

Relations between microhabitat use and limb shape in phrynosomatid lizards

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With the exception of the well-documented case for anoline lizards, recent studies have found few evolutionary relationships between morphology and habitat use in lizards despite clear-cut biomechanical predictions. One of the factors typically hampering these analyses is the clustering of habitat use within evolutionary lineages. In the present study, body shape was quantified for male and female lizards of 30 species of phrynosomatid lizards. This group was selected as little clustering of ecological variables seemed to be present. The results of traditional analyses indicate that evolutionary correlates of habitat use were prominent in the hindlimbs of both sexes. Species living in open habitats are characterized by longer femurs, and longer hindlimbs relative to the forelimb. Moreover, males from ground-dwelling species utilizing open habitats have longer toes on the hind foot than males from climbing species. Phylogenetic analyses indicated strong evolutionary associations between habitat use and the relative length of front and hindlimbs, with species from open terrestrial habitats having significantly shorter frontlimbs relative to their hindlimb than rock or tree climbing species. Evolutionary associations between morphology and habitat use were generally stronger for male lizards, indicating a potentially important contribution of sexual selection to the evolution of differences in limb proportions. © 2002 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2002, 77, 149–163.

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INTRODUCTION

Ever since Arnold (1983) proposed a rigorous framework to test for the adaptive nature of relations between ecology and morphology, ecomorphological studies have flourished (see Wainwright & Reilly, 1994; Irschick & Garland, 2001 for an overview). Moreover, since the development of statistical methods that take into account the relationships between the groups under investigation (Felsenstein, 1985, 1986; Harvey & Pagel, 1991; Garland, Harvey & Ives, 1992; Garland *et al.*, 1993; Losos & Miles, 1994) interspecific studies have flourished. In the past decade or two, lizard locomotion has become one of the show-

cases of ecomorphological theory (e.g. see Losos, Warheit & Schoener, 1997) and nearly all aspects of the adaptive chain have been investigated in one or other group (e.g. morphology/performance: Garland & Losos, 1994; Bonine & Garland, 1999; Melville & Swain, 2000; Vanhoooydonck, Van Damme & Aerts, 2000; Zani, 2000; performance/fitness: Irschick & Losos, 1998; Miles, Sinervo & Frankino, 2000; the genetic basis of differences in morphology and performance: Van Berkum & Tsuji, 1987; Tsuji *et al.*, 1989; Sorci *et al.*, 1995). The relationships between morphology and locomotor performance have been well studied, both through biomechanical analyses and *in vivo* correlates of morphology and performance (see Aerts *et al.*, 2000; Van Damme & Vanhoooydonck, 2001 for an overview). As a result of these studies, specific predictions about the relations between habitat use and morphology are possible.

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Biomechanical theory predicts clear relationships between morphology and habitat use as the physical demands acting on the locomotor system are distinct in different habitats. Consequently, specializations into climbing niches are expected to be accompanied by adaptive morphological evolution (Vanhooydonck & Van Damme, 1999; Zaaf & Van Damme, 2001). Biomechanical models suggest that climbers should have a flat body and head to keep the centre of mass as close to the substrate as possible (see Vitt *et al.*, 1997; Vanhooydonck & Van Damme, 1999; Zaaf & Van Damme, 2001). Moreover, climbers are expected to have relatively short limbs to keep the body close to the substrate (Vanhooydonck & Van Damme, 1999; Zaaf *et al.*, 1999). Given the importance of the forelimbs while climbing (delivering propulsion by pulling and keeping the body close to the substrate) differences in length between front and hindlimbs are expected to be minimal (Zaaf *et al.*, 1999; Zaaf & Van Damme, 2001). Ground-dwelling lizards, on the other hand, do not seem to be constrained for body or head height but may show short forelimbs relative to the hindlimbs (so as not to interfere while running) and long distal segments on the propulsive limb pair (i.e. the hindlimbs) to maximize the duration of the acceleratory phase (Snyder, 1954, 1962; Hildebrand, 1985; Losos, 1990a,b).

However, within these broad ecological groups (climbing vs. level running) further differentiation depending on the habitat structure is expected. Tree climbers are likely to be different from rock climbers as the surface of most trees and branches provides lizards with a substrate providing much larger frictional forces (Zani, 2000), thus lessening constraints on limb and body shape. Animals frequently running on branches are expected to have narrower bodies and heads and shorter limbs to prevent them from falling (Sinervo & Losos, 1991; Losos & Irschick, 1996). Similarly, ground-dwelling lizards moving in open habitats likely face different challenges than animals moving in densely vegetated habitats (e.g. see Schneider *et al.*, 1999). Here, too, specific predictions regarding the relations between the microhabitat and morphology can be made. Animals dwelling in terrestrial vegetation are expected to have a relatively narrow body and head which should increase manoeuvrability (Vanhooydonck & Van Damme, 1999; Vanhooydonck *et al.*, 2000). Moreover, legs are expected to be shorter in vegetated habitats, as long legs might become entangled in the vegetation (Jaksic, Nuñez & Ojeda, 1980). Also, the forelimbs can be expected to be relatively long compared to hindlimbs as this is likely to enhance turning ability (Vanhooydonck *et al.*, 2000). For ground-dwellers in open habitats, on the other hand, forelimbs are expected to be short as they might otherwise interfere with the rela-

tively long hindlimbs that provide the thrust for locomotion (see above).

Several recent studies have examined evolutionary relationships between morphology and habitat use in lizards (*Liolaemus* sp., Jaksic *et al.*, 1980; *Anolis* sp., Losos, 1990a,b, 1992; sceloporines, Miles, 1994; Lacertidae, Vanhooydonck & Van Damme, 1999; *Niveoscincus* sp. Melville & Swain, 2000; *Tropidurus* sp., Kohlsdorf, Garland & Navas, 2001; Gekkonidae, Zaaf & Van Damme, 2001). Surprisingly, the results from the majority of these studies (with the exception of the classical example of the Caribbean anoles (Losos, 1990a,b; Losos *et al.*, 1997) and *Niveoscincus* lizards (Melville & Swain, 2000)), indicate little association between habitat use and body shape. Thus, at first sight, few or no adaptive relations between morphology and ecology exist. However, potential problems associated with the analyses cited above include low statistical power due to clustering of ecological variables (Vanhooydonck & Van Damme, 1999; Kohlsdorf *et al.*, 2001), badly resolved phylogenies including multiple soft polytomies (e.g. Kohlsdorf *et al.*, 2001) and the lack of accurate information on habitat use resulting in an oversimplified characterization of the habitat (e.g. Kohlsdorf *et al.*, 2001; Zaaf & Van Damme, 2001).

One other aspect that has typically been ignored is the difference between sexes (but see Schneider *et al.*, 1999). In most studies both male and female lizards have been pooled, thus ignoring potential differences between sexes (Jaksic *et al.*, 1980; Miles, 1994; Melville & Swain, 2000; Zaaf & Van Damme, 2001), or only male lizards have been used (Vanhooydonck & Van Damme, 1999; Kohlsdorf *et al.*, 2001) thus biasing the analysis. However, sexes might differ as different selective pressures (natural and sexual) are likely to operate on male and female lizards (Zucker, 1986; Wikelski & Trillmich, 1997; Fox, Conder & Smith, 1998; Snell *et al.*, 1988). In female lizards, for example, selection for fecundity would be expected to result in an increase in body length and width to accommodate a maximal number of eggs. However, this might trade off with the ability to use narrow perches, or with moving swiftly through vegetation (see above). Similarly, sexual selection acting on males might constrain head shape. Sexual selection (e.g. male–male combat) results in increased head size in male lizards of many species, which might be particularly problematic for climbers as these are expected to have flat heads and bodies to keep the centre of mass close to substrate. Moreover, as males of many lizard species, including phrynosomatids, tend to defend territories (e.g. Zucker, 1986; Marler *et al.*, 1995; Fox *et al.*, 1998; Robson & Miles, 2000) associations between morphology and habitat use can be expected to be stronger for male lizards. It has been demonstrated that strong

associations between territoriality and locomotor performance exist in phrynosomatid lizards (Robson & Miles, 2000).

In the present study, we examine the evolutionary relationships between habitat use and morphology in phrynosomatid lizards. We chose this group of lizards because a good consensus on the relationships between the species exists (few polytomies). Additionally, habitat use has been well documented for these lizards and tends not to cluster within certain clades. More specifically, we predict that climbing lizards (i.e. rock and tree climbers) will have flatter bodies and heads compared to ground-dwelling species, and that vegetation-dwellers will have a narrower head and body than animals from open habitats (i.e. rock climbers, and ground-dwellers in open habitats). Moreover, we predict that climbing lizards will have relatively longer forelimbs, relatively short distal segments on the hindlimb, and relatively longer frontlimbs relative to their hindlimbs. Ground-dwellers in vegetation are predicted to show relatively long forelimbs, relatively short hindlimbs, and short distal hindlimb segments. Moreover the forelimb to hindlimb ratio should be large for vegetation-dwellers. These ecomorphological relationships are examined for both sexes separately to investigate whether similar selection pressures act on male and female lizards.

MATERIAL AND METHODS

MORPHOMETRY

Thirty species of phrynosomatid lizards, and four populations of the species *Urosaurus ornatus* (Phrynosomatidae) were included in the analysis (see Tables 1 and 2). Morphometric data were gathered for both preserved and live specimens. The following morphological measurements were taken for every individual to the nearest 0.01 mm using digital callipers (Mitutoyo CD-15DC; Mitutoyo Ltd, Telford, UK): snout-vent length, tail length, head length, head width, head height, body length, body width, body height, femur length, tibia length, metatarsus length, longest toe of the hindfoot (always the fourth toe), humerus length, radius length, and metacarpus length. Two additional morphometric variables were calculated from the original ones: hindlimb length being the sum of all hindlimb segments, and forelimb length being the sum of all forelimb segments. Only animals with all measured segments intact were included into the analysis.

MICROHABITAT USE

Species were classified as belonging to one of four habitat use categories (ground-dwelling in open habi-

Table 1. Morphometrical characterization of head and body for both sexes. Table entries are averages \pm standard deviations in mm. SVL, snout-vent length

Species	Sex	N	SVL	Head width	Head height	Body width	Body height
<i>Callisaurus draconoides</i>	♂	14	75.29 \pm 8.42	12.24 \pm 1.11	9.06 \pm 1.00	20.15 \pm 2.88	12.20 \pm 2.72
<i>Cophosaurus texanus</i>	♂	8	62.64 \pm 5.57	11.06 \pm 0.81	8.29 \pm 0.53	17.61 \pm 2.07	9.85 \pm 1.55
	♀	3	47.57 \pm 2.37	9.07 \pm 0.06	5.80 \pm 0.78	12.73 \pm 2.27	7.13 \pm 0.15
<i>Holbrookia maculata</i>	♂	5	53.12 \pm 1.23	10.04 \pm 0.69	6.85 \pm 0.53	15.03 \pm 2.17	7.44 \pm 0.53
	♀	3	51.25 \pm 3.05	9.49 \pm 0.66	6.55 \pm 0.41	13.46 \pm 1.08	6.94 \pm 0.58
<i>Petrosaurus thalassinus</i>	♂	13	107.23 \pm 26.48	18.62 \pm 4.24	11.56 \pm 2.97	30.54 \pm 9.99	12.46 \pm 3.64
	♀	7	99.15 \pm 14.55	17.44 \pm 2.44	10.65 \pm 1.48	31.42 \pm 6.28	11.94 \pm 1.95
<i>Sator angustatus</i>	♂	7	70.45 \pm 9.18	12.84 \pm 2.02	9.35 \pm 1.55	15.03 \pm 2.22	10.47 \pm 2.38
	♀	8	64.79 \pm 4.38	11.05 \pm 0.45	7.98 \pm 0.33	14.67 \pm 1.78	8.91 \pm 0.73
<i>Sceloporus clarkii</i>	♂	12	94.53 \pm 14.91	19.62 \pm 3.13	13.31 \pm 2.37	27.96 \pm 4.91	17.32 \pm 4.25
	♀	8	97.38 \pm 12.13	18.69 \pm 1.45	12.68 \pm 1.71	31.06 \pm 3.34	16.98 \pm 2.18
<i>Sceloporus graciosus</i>	♂	8	57.36 \pm 2.38	9.80 \pm 0.48	6.67 \pm 0.34	16.00 \pm 0.48	8.59 \pm 0.54
	♀	12	58.46 \pm 3.87	9.56 \pm 0.62	6.44 \pm 0.57	16.36 \pm 2.09	8.37 \pm 0.91
<i>Sceloporus grammicus</i>	♂	11	63.51 \pm 8.56	11.54 \pm 1.45	8.13 \pm 0.93	17.90 \pm 4.78	9.61 \pm 2.06
	♀	8	55.05 \pm 8.06	10.18 \pm 1.15	6.38 \pm 0.86	16.11 \pm 3.03	7.89 \pm 1.29
<i>Sceloporus jarrovi</i>	♂	8	72.99 \pm 4.70	16.95 \pm 1.53	10.60 \pm 1.06	24.75 \pm 2.63	11.90 \pm 1.28
	♀	14	67.72 \pm 8.78	14.79 \pm 1.13	9.26 \pm 2.62	23.13 \pm 3.24	9.48 \pm 1.29
<i>Sceloporus magister</i>	♂	8	92.37 \pm 15.59	18.26 \pm 3.92	13.11 \pm 3.22	28.65 \pm 6.41	18.49 \pm 5.29
	♀	2	87.82 \pm 6.45	17.12 \pm 1.05	11.94 \pm 1.07	24.27 \pm 2.02	18.20 \pm 2.27
<i>Sceloporus malachitus</i>	♂	6	67.21 \pm 8.04	14.82 \pm 1.99	10.00 \pm 1.36	20.42 \pm 2.27	12.35 \pm 2.01
	♀	13	60.45 \pm 7.44	13.01 \pm 1.66	8.78 \pm 1.04	19.86 \pm 2.58	10.51 \pm 1.18
<i>Sceloporus merriami</i>	♂	8	47.51 \pm 2.07	8.71 \pm 0.39	5.83 \pm 0.46	11.47 \pm 1.69	6.02 \pm 0.48
	♀	9	45.26 \pm 2.44	8.46 \pm 0.37	5.60 \pm 0.31	11.89 \pm 1.54	6.03 \pm 0.44

Table 1 Continued

Species	Sex	N	SVL	Head width	Head height	Body width	Body height
<i>Sceloporus occidentalis</i>	♂	9	65.88 ± 7.15	12.63 ± 1.45	9.00 ± 1.12	18.57 ± 2.47	11.34 ± 1.95
	♀	9	61.85 ± 6.07	11.40 ± 0.91	8.00 ± 0.83	18.27 ± 2.11	9.77 ± 1.14
<i>Sceloporus olivaceus</i>	♂	8	74.21 ± 14.75	14.61 ± 3.13	10.62 ± 2.53	22.86 ± 6.85	13.97 ± 3.67
	♀	16	85.83 ± 11.81	16.72 ± 2.06	11.87 ± 1.66	27.49 ± 6.31	15.62 ± 2.95
<i>Sceloporus orcutti</i>	♂	10	90.23 ± 8.11	18.14 ± 1.65	11.84 ± 1.16	28.29 ± 2.66	14.07 ± 2.75
	♀	13	79.46 ± 8.60	15.48 ± 1.72	10.67 ± 1.27	25.58 ± 3.65	13.38 ± 2.53
<i>Sceloporus parvus</i>	♂	9	42.78 ± 2.58	8.32 ± 0.50	5.98 ± 0.35	12.07 ± 1.51	6.29 ± 0.37
	♀	6	41.87 ± 2.87	7.68 ± 0.43	5.38 ± 0.38	12.91 ± 1.74	6.38 ± 0.49
<i>Sceloporus poinsetti</i>	♂	9	96.84 ± 9.53	22.34 ± 2.09	13.69 ± 1.75	31.89 ± 3.17	15.77 ± 1.10
	♀	9	90.51 ± 12.24	20.10 ± 2.80	10.97 ± 2.05	30.75 ± 5.25	13.27 ± 3.43
<i>Sceloporus scalaris</i>	♂	7	48.43 ± 5.23	8.63 ± 1.07	6.75 ± 0.70	12.20 ± 2.42	7.46 ± 0.83
	♀	9	50.57 ± 5.91	8.73 ± 1.01	6.74 ± 0.98	13.86 ± 2.38	7.35 ± 0.91
<i>Sceloporus serrifer</i>	♂	9	99.47 ± 12.44	20.72 ± 3.00	12.70 ± 1.91	30.93 ± 4.24	15.90 ± 2.39
	♀	9	91.57 ± 11.31	18.75 ± 2.49	11.58 ± 1.65	29.24 ± 5.32	13.74 ± 2.72
<i>Sceloporus siniferus</i>	♂	11	48.31 ± 3.32	9.19 ± 0.64	7.21 ± 0.53	11.13 ± 1.02	8.45 ± 1.07
	♀	7	43.36 ± 3.22	8.49 ± 0.54	6.48 ± 0.44	11.36 ± 1.05	7.71 ± 0.34
<i>Sceloporus torquatus</i>	♂	3	104.69 ± 7.66	22.84 ± 2.53	14.70 ± 0.39	35.34 ± 0.92	16.28 ± 1.29
	♀	8	93.65 ± 2.97	20.80 ± 0.97	13.29 ± 1.13	33.56 ± 2.04	14.38 ± 1.15
<i>Sceloporus undulatus</i>	♂	17	58.98 ± 5.32	10.78 ± 0.97	7.16 ± 0.72	17.85 ± 2.45	9.37 ± 1.12
	♀	7	66.61 ± 3.91	11.49 ± 0.99	7.76 ± 0.92	21.78 ± 1.31	10.97 ± 1.43
<i>Sceloporus variabilis</i>	♂	12	48.13 ± 5.23	9.10 ± 0.43	6.91 ± 0.28	13.61 ± 1.22	8.11 ± 0.75
	♀	9	45.36 ± 5.49	8.05 ± 0.55	6.05 ± 0.55	12.95 ± 2.31	7.33 ± 0.91
<i>Sceloporus virgatus</i>	♂	11	48.84 ± 4.56	10.49 ± 0.60	7.86 ± 0.67	15.33 ± 1.26	9.84 ± 3.28
	♀	9	52.72 ± 5.65	11.12 ± 0.81	8.28 ± 0.78	17.49 ± 2.09	9.58 ± 0.60
<i>Uma inornata</i>	♂	4	82.65 ± 18.50	13.95 ± 2.88	9.70 ± 1.83	22.45 ± 7.96	12.03 ± 3.87
	♀	2	53.25 ± 1.06	11.15 ± 1.34	7.40 ± 0.71	17.40 ± 0.28	7.70 ± 0.42
<i>Urosaurus auriculatus</i>	♂	13	62.04 ± 4.78	10.69 ± 0.81	7.59 ± 0.77	14.53 ± 1.66	9.03 ± 1.44
	♀	4	47.75 ± 6.70	8.34 ± 0.86	5.76 ± 0.55	10.54 ± 1.51	6.58 ± 0.70
<i>Urosaurus graciosus</i>	♂	14	51.89 ± 4.04	9.36 ± 0.49	6.63 ± 0.62	10.91 ± 0.86	7.39 ± 1.16
	♀	5	48.88 ± 3.64	8.64 ± 0.48	6.35 ± 0.54	11.73 ± 2.78	6.77 ± 0.64
<i>Urosaurus lahtelai</i>	♂	11	44.76 ± 4.14	7.68 ± 0.68	5.29 ± 0.55	9.84 ± 1.27	5.67 ± 0.87
	♀	9	40.69 ± 5.73	7.12 ± 0.41	4.77 ± 0.48	9.52 ± 1.14	5.36 ± 0.70
<i>Urosaurus microscutatus</i>	♂	13	43.49 ± 2.41	7.76 ± 0.44	5.26 ± 0.22	11.17 ± 1.15	6.06 ± 0.44
	♀	6	37.21 ± 3.15	6.59 ± 0.54	4.55 ± 0.35	9.01 ± 0.64	5.09 ± 0.44
<i>Urosaurus nigricaudus</i>	♂	8	48.83 ± 4.60	8.84 ± 0.52	6.33 ± 0.31	12.11 ± 0.94	6.57 ± 0.61
	♀	8	44.75 ± 6.44	8.06 ± 0.51	5.68 ± 0.49	13.14 ± 1.82	5.93 ± 0.33
<i>Urosaurus ornatus</i> (1)	♂	6	50.13 ± 2.10	8.09 ± 0.28	4.91 ± 0.29	13.13 ± 1.17	6.22 ± 0.44
	♀	3	50.12 ± 1.77	7.86 ± 0.18	4.76 ± 0.25	14.29 ± 1.30	6.08 ± 0.74
<i>Urosaurus ornatus</i> (2)	♂	7	54.67 ± 0.82	9.22 ± 0.37	6.13 ± 0.34	13.20 ± 1.08	7.54 ± 0.68
	♀	5	51.79 ± 2.60	8.13 ± 0.28	5.22 ± 0.15	13.48 ± 2.02	6.27 ± 0.54
<i>Urosaurus ornatus</i> (3)	♂	12	48.67 ± 2.36	8.21 ± 0.36	4.85 ± 0.37	12.86 ± 0.79	6.03 ± 0.40
	♀	2	48.60 ± 2.34	7.80 ± 0.69	5.30 ± 0.26	13.90 ± 2.55	7.37 ± 1.52
<i>Urosaurus ornatus</i> (4)	♂	8	51.05 ± 2.38	9.80 ± 0.45	6.30 ± 0.22	15.90 ± 1.80	7.90 ± 0.88
	♀	3	47.75 ± 6.70	8.34 ± 0.86	5.76 ± 0.55	10.54 ± 1.51	6.58 ± 0.70

tats, ground-dwelling in vegetation, rock-climbing and tree-climbing) based on literature data (see Table 3).

ANALYSES

As closely related species share a large part of their evolutionary history, they cannot be considered independent data points (Felsenstein, 1985, 1986; Harvey

& Pagel, 1991). To take the evolutionary history of the species into account, phylogenetic analyses were used. As these methods require information on the relationships between the species in the analysis, we constructed a tree depicting these relationships based on literature data (Wiens, 1993; Reeder & Wiens, 1996; Wiens & Reeder, 1997; see Fig. 1). The relationships between the four populations of *Urosaurus* were

Table 2. Morphometrical characterization of the limbs for both sexes. Table entries are averages \pm standard deviations. The first row for each species denotes the results for male lizards, the second row for females

Species	Femur length	Tibia length	Metatarsus length	Longest toe length	Humerus length	Radius length	Meta carpus length	Hind limb length	Fore limb length
<i>Callisaurus draconoides</i>	20.56 \pm 1.62	22.24 \pm 2.82	12.52 \pm 0.90	20.95 \pm 2.21	16.89 \pm 1.91	14.08 \pm 1.56	5.39 \pm 0.58	76.27 \pm 6.50	36.35 \pm 3.66
<i>Cophosaurus texanus</i>	16.49 \pm 1.35	16.61 \pm 1.97	8.88 \pm 1.05	17.73 \pm 2.15	14.03 \pm 1.63	10.68 \pm 1.29	4.28 \pm 0.43	59.70 \pm 5.89	28.98 \pm 2.97
<i>Holbrookia maculata</i>	12.50 \pm 1.15	8.98 \pm 6.84	6.50 \pm 0.82	14.00 \pm 0.46	10.63 \pm 1.25	7.20 \pm 0.79	3.30 \pm 0.35	41.98 \pm 8.35	21.13 \pm 2.27
	12.46 \pm 0.86	11.20 \pm 0.55	8.16 \pm 0.35	10.70 \pm 0.77	10.60 \pm 0.54	7.62 \pm 0.30	3.83 \pm 0.95	42.53 \pm 1.84	22.05 \pm 1.19
<i>Petrosaurus thalassinus</i>	12.10 \pm 0.69	10.23 \pm 0.17	7.47 \pm 0.58	10.59 \pm 0.69	10.08 \pm 0.32	7.80 \pm 0.20	3.63 \pm 0.13	40.38 \pm 0.86	21.51 \pm 0.35
	26.41 \pm 6.31	23.25 \pm 5.40	11.89 \pm 1.93	17.59 \pm 3.27	19.96 \pm 4.69	15.33 \pm 3.39	6.79 \pm 1.30	79.14 \pm 16.52	42.08 \pm 9.23
<i>Sator angustatus</i>	23.44 \pm 3.90	21.98 \pm 3.79	10.91 \pm 1.48	14.52 \pm 2.61	18.23 \pm 2.61	14.25 \pm 1.75	6.24 \pm 0.83	70.86 \pm 11.40	38.71 \pm 4.96
	17.88 \pm 2.86	18.64 \pm 2.22	11.13 \pm 1.25	15.50 \pm 1.20	13.85 \pm 1.96	11.66 \pm 2.08	4.75 \pm 0.86	63.15 \pm 7.11	30.26 \pm 4.70
<i>Sceloporus clarkii</i>	14.69 \pm 0.95	16.16 \pm 0.60	9.22 \pm 0.57	13.25 \pm 0.96	11.89 \pm 0.55	9.39 \pm 1.12	3.88 \pm 0.45	53.31 \pm 2.41	25.15 \pm 1.80
	21.19 \pm 3.23	18.11 \pm 4.20	10.92 \pm 1.17	14.77 \pm 1.91	17.81 \pm 3.32	14.47 \pm 2.80	6.18 \pm 0.81	64.99 \pm 9.19	38.47 \pm 6.63
<i>Sceloporus graciosus</i>	20.35 \pm 2.66	17.39 \pm 2.94	11.22 \pm 1.16	15.00 \pm 1.08	17.72 \pm 1.62	14.69 \pm 1.31	6.26 \pm 0.82	63.95 \pm 5.78	38.67 \pm 3.21
	11.35 \pm 0.84	9.66 \pm 0.69	6.71 \pm 0.48	11.13 \pm 1.00	9.37 \pm 0.84	6.93 \pm 0.38	3.57 \pm 0.23	38.84 \pm 1.50	19.86 \pm 1.11
<i>Sceloporus grammicus</i>	11.49 \pm 0.61	8.60 \pm 0.78	6.58 \pm 0.40	10.46 \pm 0.65	8.85 \pm 0.64	6.72 \pm 0.54	3.75 \pm 0.69	37.14 \pm 1.64	19.32 \pm 1.20
	13.58 \pm 1.72	11.04 \pm 1.14	7.13 \pm 0.65	10.61 \pm 1.18	11.26 \pm 1.48	8.94 \pm 0.98	4.26 \pm 0.46	42.37 \pm 3.66	24.47 \pm 2.46
<i>Sceloporus jarrovi</i>	11.03 \pm 1.89	9.23 \pm 1.20	6.01 \pm 0.78	8.92 \pm 1.35	9.72 \pm 1.58	7.50 \pm 0.89	3.90 \pm 1.16	35.20 \pm 4.62	21.12 \pm 3.04
	17.81 \pm 2.08	13.50 \pm 1.42	8.83 \pm 0.75	12.06 \pm 1.11	13.70 \pm 1.08	11.23 \pm 0.94	5.75 \pm 1.38	52.19 \pm 3.33	30.69 \pm 1.14
<i>Sceloporus magister</i>	16.28 \pm 1.99	12.87 \pm 1.45	7.65 \pm 0.67	10.81 \pm 0.82	12.77 \pm 1.20	10.07 \pm 1.28	4.92 \pm 2.79	47.61 \pm 3.94	27.77 \pm 4.38
	21.14 \pm 3.64	16.82 \pm 5.41	12.33 \pm 1.96	15.65 \pm 2.01	16.59 \pm 3.75	13.39 \pm 3.25	6.50 \pm 1.02	65.92 \pm 11.80	36.48 \pm 7.88
<i>Sceloporus malachitius</i>	20.83 \pm 1.19	16.57 \pm 4.99	10.88 \pm 1.58	14.45 \pm 1.24	16.25 \pm 1.12	13.10 \pm 2.47	6.10 \pm 0.74	62.73 \pm 0.98	35.45 \pm 2.85
	14.46 \pm 2.16	13.76 \pm 1.90	8.98 \pm 1.12	13.59 \pm 2.24	13.14 \pm 1.94	10.75 \pm 1.55	4.07 \pm 0.76	50.79 \pm 7.34	27.97 \pm 3.98
<i>Sceloporus merriami</i>	12.86 \pm 1.51	12.23 \pm 1.60	8.08 \pm 0.88	12.39 \pm 1.49	11.85 \pm 1.34	9.27 \pm 1.06	4.06 \pm 0.58	45.56 \pm 5.01	25.18 \pm 2.76
	11.61 \pm 0.81	10.57 \pm 0.83	7.28 \pm 0.67	8.44 \pm 0.73	9.60 \pm 0.78	7.98 \pm 0.67	3.23 \pm 0.39	37.90 \pm 2.53	20.80 \pm 0.94
<i>Sceloporus occidentalis</i>	10.14 \pm 0.50	9.56 \pm 0.38	6.40 \pm 0.37	7.55 \pm 0.73	8.88 \pm 0.85	7.29 \pm 0.39	3.17 \pm 0.33	33.65 \pm 1.17	19.33 \pm 1.02
	15.52 \pm 1.95	15.53 \pm 2.41	9.29 \pm 0.89	13.89 \pm 1.60	12.69 \pm 1.98	10.41 \pm 1.32	4.55 \pm 0.48	54.24 \pm 6.58	27.66 \pm 3.57
<i>Sceloporus olivaceus</i>	13.78 \pm 1.29	13.89 \pm 1.66	8.71 \pm 0.70	12.20 \pm 0.88	11.67 \pm 0.90	9.71 \pm 1.12	4.21 \pm 0.25	48.59 \pm 4.23	25.59 \pm 2.00
	16.59 \pm 3.43	15.38 \pm 3.20	10.40 \pm 1.52	13.96 \pm 2.07	13.48 \pm 2.62	11.05 \pm 1.92	4.76 \pm 0.67	56.34 \pm 9.37	29.29 \pm 4.53
<i>Sceloporus orcutti</i>	19.15 \pm 2.20	17.84 \pm 2.08	12.50 \pm 1.05	15.78 \pm 1.22	16.06 \pm 2.14	13.58 \pm 1.83	5.91 \pm 0.80	65.26 \pm 5.52	35.54 \pm 4.52
	20.38 \pm 1.76	20.39 \pm 1.84	11.38 \pm 0.94	15.20 \pm 0.87	17.27 \pm 1.47	14.50 \pm 1.48	6.33 \pm 1.09	67.34 \pm 4.38	38.11 \pm 3.00
<i>Sceloporus parvus</i>	18.37 \pm 2.45	17.90 \pm 1.79	10.54 \pm 0.95	13.66 \pm 1.11	15.51 \pm 2.03	12.84 \pm 2.39	5.76 \pm 0.58	60.47 \pm 5.69	34.10 \pm 4.60
	9.92 \pm 0.67	9.19 \pm 0.67	5.07 \pm 0.40	8.78 \pm 0.63	7.38 \pm 0.33	5.47 \pm 0.47	2.51 \pm 0.28	32.95 \pm 1.31	15.36 \pm 0.73
<i>Sceloporus poinsetti</i>	8.94 \pm 1.00	8.36 \pm 0.43	4.56 \pm 0.59	8.04 \pm 1.07	6.67 \pm 0.52	5.61 \pm 0.49	2.82 \pm 1.09	29.89 \pm 2.01	15.09 \pm 1.63
	23.41 \pm 2.26	19.00 \pm 2.65	11.55 \pm 0.63	14.29 \pm 0.99	18.51 \pm 2.42	12.62 \pm 1.69	6.34 \pm 1.03	68.24 \pm 5.45	37.47 \pm 4.41
<i>Sceloporus serrifer</i>	20.82 \pm 2.26	17.20 \pm 3.25	10.90 \pm 1.27	12.92 \pm 2.12	15.42 \pm 2.70	11.60 \pm 1.90	5.47 \pm 0.72	61.83 \pm 8.05	32.49 \pm 4.82
	23.29 \pm 3.01	19.63 \pm 3.54	12.13 \pm 1.73	15.40 \pm 1.43	18.20 \pm 3.05	13.15 \pm 2.55	6.21 \pm 0.85	70.46 \pm 8.63	37.56 \pm 6.08
	21.50 \pm 2.72	17.30 \pm 3.42	11.01 \pm 1.39	14.90 \pm 1.65	16.88 \pm 2.71	12.71 \pm 2.48	6.05 \pm 1.13	64.71 \pm 8.65	35.94 \pm 5.94

Table 2. Continued

Species	Femur length	Tibia length	Metatarsus length	Longest toe length	Humerus length	Radius length	Meta carpus length	Hind limb length	Fore limb length
<i>Sceloporus scalaris</i>	9.71 ± 1.34	8.24 ± 1.60	5.63 ± 0.74	8.50 ± 1.30	8.06 ± 1.23	5.96 ± 0.70	2.83 ± 0.32	32.08 ± 4.36	16.86 ± 1.93
<i>Sceloporus siniferus</i>	9.11 ± 0.90	7.40 ± 1.78	5.09 ± 0.95	8.02 ± 1.31	7.51 ± 1.12	5.80 ± 0.84	2.73 ± 0.52	29.62 ± 4.61	16.04 ± 2.35
<i>Sceloporus torquatus</i>	11.18 ± 0.90	13.05 ± 1.01	8.39 ± 0.59	12.34 ± 1.05	9.45 ± 0.90	7.89 ± 0.58	3.03 ± 0.35	44.95 ± 3.05	20.37 ± 1.44
<i>Sceloporus undulatus</i>	10.21 ± 0.95	11.50 ± 1.08	7.39 ± 0.64	10.91 ± 1.06	7.99 ± 0.59	6.88 ± 0.51	2.59 ± 0.27	40.00 ± 3.47	17.46 ± 1.12
<i>Sceloporus variabilis</i>	23.31 ± 1.85	21.09 ± 1.87	10.48 ± 1.86	14.31 ± 0.96	17.88 ± 4.26	12.94 ± 1.13	6.50 ± 0.74	69.19 ± 6.12	37.32 ± 5.77
<i>Sceloporus virgatus</i>	22.91 ± 1.82	19.81 ± 1.04	9.89 ± 1.06	14.90 ± 1.71	18.52 ± 1.27	13.74 ± 0.96	5.87 ± 0.74	67.52 ± 4.10	38.13 ± 1.86
<i>Uma inornata</i>	12.55 ± 1.48	10.51 ± 1.95	7.01 ± 0.85	10.30 ± 0.97	9.00 ± 1.17	7.32 ± 1.11	3.75 ± 0.37	40.36 ± 3.84	20.06 ± 2.16
<i>Urosaurus auriculatus</i>	13.37 ± 1.12	10.57 ± 1.22	7.08 ± 0.72	9.86 ± 0.83	9.38 ± 1.12	7.74 ± 0.58	3.76 ± 0.40	40.88 ± 2.14	20.88 ± 1.77
<i>Urosaurus graciosus</i>	10.48 ± 0.90	11.43 ± 0.60	7.19 ± 0.33	9.40 ± 0.89	9.08 ± 0.57	7.43 ± 0.78	2.86 ± 0.44	38.50 ± 1.86	19.37 ± 1.13
<i>Urosaurus lahtelai</i>	9.24 ± 0.94	9.50 ± 0.39	6.59 ± 0.55	8.93 ± 0.51	7.92 ± 0.59	6.13 ± 0.75	2.67 ± 0.21	34.26 ± 1.36	16.73 ± 1.25
<i>Urosaurus microscutatus</i>	12.75 ± 1.44	9.88 ± 1.26	6.21 ± 0.63	9.22 ± 0.72	9.56 ± 0.94	7.23 ± 0.72	3.41 ± 1.55	38.06 ± 3.46	20.20 ± 2.27
<i>Urosaurus nigricaudus</i>	12.92 ± 1.04	10.19 ± 0.59	6.00 ± 0.40	9.34 ± 0.61	10.10 ± 0.86	7.96 ± 0.88	2.85 ± 0.68	38.45 ± 1.91	20.91 ± 1.46
<i>Urosaurus ornatus</i> (1)	18.15 ± 3.63	18.63 ± 5.01	9.23 ± 1.93	17.18 ± 2.84	15.95 ± 2.98	11.38 ± 1.95	5.05 ± 1.16	63.18 ± 12.81	32.38 ± 5.76
<i>Urosaurus ornatus</i> (2)	14.00 ± 0.99	13.10 ± 1.56	8.10 ± 0.99	12.75 ± 1.63	11.75 ± 2.05	8.85 ± 2.33	4.15 ± 0.78	47.95 ± 5.16	24.75 ± 5.16
<i>Urosaurus ornatus</i> (3)	12.97 ± 1.13	12.89 ± 1.12	7.84 ± 0.80	11.24 ± 1.26	11.42 ± 1.03	8.70 ± 0.57	4.18 ± 0.46	44.94 ± 3.68	24.30 ± 1.66
<i>Urosaurus ornatus</i> (4)	10.05 ± 1.25	9.69 ± 0.89	6.18 ± 0.88	9.36 ± 1.07	8.29 ± 1.51	6.64 ± 1.18	3.25 ± 0.31	35.27 ± 3.78	18.18 ± 2.85
	10.91 ± 0.85	9.44 ± 0.87	5.43 ± 0.57	10.38 ± 0.68	8.45 ± 0.92	6.64 ± 0.48	2.71 ± 0.45	36.15 ± 2.29	17.80 ± 1.37
	8.79 ± 0.78	8.79 ± 0.74	4.40 ± 0.52	9.81 ± 0.63	8.33 ± 0.66	6.65 ± 0.84	2.73 ± 0.38	31.79 ± 2.07	17.71 ± 1.28
	10.21 ± 1.13	9.58 ± 0.98	5.66 ± 0.59	8.56 ± 1.16	8.12 ± 0.84	6.43 ± 0.56	2.39 ± 0.34	34.01 ± 3.51	16.95 ± 1.59
	8.49 ± 0.72	8.35 ± 0.49	5.03 ± 0.49	7.91 ± 0.90	7.36 ± 0.49	5.69 ± 0.40	2.17 ± 0.20	29.77 ± 2.15	15.22 ± 0.90
	10.00 ± 0.82	9.25 ± 0.64	5.08 ± 0.59	8.09 ± 0.44	8.06 ± 0.45	6.45 ± 0.51	2.52 ± 0.30	32.41 ± 2.16	17.03 ± 1.10
	7.54 ± 0.55	7.20 ± 0.74	4.26 ± 0.25	6.78 ± 0.40	6.48 ± 0.52	5.32 ± 0.46	1.96 ± 0.29	25.78 ± 1.39	13.76 ± 1.25
	10.11 ± 0.68	8.34 ± 0.48	4.43 ± 0.47	8.86 ± 1.06	8.36 ± 0.56	6.46 ± 0.47	2.44 ± 0.36	31.74 ± 1.67	17.26 ± 0.86
	9.04 ± 1.05	7.23 ± 0.69	4.16 ± 0.32	7.58 ± 0.54	7.43 ± 0.48	5.85 ± 0.39	2.26 ± 0.23	28.01 ± 1.80	15.54 ± 0.85
	11.10 ± 0.47	6.75 ± 0.22	4.93 ± 0.24	8.24 ± 0.52	7.99 ± 0.13	5.59 ± 0.53	3.35 ± 0.95	31.02 ± 0.66	16.93 ± 1.05
	10.33 ± 0.55	6.22 ± 0.66	4.52 ± 0.78	7.01 ± 1.10	7.16 ± 0.26	5.41 ± 0.08	3.33 ± 1.23	28.07 ± 1.24	15.90 ± 1.11
	12.48 ± 0.84	8.56 ± 0.85	6.35 ± 0.74	9.67 ± 0.86	9.15 ± 0.72	6.89 ± 0.50	3.83 ± 0.51	37.06 ± 2.22	19.87 ± 0.85
	11.94 ± 0.57	7.71 ± 0.76	5.86 ± 0.45	8.32 ± 0.60	8.41 ± 0.52	6.44 ± 0.88	3.43 ± 0.23	33.83 ± 1.48	18.28 ± 0.61
	12.03 ± 0.71	7.10 ± 0.84	5.31 ± 0.48	8.10 ± 0.75	8.49 ± 0.55	5.89 ± 0.45	2.96 ± 0.24	32.53 ± 2.02	17.34 ± 0.93
	11.19 ± 0.53	6.31 ± 0.30	5.03 ± 0.35	7.31 ± 0.37	8.03 ± 0.00	5.82 ± 0.15	2.68 ± 0.37	29.83 ± 0.85	16.53 ± 0.22
	10.93 ± 0.90	7.63 ± 1.30	5.80 ± 0.58	9.08 ± 0.51	7.00 ± 0.73	6.38 ± 0.67	2.73 ± 0.21	33.43 ± 2.63	16.10 ± 1.28
	10.37 ± 0.55	6.60 ± 0.26	5.20 ± 0.61	8.10 ± 0.87	5.80 ± 0.87	5.50 ± 0.36	2.53 ± 0.12	30.27 ± 0.96	13.83 ± 1.12

Table 3. Habitat use in the species examined in this study

Species	Habitat use	Reference
<i>Callisaurus draconoides</i>	Ground-dweller in open habitats	Stebbins (1985); McPeck 2000
<i>Cophosaurus texanus</i>	Ground-dweller in open habitats	Conant (1975); Stebbins (1985)
<i>Holbrookia maculata</i>	Ground-dweller in open habitats	Conant (1975); Stebbins (1985); Ballinger & Watts (1995)
<i>Petrosaurus thalassinus</i>	Rock-climber	Stebbins (1985); McPeck 2000
<i>Sator angustatus</i>	Ground-dweller in open habitats	McPeck 2000
<i>Sceloporus clarki</i>	Tree-climber	Stebbins (1985)
<i>Sceloporus graciosus</i>	Ground-dweller in vegetation	Conant (1975); Stebbins (1985)
<i>Sceloporus grammicus</i>	Tree-climber	Conant (1975); Ortega-Rubio & Arriaga (1990)
<i>Sceloporus jarrovi</i>	Rock-climber	Stebbins (1985); Morrison <i>et al.</i> (1995)
<i>Sceloporus magister</i>	Tree-climber	Conant (1975); Stebbins (1985)
<i>Sceloporus malachitus</i>	Rock-climber	Köhler (1993)
<i>Sceloporus merriami</i>	Rock-climber	Conant (1975)
<i>Sceloporus occidentalis</i>	Ground-dweller in open habitats	Stebbins (1985); Grover (1996); Block & Morrison (1998)
<i>Sceloporus olivaceus</i>	Tree-climber	Conant (1975)
<i>Sceloporus orcutti</i>	Rock-climber	Stebbins (1985)
<i>Sceloporus parvus</i>	Rock-climber (but see Mink & Sites, 1996)	Ivan Rubio Perez, pers. comm.
<i>Sceloporus poinsetti</i>	Rock-climber	Conant (1975); Stebbins (1985)
<i>Sceloporus scalaris</i>	Ground-dweller in vegetation	Stebbins (1985); Mink & Sites (1996); Ortega-Rubio & Arriaga (1990); Bock <i>et al.</i> (1990)
<i>Sceloporus serrifer</i>	Rock-climber	Conant (1975); Lee (1996)
<i>Sceloporus siniferus</i>	Ground-dweller in vegetation	Alvarez del Toro (1982)
<i>Sceloporus torquatus</i>	Rock-climber	Burquez, Flores-Villela & Hernandez 1986
<i>Sceloporus undulatus</i>	Ground-dweller in open habitats	Conant (1975); Stebbins (1985); Pounds & Jackson (1983); Ballinger & Watts (1995); Grover (1996)
<i>Sceloporus variabilis</i>	Ground-dweller in vegetation	Conant (1975)
<i>Sceloporus virgatus</i>	Ground-dweller in open habitats	Stebbins (1985); Smith (1995); (1998)
<i>Uma inornata</i>	Ground-dweller in open habitats	Stebbins (1985)
<i>Urosaurus auriculatus</i>	Rock-climber	Ortega-Rubio <i>et al.</i> (1991)
<i>Urosaurus graciosus</i>	Ground-dweller in vegetation	Stebbins (1985)
<i>Urosaurus lahtelai</i>	Rock-climber	Stebbins (1985); McPeck 2000
<i>Urosaurus microscutatus</i>	Rock-climber	Stebbins (1985)
<i>Urosaurus nigricaudus</i>	Tree-climber	Stebbins (1985); McPeck 2000
<i>Urosaurus ornatus</i> (1)	Tree-climber	Herrel <i>et al.</i> (2001)
<i>Urosaurus ornatus</i> (2)	Rock-climber	Herrel <i>et al.</i> (2001)
<i>Urosaurus ornatus</i> (3)	Rock-climber	Herrel <i>et al.</i> (2001)
<i>Urosaurus ornatus</i> (4)	Ground-dweller in open habitats	Herrel <i>et al.</i> (2001)

The habitat used by the species studied was grouped into one of four classes: rock-climbing, tree-climbing, ground-dwelling and ground-dwelling in vegetation.

included in the phylogeny as a hard polytomy (Fig. 1; see Purvis & Garland, 1993). Two sets of analyses were performed, one to test whether body and head shape differ between species occupying different habitats, and one to test for differences in leg shape between species from different habitat groups.

The species means of all traits were calculated for both sexes separately and \log_{10} -transformed. As shape differences were of special interest, we regressed the

species means of all variables for each sex separately against snout–vent length, and calculated the residuals. In addition, we regressed the species mean for forelimb length against the species mean of hindlimb length for each sex and calculated residuals. The residuals of the morphometric traits, of forelimb length vs. hindlimb length, and snout–vent length (\log_{10} transformed) were then used as input for the simulation analysis.

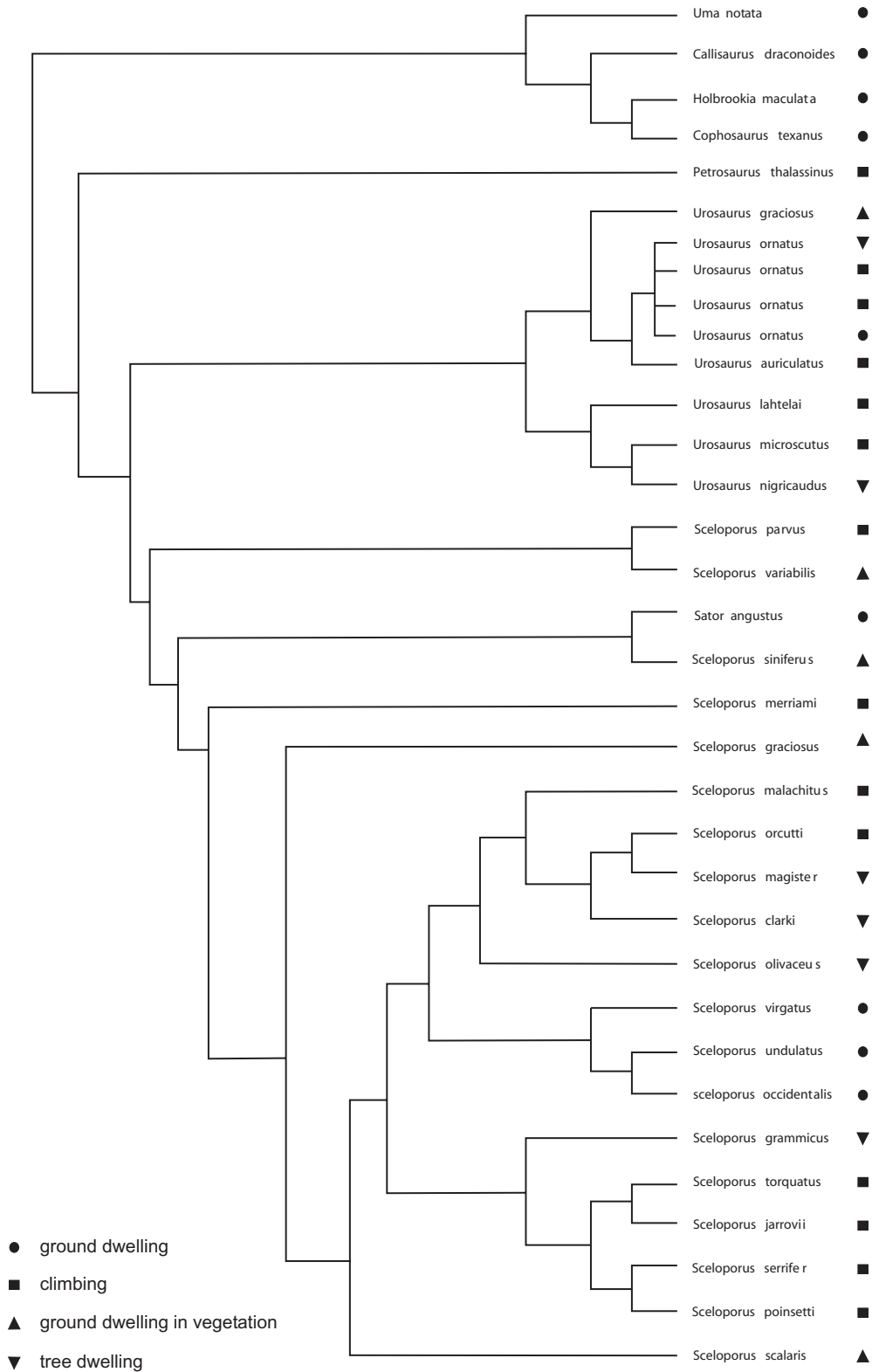


Figure 1. Phylogenetic tree used for comparative analyses. The relationships between the species are based on Wiens (1993), Reeder & Wiens (1996) and Wiens & Reeder (1997). The classification of species into one of four habitat categories was based on literature data (Table 3). Species belonging to different habitat categories are indicated by symbols: ●, ground-dwelling in open area; ■, rock-climbing; ▲, ground-dwelling in vegetation; ▼, tree-climbing.

All phylogenetic analyses were performed using the PDTREE, PDSIMUL and PDANOVA programs (Garland, Midford & Ives, 1999). In the analyses branch lengths were set to unity as data concerning the divergence times of all species were not available (see also Diaz-Uriarte & Garland, 1998). We inspected diagnostics graphs and statistics in the PDTREE program (Garland *et al.*, 1999) to verify that branch lengths were indeed adequate for all traits. Where necessary, branch lengths were transformed using the Pagel transformation (Garland *et al.*, 1999).

The PDSIMUL program was used to create an empirical null distribution based on the phylogenetic relationships between the species. We ran 1000 unbounded simulations and used the Brownian motion model as our model for evolutionary change. Next the PDANOVA program was used to create a new distribution of F -values based on the simulation data. Differences between groups were considered significant if the F -value of our analysis on the original data exceeded the F_{95} value of the empirically-derived distribution.

RESULTS

Both traditional and phylogenetic analyses indicated that lizards from different habitat categories did not differ in snout-vent length (Tables 1 and 4). Moreover, none of the head and body shape variables that were measured differed between species occupying different habitats. Using traditional statistics, only differences

in body height approached significance, but all trends disappeared when taking into account the relationships between species (Table 4).

Traditional analyses indicated significant differences in hindlimb shape (residual femur length, residual longest toe length, residual hindlimb length, and the residual of forelimb length against hindlimb length) between male lizards from different habitats (Tables 2 and 4). For female lizards, only differences in femur length and the ratio of front against hindlimb length were significantly different for animals utilizing different habitats (Tables 2 and 4). Post-hoc tests indicated that both male and female lizards from open terrestrial habitats had a significantly longer femur than ground-dwelling lizards from vegetated habitats or tree-climbers (Figs 2,3). Male lizards from open terrestrial habitats also had longer toes than rock or tree-climbers, and longer hindlimbs than males from tree-climbing species (Fig. 2). Both male and female lizards from open terrestrial habitats had a smaller residual forelimb length to hindlimb length than both rock and tree-climbers (Figs 2,3). However, differences in residual femur length and residual hindlimb length for males, and differences in residual longest toe length for females were no longer significant after Bonferroni correction (Table 4).

When taking into account the relationships among the species studied, only differences in residual frontlimb to hindlimb length remained significant for both sexes. Additionally, for male lizards residual longest toe length showed differences between habitat

Table 4. Phylogenetic analysis of the morphometric data for the phrynosomatids included in the study

	F_{95}		P		F_{phyl}		P	
	male	female	male	female	male	female	male	female
Head and body shape								
Log SVL	1.33	1.23	0.28	0.32	4.51	3.78	0.43	0.39
Residual head width	0.52	0.57	0.67	0.64	4.69	3.78	0.78	0.74
residual head height	0.62	0.74	0.61	0.54	4.21	4.36	0.73	0.59
residual body width	0.28	0.19	0.84	0.90	4.28	3.89	0.90	0.94
residual body height	1.75	1.69	0.18	0.19	4.59	3.73	0.32	0.28
Limb proportions								
Residual femur length	4.50	5.05	0.01	0.006*	4.53	4.00	0.052	0.027
Residual tibia length	2.71	1.18	0.06	0.34	4.66	4.09	0.15	0.45
Residual longest toe length	5.41	2.32	0.004*	0.10	4.21	3.74	0.027	0.16
Residual front limb length	1.04	0.69	0.39	0.57	4.04	3.68	0.53	0.63
Residual hind limb length	3.88	2.02	0.02	0.13	4.20	3.66	0.062	0.20
Residual fl/hll	8.40	6.17	0.0003*	0.002*	4.38	3.73	0.004*	0.008*

F and P -values are for non-phylogenetic and phylogenetic ANOVA's for analyses performed on head and body, and limb shape data. Results of the phylogenetic analysis are considered significant if the phylogenetic F -values are larger than the traditional F_{95} values. *indicates significant differences at the $\alpha = 0.05$ level after sequential Bonferroni correction. SVL, snout-vent length; residual fl/hll, residual front limb length relative to hindlimb length.

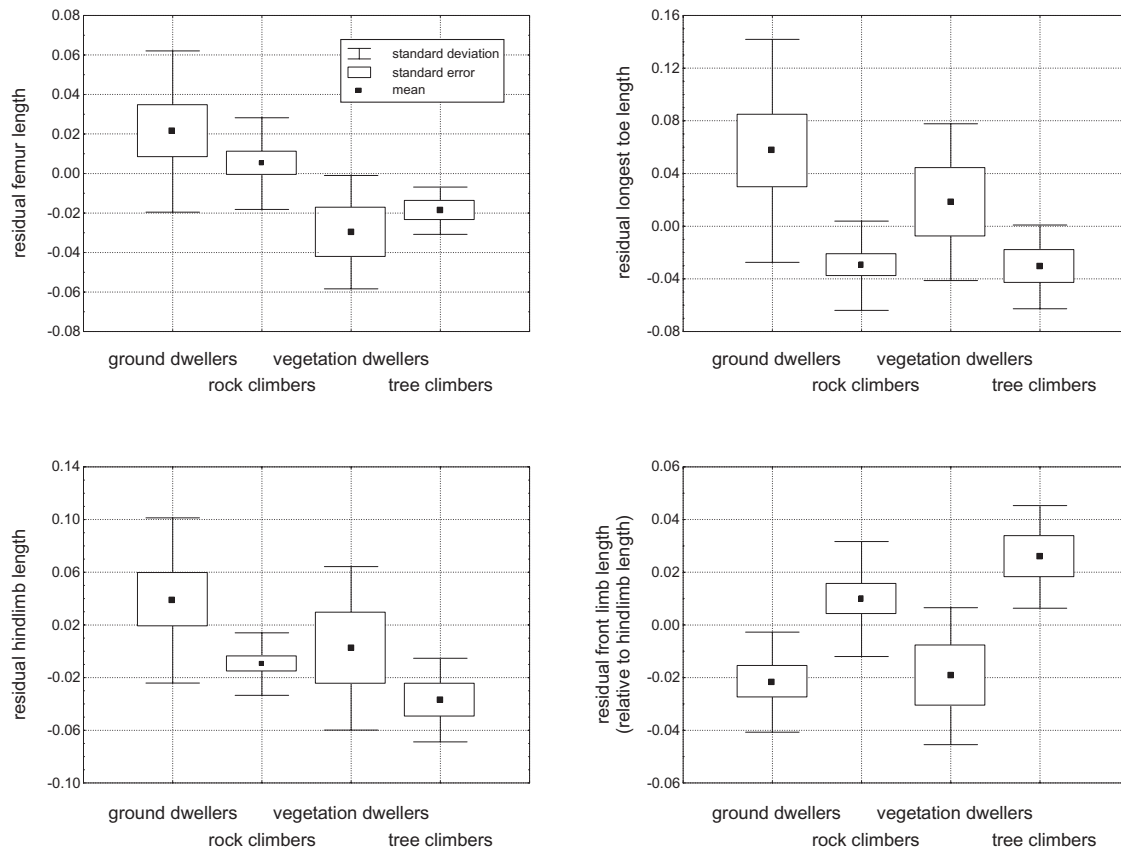


Figure 2. Box plots illustrating morphometric differences among habitat categories for male lizards. Although differences were significant for all variables illustrated using non-phylogenetic analysis, only differences in longest toe length and residual forelimb length were significant when using phylogenetically informed analyses. Ground-dwellers have significantly longer toes than either rock or tree-climbers, and relatively shorter frontlimbs (compared to the hindlimbs) than either rock or tree-climbers.

groups, and for female lizards, femur length was significantly different between species occupying different habitats. However, these differences were no longer significant after Bonferroni correction (Table 4).

DISCUSSION

The predicted correlations between habitat use and morphology were only partially confirmed by our results. Surprisingly none of the head or body shape variables showed any relations with habitat use in the phrynosomatids examined in this study. Yet, in a population-level analysis, significant differences in head and body shape between populations of the species *Urosaurus ornatus* were present (Herrel, Meyers & Vanhooydonck, 2001). In *U. ornatus*, lizards from climbing populations had flatter bodies and heads than species from a ground-dwelling population. Also for lacertid lizards (Vanhooydonck & Van Damme, 1999) and populations of *Tropidurus* lizards (Vitt *et al.*,

1997), a tendency towards flatter heads and bodies in climbing or rock-dwelling species was observed. Why this does not seem to be true in phrynosomatids remains unclear. Either our measurements were not accurate enough to detect small differences in head and body shape, our predictions were inaccurate, or selection on these characteristics is largely unaffected by habitat use as both head and body are likely to be constrained by many other functions besides locomotion (e.g. feeding, reproduction). Further analysis investigating whether negative correlations between head and body height and climbing performance exist in phrynosomatid lizards might be particularly useful in shedding some light on this matter.

Differences in limb shape, on the other hand, were largely supported by the conventional analyses. Male lizards from species that live in open terrestrial habitats had a longer fourth toe on the hind foot than rock or tree-climbing species, and longer hindlimbs than tree-climbers, both as predicted. Additionally, both male and female lizards from species utilizing open

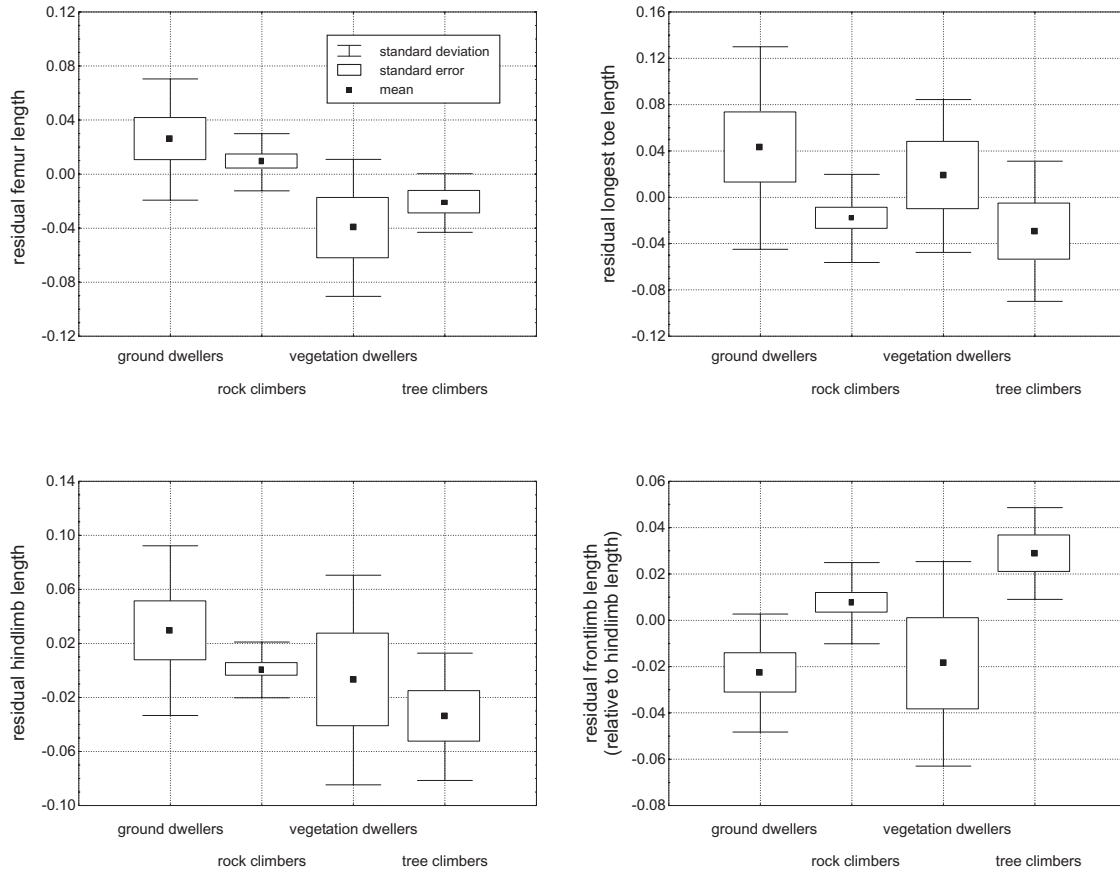


Figure 3. Box plots illustrating morphometric differences among habitat categories for female lizards. Although differences were significant for most variables illustrated using non-phylogenetic analysis, only differences in residual forelimb length and femur length were significant when using phylogenetically informed analyses (note that differences in femur length are no longer significant after Bonferroni correction). Ground-dwellers have relatively shorter frontlimbs (compared to the hindlimbs) than either rock or tree-climbers, and have significantly longer femurs than both vegetation-dwellers and tree-climbers.

terrestrial habitats had relatively short forelimbs compared to their hindlimbs, in contrast to rock or tree-climbing species. The observation that relatively short femurs occurred in species that were ground-dwellers in vegetation or tree-climbers, compared to those of species utilizing more open terrestrial habitats, was not in accordance with our predictions. Although shorter femurs are likely to allow both tree-climbers moving on branches and vegetation-dwellers to position the feet closer to the body, it was expected that ground-dwellers would show an increase in the length of the distal limb segments. Still, lengthening of the femur might be important in specialized runners to provide an increased area of attachment for the caudofemoralis muscle which powers locomotion in lizards (Russell & Bauer, 1992; Reilly, 1995, 1998; Zaaf *et al.*, 1999).

The phylogenetic analysis indicated that only relative leg length (front to hindlimb) showed a strong

adaptive response to habitat use, with rock and tree-climbers having relatively longer forelimbs compared to the hindlimbs, and ground-dwellers in open habitats having short forelimbs relative to their hindlimbs. It appears that the physical constraints imposed by gravitational forces during climbing are important in shaping the locomotor apparatus in phrynosomatid lizards. This is in sharp contrast to the results of two previous studies where the relative length of fore- to hindlimbs was included in the analyses (lacertids: Vanhooydonck & Van Damme, 1999; geckos: Zaaf & Van Damme, 2001). In the case of the lacertid lizards, the clustering of habitat groups within certain clades seems to be crucial in the absence of any correlation (i.e. lack of statistical power, see Vanhooydonck & Van Damme, 1999). In geckoes, however, the presence of highly specialized adhesive structures such as toe pads probably reduces the constraints imposed by gravity during climbing (see Zaaf & Van Damme,

2001). Adhesive structures such as toe pads have consequently been explained as key innovations, forming the basis of the adaptive morphological radiation of anoline lizards (Warheit *et al.*, 1999).

Other limb shape variables such as femur length in female lizards (with species from open terrestrial habitats having longer femurs than species from vegetated terrestrial habitats and tree-climbers) and longest toe length in male lizards (ground-dwellers from open habitat having longer longest toes than rock or tree-climbers) showed fairly strong differences between habitat groups. Similar results have been found in lizards of the genus *Anolis* and *Tropidurus*, where branch-dwellers tended to have shorter hindlimbs (Losos, 1994; Losos *et al.*, 1997; Kohlsdorf *et al.*, 2001), and *Tropidurus* species from sandy, open habitats tended to have longer feet (Kohlsdorf *et al.*, 2001). Also in *Niveoscincus* and *Liolaemus*, species occupying open microhabitats had longer limbs than species from vegetated habitats (Jaksic *et al.*, 1980; Melville & Swain, 2000).

Despite these results, the statistical power of our data set (compared to conventional analyses) was lower than expected, especially given the strong associations observed between habitat use and morphology in populations of the phrynosomatid species *Urosaurus ornatus* (Herrel *et al.*, 2001). Although these differences at the population level might be the result of a phenotypically plastic response to differences in habitat (e.g. Losos *et al.*, 2000), the strong correspondence of both leg and body shape to a priori predictions is indicative of an adaptive response. However, upon examination in the wild of several of the species used in the present study, it was noted that several of them may occupy habitats which are radically different from those reported in the literature. For example, populations of *Sceloporus serrifer* living variously on rocks, trees and on the ground were all encountered within a fairly close geographical range. Also for other species such as *S. clarkii*, *U. ornatus* and *S. undulatus* populations differing largely in habitat use were encountered. As most studies (the present one included) typically use museum collections to quantify morphometric traits (including lizards from different populations) which are then related to literature data on ecological variables, the adaptive characters which are potentially present might not be detected. Moreover, by utilizing broad habitat categories based on literature data additional error is introduced into the data (see also Kohlsdorf *et al.*, 2001). Ideally both habitat use and morphometry should be quantified for animals from the same population.

Not unexpectedly, we found some differences in the strength of the adaptive response between male and female lizards. Although both sexes responded similarly to differences in habitat (Table 4), male lizards

generally showed stronger responses (especially when considering the conventional analysis). Although previous studies have indicated how plastic responses in hindlimb length may vary between sexes (Losos *et al.*, 2000), no studies have examined differences between sexes in their evolutionary response to habitat structure. As male lizards need to defend territories, and as territoriality is strongly correlated with locomotor capacity in some phrynosomatid lizards (Robson & Miles, 2000) both natural and sexual selection will probably thus act in concert to maximize locomotor performance in male lizards. For territorial species, male locomotor performance might be essential to defend crucial resources that allow them to gain access to females. Although possibly not directly linked (Garland, Hankins & Huey, 1990; Robson & Miles, 2000), males that do not perform well will most likely have fewer offspring. Females on the other hand will probably have some reproductive success even when they are not performing optimally (e.g. Fox *et al.*, 1981; 1998). Thus, in male lizards, selection on morphological traits will presumably occur more rapidly than on female lizards. Yet, whereas males typically showed stronger responses to habitat structure, females from species utilizing different habitats showed larger differences in femur length. Although this might be the result of females being under strong selective pressure, it might alternatively be that femur length is constrained in male lizards (e.g. by the insertion of the m. caudofemoralis). Given that males are probably under strong selective pressure to optimize their locomotor performance, it can be expected that differences in femur length between species living in different habitats will be small.

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