) on contrasts of log(SVL), whereas the best model for females (B) was an ordinary least squares regression including clade.

SEGMENT LENGTHS AND BIOMECHANICS

Although the length of the whole limb was an important predictor of all segment lengths, the lengths of the segments do not all scale isometrically with hind limb length (Tables 6, 7). For both male and female lizards, the thigh is significantly shorter in longer-limbed species than would be expected based on isometry. This is in agreement with what we predicted for the more proximal segments. A relatively shorter thigh in longer-limbed species may allow for an increase in the length of the limb as a whole at the same time as not greatly increasing the size of the most massive segment. However, the thigh is the site of attachment for the caudofemoralis, which is generally considered the major propulsive muscle for lizard locomotion (Brinkman, 1981; Rewcastle, 1981; Zani, 1996; Fieler & Jayne, 1998; Reilly, 1998). Given the importance of this segment and its associated muscles, a shortening relative to the rest of the hind limb may cause changes to the kinematics and kinetics of locomotion. Future studies should compare the locomotion of lizards possessing relatively short thighs with species possessing relatively long thighs to better understand the role thigh length plays.

In males, *Phrynosoma* species in clade 2 with longer hind limbs have relatively shorter toes, which is expected based on the behaviour and kinematics of this clade (see below). For these horned lizards, selection for increased running speed is not likely to be pervasive, yet some species do have longer limbs for their body size than others. The selective factors that might result in limb elongation (relative to body size) in horned lizards are unknown.

HABITAT

Performance can differ among closely-related species that occupy different habitats (Losos, 1990a,b; Garland, 1994; Bonine & Garland, 1999; Irschick & Losos, 1999; Melville & Swain, 2000; Vanhooydonck & Van Damme, 2003; Mattingly & Jayne, 2004; Vanhooydonck *et al.*, 2005; Goodman *et al.*, 2008; Higham & Russell, 2010; Johnson, Revell & Losos, 2010; Bonino *et al.*, 2011; Fuller, Higham & Clark, 2011; Tulli *et al.*, 2012), which suggests that morphology could change in response to selection to optimize performance in those habitats (Goodman *et al.*, 2008). For example, in the well-studied *Anolis* lizards, limb length is related to habitat use (Losos, 1990b, 1995; Irschick *et al.*, 1997; Irschick & Losos, 1999) and this morphological difference is at least part of the mechanistic basis for performance differences between habitats (Losos, 1990a, b; Irschick *et al.*, 2005a, b). Species with longer limbs prefer to move more often on broad surfaces in their natural habitat, whereas shorter limbed species tend to prefer narrow diameter perches (Losos, 1995; Irschick & Losos, 1999). Similarly, limb dimensions differ in lizard species that burrow compared to species that

Table 5. Model significance and effect tests for both males and females from the best multiple regression models predicting hind limb segment measures (Tables 3, 4)

| Dependent	Sex	Model type	r^2	F	Independent	F	P
Thigh	Male	OLS	0.291	18.058	HL – Thigh	18.058	< 0.001
	Female	OLS	0.432	33.465	HL – Thigh	33.465	< 0.001
Crus	Male	PGLS	0.403	29.641	HL – Crus	29.641	< 0.001
	Female	OLS	0.723	8.049	HL – Crus	12.169	0.0014
					Habitat	3.425	0.013
					HL – Crus * Habitat	6.060	< 0.001
Pes	Male	OLS	0.541	9.418	HL – Pes	25.859	< 0.001
					Clade	2.739	0.0419
	Female	OLS	0.640	78.385	HL – Pes	78.385	< 0.001
Toe	Male	OLS	0.875	28.059	HL – Toe	0.182	0.6726
					Clade	50.464	< 0.001
					HL – Toe * Clade	3.745	0.012
	Female	OLS	0.745	23.414	HL – Toe	12.101	0.0012
					Clade	22.299	< 0.001
log(HL)	Male	PGLS	0.877	17.706	log(SVL)	17.706	< 0.001
	Female	OLS	0.907	78.192	log(SVL)	259.977	< 0.001
					Clade	6.017	< 0.001

For all models, $P < 0.001$. OLS, ordinary least squares; PGLS, phylogenetic generalized least squares.

use existing habitat structure as retreats (Thompson & Withers, 2005; Thompson *et al.*, 2008). Species of *Ctenophorus* lizards that dig burrows have shorter hind limbs compared to those that retreat to other structures (Thompson & Withers, 2005). In skinks, species occupying open habitats have elevated sprinting abilities and longer hind limbs, whereas species living in more constrained habitats have shorter limbs and slower maximal sprint speeds (Melville & Swain, 2000). However, these trends are not as obvious in other groups of lizards, including lacertids (Vanhooydonck & Van Damme, 1999), phrynosomatids (Herrel *et al.*, 2002), and liolaemids (Schulte *et al.*, 2004; Tulli *et al.*, 2012), possibly because characteristics of the individual segments are more important than total limb length for determining performance in a particular habitat.

Overall, habitat was not an important predictor of hind limb segment lengths in phrynosomatid lizards, despite its importance for explaining total hind limb length in other lizard groups (Losos, 1990b, 1995; Irschick *et al.*, 1997; Irschick & Losos, 1999; Melville & Swain, 2000). Our results do not support the initial prediction that arboreal lizards should have shorter limbs overall, nor the prediction that thighs should be shorter in more vegetated or rocky habitats. Habitat was only important in explaining the length of the crus in female lizards, with females in open terrestrial habitats having longer crura than females in arboreal habitats (Fig. 2). Because the terrestrial habitat is predicted to place relatively few constraints on limb lengthening, the crus may be

free to contribute to limb elongation in response to selection. On the other hand, in the arboreal habitat, the relatively shorter crus may reduce the distance of the body from the substrate, which can reduce pitching moments on inclined surfaces or toppling moments on narrow perches (Cartmill, 1985; Sinervo & Losos, 1991; Losos & Irschick, 1996; Kohlsdorf *et al.*, 2001; Grizante *et al.*, 2010).

A lack of associations between other aspects of hind limb morphology and habitat could suggest that the limb morphology of phrynosomatid lizards is suited for locomotion in many situations rather than being optimized for one habitat (Tulli *et al.*, 2012). Selection may favour the ability to transition from one substrate to another without changes in performance, rather than maximizing performance on one substrate. An alternative explanation may be that microhabitat usage is more subtle and complicated than we understand (Bartholomew, 1987). For example, in studies of Tropidurin lizards, species that often moved on tree trunks had longer femurs than other arboreal species, including those that moved primarily on branches (Kohlsdorf *et al.*, 2001; Grizante *et al.*, 2010). This distinction may explain the lack of support for our prediction that arboreal lizards would have shorter hind limbs overall. Similarly, two species of phrynosomatid lizards living in rocky habitats may experience greatly different demands on the locomotor system depending on the specific microhabitat that they use. A lizard that spends its time on vertical rock faces will experience very different constraints on locomotion than one
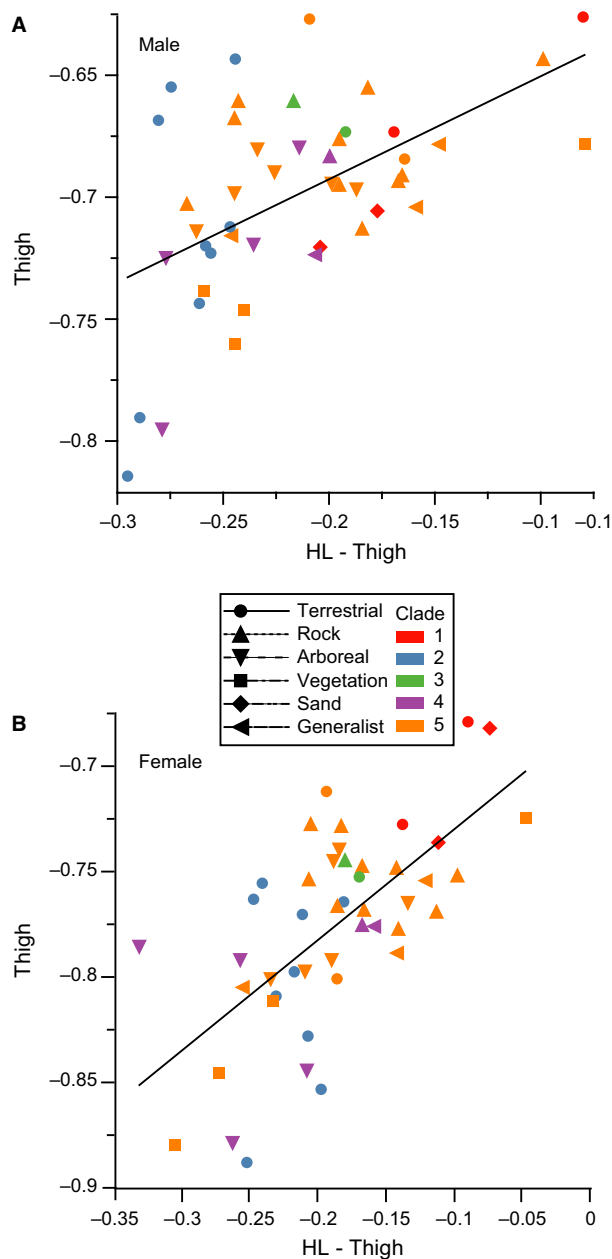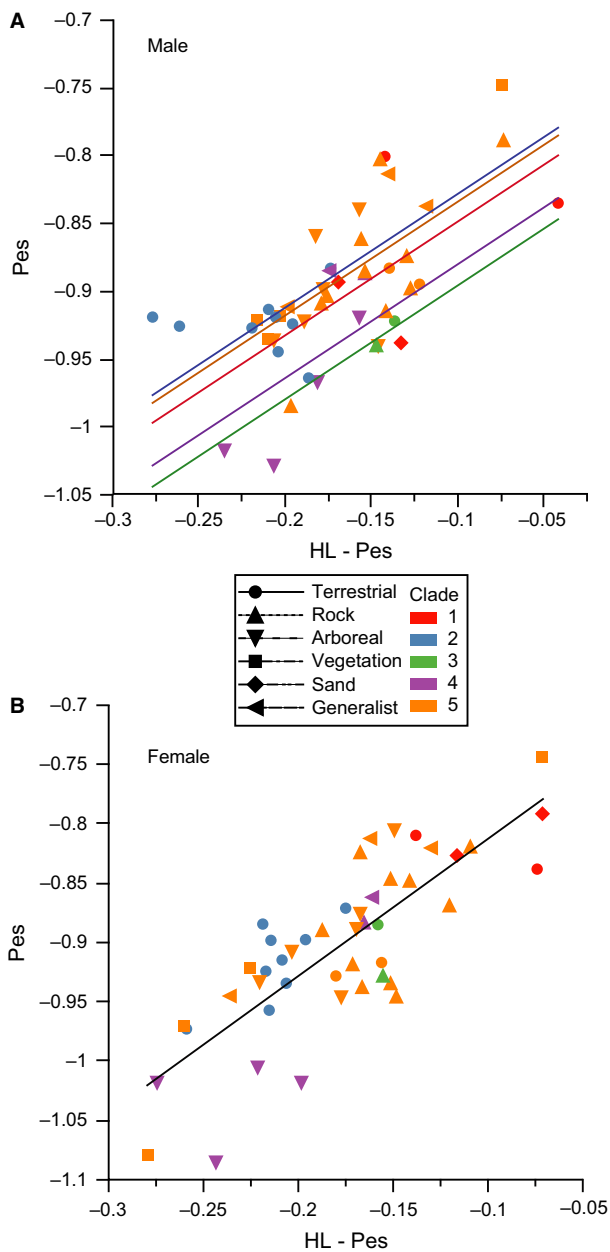
Figure 3. The relationship between thigh length and remainder hind limb length. For males (A) and females (B) the best model was an ordinary least squares regression. HL, hind limb length.

inhabiting relatively flat sheet rock (Howard & Hailey, 1999). Variation in limb kinematics among species could also explain the lack or correlation between limb morphology and habitat use in these lizards (Clemente *et al.*, 2013). More detailed data on the microhabitat use by these species and the possible constraints they impose are necessary to explain
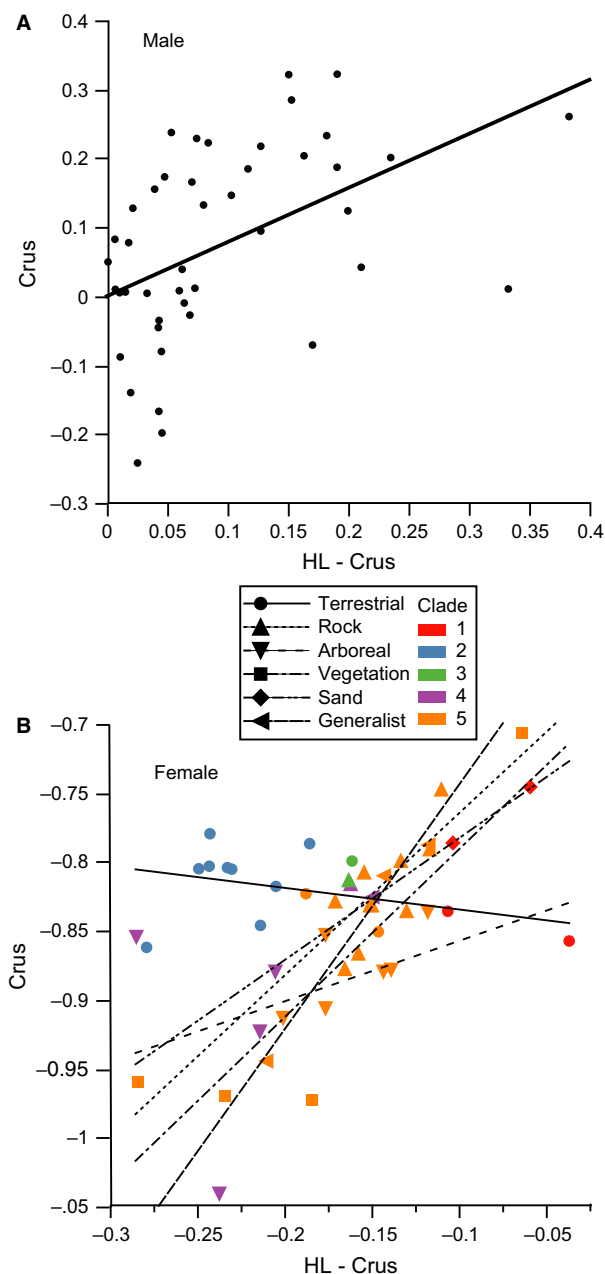
Figure 4. The relationship between crus length and remainder hind limb length. For males (A), the best model was a phylogenetic generalized least squares regression, as represented by phylogenetic independent contrasts of crus length vs. contrasts of remainder hind limb length. For females (B), the best model was an ordinary least squares regression that included habitat and the interaction with remainder hind limb length. Female lizards in open terrestrial habitat had significantly longer crura than females in arboreal habitats (Tukey–Kramer honestly significant difference, $P = 0.0064$). HL, hind limb length.
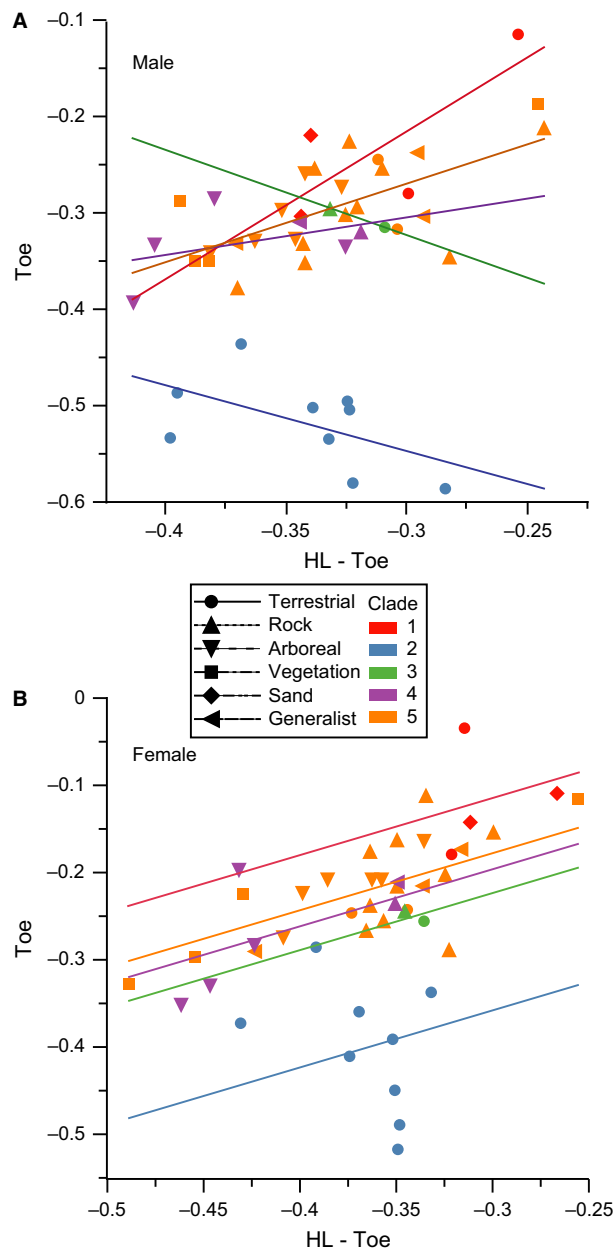
Figure 5. The relationship between pes length and remainder hind limb length. For males (A), the best model was an ordinary least squares (OLS) regression including clade, although there were no significant pair-wise differences. The best model for females (B) was an OLS regression. HL, hind limb length.

the relationship between limb morphology, kinematics, and habitat use.

PHYLOGENY

Shared evolutionary history in the form of the phylogeny from Pyron *et al.* (2013) was associated with

Figure 6. The relationship between toe length and remainder hind limb length. For males (A), the best model was an ordinary least squares (OLS) regression including clade and the interaction with remainder hind limb length. Male lizards in clade 2 have significantly shorter toes than males in clade 1 [Tukey–Kramer honestly significant difference (HSD), $P < 0.0001$], clade 3 ($P < 0.001$), clade 4 ($P < 0.0001$), and clade 5 ($P < 0.0001$). For females (B), the best model was an OLS regression including clade. Female lizards in clade 2 have significantly shorter toes than females in clade 1 (Tukey–Kramer HSD, $P < 0.0001$), clade 3 ($P = 0.022$), clade 4 ($P < 0.0001$), and clade 5 ($P < 0.0001$). HL, hind limb length.

Table 6. Estimated slopes for hind limb length (HL) – segment from the best regression models predicting hind limb segment measures for male lizards (Table 3)

Dependent variable	Independent variables	Model type	Slope	SE	t	P	d.f.
Thigh	HL – Thigh	OLS	0.433	0.102	−5.574	<0.001	44
Crus	HL – Crus	PGLS	0.785	0.144	−1.493	0.143	44
Pes	HL – Pes	OLS	0.839	0.165	−0.974	0.336	40
Toe – Clade 1	HL – Toe	OLS	1.532	0.914	0.582	0.601	3
Toe – Clade 2	HL – Toe	OLS	−0.683	0.399	−4.213	0.003	8
Toe – Clade 3	HL – Toe	OLS	–	–	–	–	1*
Toe – Clade 4	HL – Toe	OLS	0.389	0.401	−1.521	0.189	5
Toe – Clade 5	HL – Toe	OLS	0.814	0.196	−0.950	0.352	24
log(HL)	log(SVL)	PGLS	0.961	0.054	−0.710	0.481	44

Partial regression coefficients are presented for models with more than one independent variable with appropriately reduced degrees of freedom. Slopes for interactions terms were determined from separate linear regressions for each grouping. A t-test was performed between the measured slope and a null slope of one representing isometric scaling.
*Clade 3 included only two species.
OLS, ordinary least squares; PGLS, phylogenetic generalized least squares.

Table 7. Estimated regression slopes for hind limb length (HL) – segment from the best regression models predicting hind limb segment measures for female lizards (Table 4)

Dependent variable	Independent variable	Model type	Slope	SE	t	P value	d.f.
Thigh	HL – Thigh	OLS	0.522	0.090	−5.290	< 0.001	44
Crus – Terrestrial	HL – Crus	OLS	−0.158	0.111	−10.475	< 0.001	13
Crus – Rock	HL – Crus	OLS	1.184	0.395	0.465	0.651	11
Crus – Arboreal	HL – Crus	OLS	0.441	0.379	−1.473	0.175	9
Crus – Vegetation	HL – Crus	OLS	1.226	0.460	0.491	0.657	3
Crus – Sand	HL – Crus	OLS	–	–	–	–	1*
Crus – Generalist	HL – Crus	OLS	1.785	0.173	4.534	0.020	3
Pes	HL – Pes	OLS	1.157	0.131	1.205	0.235	44
Toe	HL – Toe	OLS	0.652	0.187	−1.858	0.071	40
log(HL)	log(SVL)	OLS	0.987	0.061	−0.220	0.827	40

Partial regression coefficients are presented for models with more than one independent variable with appropriately reduced degrees of freedom. Slopes for interactions terms were determined from separate linear regressions for each grouping. A t-test was performed between the measured slope and a null slope of one representing isometric scaling.
*The Sand group included only two species.
OLS, ordinary least squares; PGLS, phylogenetic generalized least squares.

variation in total hind limb length and crus length in male lizards, and broad clade differences were important in models of the female hind limb, male pes, and the toes of both males and females (Tables 3, 4). Clade differences may reflect the evolution of unmeasured physiological or behavioural features within clades, as well as shared ancestral features that affect evolution. Both male and female lizards in the *Phrynosoma* clade had significantly shorter toes than those of other clades, which appears to be reasonable given that horned lizards generally do not rely on an ability to run quickly for prey capture or predator escape (Sherbrooke, 2003). Although many studies measure the total length of the hind limb and relate that to performance (Bonine & Garland, 1999; Vanhooydonck & Van Damme, 2001; Herrel *et al.*, 2002; Goodman *et al.*, 2008), the length of the hind limb that is actually contributing to forward locomotion (effective limb length) may be quite different (Fieler & Jayne, 1998). At slow speeds, lizards have a plantigrade posture where the body is supported on the bones of the pes (Brinkman, 1981; Rewcastle, 1981; Reilly & Delancey, 1997b; Fieler & Jayne, 1998; Irschick & Jayne, 1999). In this posture, the length of the pes and the toe may not contribute at all to stride length or to the length of propulsive contact, both of which can increase the average

speed (Fieler & Jayne, 1998; Irschick & Jayne, 1999). Some lizards transition to a digitigrade posture at higher speeds, where the body is supported on the bones of the toe (Fieler & Jayne, 1998). In this posture, the pes is oriented in a more forward direction and the lengths of the pes and toe segments may contribute more to the effective limb length (Fieler & Jayne, 1998). Lizards in the genus *Phrynosoma*, however, do not use a digitigrade posture during running (Irschick & Jayne, 1999) and are more likely to rely on crypsis than running during predator–prey interactions (Sherbrooke, 2003). The length of the toe may therefore have no important effect on sprinting performance and, moreover, sprinting performance may have relatively little effect on Darwinian fitness for species in this group. This speculation can be viewed in the context of the idea that behaviour can serve as a 'filter' between performance and fitness (Garland & Losos, 1994; Careau & Garland, 2012; Lailvaux & Husak, 2014).

Our results suggest that different species of lizards are able to arrive at the same solution (limb elongation) through different combinations of morphological characteristics (i.e. multiple solutions: Garland *et al.*, 2011; Linnen *et al.*, 2013; Losos, 2011). However, the analysis in the present study is based on the assumption that populations are responding to some form of selection with evolutionary changes in hind limb length. Hind limb length in phrynosomatid lizards is significantly positively related to laboratory measures of maximum sprint speed (Bonine & Garland, 1999). In some species, sprint speed has been correlated with different aspects of Darwinian fitness, including survival and reproduction (Husak & Fox, 2006; Husak *et al.*, 2006, 2008). However, it is possible that the selective factors leading to limb elongation differ among species. For example, long limbs are useful for increasing jump performance, as well as sprint performance, although the precise mechanisms of jump performance may require different limb segment morphology than running. Long limbs could also be beneficial during climbing, and the response to selection for climbing performance may involve a different suite of hind limb traits. Clade-level patterns of variation may therefore represent not only differences in how limb morphology changes in response to selection, but also differences in past selective factors acting on limb function.

SEXUAL DIMORPHISM

Although the ultimate causes remain unclear, we conclude that the patterns of limb morphology evolution differ between the sexes in phrynosomatid lizards. Phylogenetic analyses reveal differences in the patterns of hind limb segment evolution between the sexes that may reflect differences in selective regimes. In a study of sexual dimorphism in Iguanian lizards, differences between digit ratios were suggested to be related to habitat use, although the ecological data were not available to confirm this (Gomes & Kohlsdorf, 2011). In the present study, habitat is an important predictor of crus length in female lizards but, in males, crus length is explained only by shared evolutionary history. This result suggests that sexual dimorphism in habitat use may drive differences in limb morphology. If males do not utilize the habitat in the same way as females, then they may experience different types of selection. For example, male lizards that defend territories may spend more time exposed in open habitats compared to females of the same species. If the strongest selection for fast running is experienced by males during territorial behaviour (Husak & Fox, 2006), then the details of their habitat use during other behaviours may not matter, even if the relative time spent in the open is small. On the other hand, selective breeding experiments have sometimes found that even uniform selection on the sexes can result in different, sex-specific evolutionary responses (Garland *et al.*, 2011).

Our results indicate that pooling measurements from all individuals in a species or population (juveniles, females, males) when attempting to examine phylogenetic evolution may obscure general patterns. At the same time, studying only one class of individuals may fail to reveal patterns unique to other classes of individuals. Finally, to some extent, the morphological evolution of one sex is constrained by the morphology of the other sex, which may sometimes explain the presence of suboptimal or maladaptive traits. Future studies examining morphology–performance–behaviour–fitness relationships should endeavour to study the sexes separately, as well as consider the possibly unique evolutionary patterns observed in juveniles.

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APPENDIX

Table A1. Morpholometrics as means and standard deviations for each species by sex in mm

Species	Sex	N	Habitat	SVL mean	SVL SD	Thigh mean	Thigh SD	Crus mean	Crus SD	Pes mean	Pes SD	Toe mean	Toe SD
Cophosaurus	M	8	Open terrestrial[1,2]	62.64	5.57	16.49	1.35	16.61	1.97	8.88	1.05	17.73	2.15
texanus	F	3		47.57	2.37	12.50	1.15	8.98	6.84	6.50	0.82	14.00	0.46
Holbrookia	M	5	Open terrestrial[1,2]	53.12	1.23	12.46	0.86	11.20	0.55	8.16	0.35	10.70	0.77
maculata	F	3		51.26	3.05	12.10	0.69	10.23	0.17	7.47	0.58	10.59	0.69
Petrosaurus	M	13	Rock-dwelling[1,3]	107.23	26.48	26.41	6.31	23.25	5.40	11.89	1.93	17.59	3.27
thalassinus	F	7		99.15	14.55	23.44	3.90	21.98	3.79	10.91	1.48	14.52	2.61
Phrynosoma	M	19	Open terrestrial[1,4]	78.63	6.04	19.99	1.80	19.70	1.38	9.96	0.75	7.12	0.52
cornutum	F	6		87.90	5.66	20.10	1.36	19.70	0.86	9.54	0.22	7.61	0.64
Phrynosoma	M	2	Open terrestrial[1,3,4]	112.05	0.35	22.70	0.57	23.65	0.35	12.80	0.99	13.15	0.92
coronatum	F	1		119.10	–	26.80	–	26.50	–	14.00	–	11.80	–
Phrynosoma	M	1	Open terrestrial[1,4]	66.80	–	11.30	–	13.10	–	7.80	–	7.10	–
douglasii	F	3		86.60	9.30	14.60	0.44	16.97	0.35	8.60	0.56	9.83	0.32
Phrynosoma	M	2	Open terrestrial[4]	67.63	1.85	16.67	0.64	14.92	0.30	7.12	0.07	7.67	1.35
Hernandesi	F	1		85.86	–	19.21	–	19.99	–	10.78	–	10.60	–
Phrynosoma	M	2	Open terrestrial[1,4]	51.90	4.81	11.10	0.71	12.20	0.71	6.00	1.13	6.40	0.14
modestum	F	5		55.42	6.17	10.44	1.37	11.94	1.08	6.58	0.66	7.40	0.53
Phrynosoma	M	2	Open terrestrial[4]	67.85	1.06	12.15	0.64	13.00	0.00	7.80	1.27	8.00	0.28
orbiculare	F	2		85.00	6.93	15.50	0.14	17.25	1.48	10.35	0.49	11.85	0.64
Phrynosoma	M	14	Open terrestrial[1,3,4]	75.32	3.09	15.86	0.58	17.72	2.48	8.90	0.70	7.76	0.73
platyrhinos	F	9		75.49	2.99	15.53	0.70	17.69	0.83	8.59	0.43	7.48	0.77
Phrynosoma	M	4	Open terrestrial[1,3,4]	78.82	10.96	18.89	3.29	17.49	3.00	9.19	1.35	7.23	1.55
solare	F	4		73.03	23.23	16.23	3.11	16.16	5.04	8.13	1.63	6.26	1.62
Phrynosoma	M	2	Open terrestrial[4]	72.25	6.29	15.30	0.71	16.80	1.27	7.95	1.20	8.10	0.14
taurus	F	2		81.00	2.12	16.30	0.14	18.00	0.28	8.35	0.92	8.60	0.14
Sceloporus	M	3	Vegetated Terrestrial[5,6,7]	47.57	4.37	9.07	1.19	9.00	1.22	5.37	0.65	8.37	0.65
aeneus	F	4		50.05	2.43	8.33	0.88	7.50	0.37	3.93	0.71	7.40	0.69
Sceloporus	M	7	Rock- dwelling[3]	70.45	9.18	17.88	2.86	19.64	2.22	11.13	1.25	15.50	1.20
angustus	F	8		64.79	4.38	14.69	0.95	16.16	0.60	9.22	0.57	13.25	0.96
Sceloporus	M	12	Arboreal[1,6]	94.53	14.91	21.19	3.23	18.11	4.20	10.92	1.17	14.77	1.91
clarki	F	8		97.38	12.13	20.35	2.69	17.39	2.94	11.22	1.16	15.00	1.08
Sceloporus	M	5	Arboreal[6]	72.18	1.28	16.22	0.59	15.50	0.99	8.00	0.57	14.14	0.65
formosus	F	4		69.58	6.44	14.43	0.95	13.65	1.18	7.35	0.57	12.30	1.11
Sceloporus	M	8	Vegetated Terrestrial[1,2]	57.36	2.38	11.35	0.84	9.66	0.69	6.71	0.48	11.13	1.00
graciosus	F	12		58.46	3.87	11.49	0.61	8.60	0.78	6.58	0.40	10.46	0.65
Sceloporus	M	11	Arboreal[2,8]	63.51	8.56	13.58	1.72	11.04	1.14	7.13	0.65	10.61	1.18
grammicus	F	8		55.05	8.06	11.03	1.89	9.23	1.20	6.01	0.78	8.92	1.35
Sceloporus	M	14	Rock- dwelling[6]	96.95	6.06	22.16	1.29	23.44	1.37	12.54	0.84	17.91	1.01

Table A1. *Continued*

Species	Sex	N	Habitat	SVL mean	SVL SD	Thigh mean	Thigh SD	Crus mean	Crus SD	Pes mean	Pes SD	Toe mean	Toe SD
horridus	F	3		97.20	3.91	21.67	1.10	22.63	1.78	12.27	1.18	19.37	2.20
Sceloporus	M	8	Rock- dwelling[1,6,9]	72.99	4.70	17.81	2.08	13.50	1.42	8.83	0.75	12.06	1.11
jorrovii	F	14		67.72	8.78	16.28	1.99	12.87	1.45	7.65	0.67	10.81	0.82
Sceloporus	M	8	Arboreal[1,6]	92.37	15.59	21.14	3.64	16.82	5.41	12.33	1.96	15.65	2.01
magister	F	2		87.82	6.45	20.83	1.19	16.57	4.99	10.88	1.58	14.45	1.24
Sceloporus	M	6	Rock- dwelling[6]	67.21	8.04	14.46	2.16	13.76	1.90	8.98	1.12	13.59	2.24
malachiticus	F	13		60.45	7.44	12.86	1.51	12.23	1.60	8.08	0.88	12.39	1.49
Sceloporus	M	8	Rock- dwelling[2,6]	47.51	2.07	11.61	0.81	10.57	0.83	7.28	0.67	8.44	0.71
merriamai	F	9		45.26	2.44	10.14	0.50	9.56	0.38	6.40	0.37	7.55	0.71
Sceloporus	M	9	Generalist[1,10]	65.88	7.15	15.35	1.95	15.53	2.41	9.29	0.89	13.89	1.60
occidentalis	F	9		61.39	6.07	13.78	1.29	13.89	1.66	8.71	0.70	12.20	0.88
Sceloporus	M	2	Open terrestrial[6]	48.90	0.99	11.15	0.21	11.15	0.49	6.05	0.21	10.90	0.28
Ochoterenae	F	2		45.90	2.97	9.10	0.99	9.35	0.92	5.10	0.14	8.40	0.57
Sceloporus	M	8	Arboreal[2,6]	74.21	14.75	16.59	3.43	15.38	3.20	10.40	1.52	13.96	2.07
olivaceus	F	16		85.82	11.81	19.15	2.20	17.84	2.08	12.50	1.05	15.78	1.22
Sceloporus	M	10	Rock- dwelling[1,6]	90.23	8.11	20.38	1.76	20.39	1.84	11.39	0.94	15.20	0.87
orcutti	F	13		79.46	8.60	18.37	2.45	17.90	1.79	10.54	0.95	13.70	1.11
Sceloporus	M	9	Rock- dwelling[6,7]	42.78	2.58	9.92	0.67	9.19	0.37	5.07	0.40	8.78	0.63
parvus	F	6		41.87	2.87	8.94	1.00	8.36	0.43	4.56	0.59	8.04	1.07
Sceloporus	M	9	Rock- dwelling[1,2,6]	96.84	9.53	23.41	2.26	19.00	2.65	11.55	0.63	14.29	0.99
poinsetti	F	9		90.51	12.24	20.82	2.26	17.20	3.25	10.90	1.27	12.92	2.12
Sceloporus	M	9	Vegetated Terrestrial[1,6,7,8]	48.43	5.23	9.71	1.34	8.24	1.60	5.63	0.74	8.50	1.30
scalaris	F	9		50.57	5.91	9.11	0.90	7.40	1.78	5.09	0.95	8.02	1.31
Sceloporus	M	7	Arboreal[11]	99.47	12.44	23.29	3.01	19.63	3.54	12.13	1.73	15.40	1.43
serrifer	F	9		91.57	11.31	21.50	2.72	17.30	3.42	11.01	1.39	14.90	1.65
Sceloporus	M	11	Vegetated Terrestrial[6]	48.31	3.32	11.18	0.90	13.05	1.01	8.39	0.59	12.34	1.05
siniferus	F	7		43.36	3.22	10.21	0.95	11.50	1.08	7.39	0.64	10.91	1.06
Sceloporus	M	8	Rock- dwelling[6]	67.35	6.79	15.18	1.33	15.09	1.18	8.28	0.83	14.51	1.94
taeniocnemis	F	8		65.43	5.24	14.30	1.53	13.48	1.53	7.14	1.23	12.66	1.37
Sceloporus	M	3	Rock- dwelling[6,12]	104.69	7.66	23.31	1.85	21.09	1.87	10.48	1.86	14.31	0.96
toquatus	F	8		93.65	2.97	22.91	1.82	19.81	1.04	9.89	4.06	14.90	1.71
Sceloporus	M	17	Generalist[1,2,13]	58.98	5.32	12.55	1.48	10.51	1.95	7.01	0.85	10.30	0.97
undulatus	F	7		66.61	3.91	13.37	1.12	10.57	1.22	7.08	0.72	9.86	0.82
Sceloporus	M	12	Generalist[2,6,7]	48.13	5.23	10.48	0.90	11.43	0.60	7.19	0.33	9.40	0.89
variabilis	F	9		45.36	5.49	9.24	0.94	9.50	0.39	6.59	0.55	8.93	0.51
Sceloporus	M	11	Open terrestrial[1,14]	48.84	4.56	12.75	1.44	9.88	1.26	6.21	0.63	9.22	0.72
virgatus	F	9		52.72	5.65	12.92	1.04	10.19	0.59	6.00	0.40	9.34	0.61
Uma	M	4	Sand[1]	82.64	18.50	18.15	3.63	18.63	5.01	9.23	1.93	17.18	2.84
inornata	F	2		53.25	1.06	14.00	0.99	13.10	1.56	8.10	0.99	12.75	1.63
Uma	M	2	Sand[1]	100.50	3.68	21.45	0.21	22.10	2.83	12.40	0.85	16.45	0.64
scoparia	F	2		83.40	1.13	19.85	0.49	19.40	1.13	11.60	1.13	16.20	1.13
Urosaurus	M	13	Generalist[15]	62.04	4.78	12.97	1.13	12.89	1.12	7.84	0.80	11.24	1.26
auriculatus	F	4		47.75	6.70	10.05	1.25	9.69	0.89	6.18	0.88	9.36	1.07
Urosaurus	M	8	Arboreal[16]	47.39	3.65	8.30	0.65	8.99	0.88	4.41	0.47	7.55	0.68
bicarinatus	F	4		46.25	3.31	7.68	0.78	8.78	0.90	3.58	0.25	6.95	0.97
Urosaurus	M	14	Arboreal[1,16]	51.89	4.04	10.91	0.85	9.44	0.87	5.43	0.57	10.38	0.68
graciosus	F	5		48.88	3.64	8.79	0.78	8.79	0.74	4.40	0.52	9.81	0.63
Urosaurus	M	11	Rock- dwelling[1]	44.76	4.14	10.21	1.13	9.58	0.98	5.66	0.59	8.56	1.16
lahtelai	F	9		40.69	5.73	8.49	0.72	8.35	0.49	5.03	0.49	7.91	0.90

Table A1. *Continued*

Species	Sex	N	Habitat	SVL mean	SVL SD	Thigh mean	Thigh SD	Crus mean	Crus SD	Pes mean	Pes SD	Toe mean	Toe SD
Urosaurus	M	8	Arboreal[1,16]	48.83	4.60	10.11	0.68	8.34	0.48	4.43	0.47	8.86	1.06
nigricaudus	F	8		44.75	6.44	9.04	1.05	7.23	0.69	4.16	0.32	7.58	0.54
Urosaurus	M	6	Arboreal[17]	50.13	2.10	11.10	0.47	6.75	0.22	4.93	0.24	8.24	0.52
ornatus	F	3		50.12	1.77	10.33	0.55	6.22	0.66	4.52	0.78	7.01	0.10
Uta	M	5	Open terrestrial[1,2]	53.20	2.53	12.48	0.64	12.50	1.05	6.18	0.76	9.88	0.95
stansburiana	F	4		49.55	1.72	11.03	1.34	10.73	0.45	6.08	0.70	8.68	0.86

[1]Stebbins (1985); [2]Conant & Collins (1991); [3]Grismer (2002); [4]Sherbrooke (2003); [5]Lemos-Espinal *et al.* (2002); [6]Smith (1939); [7]Mink & Sites (1996); [8]Ortega-Rubio & Arriaga (1990); [9]Morrison *et al.* (1995); [10]Block & Morrison (1998); [11]Smith (1936); [12]Burquez *et al.* (1986); [13]Ballinger & Watts (1995); [14]Smith (1996); [15]Ortega-Rubio *et al.* (1992); [16]Mittleman (1942); [17]Herrel *et al.* (2002).SVL, snout–vent length.