Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis

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Recent ecomorphological studies have shown that the predicted correlations between morphology and ecology on broad taxonomic levels are often obscured when comparing more closely related groups. Among species, comparisons of lizards often indicate very little support for adaptive radiations into novel habitats. As few population level studies have been performed, we compared body, head and limb shape between four populations of *Urosaurus ornatus* living in structurally distinct habitats (cliffs, rocks, trees and boulders). Surprisingly, clear correlations between habitat use and body shape among populations were found, most of which were in good accordance with a priori biomechanical predictions (e.g. flat body and head for extreme climbers; long distal hindlimb segments for jumpers and runners; narrow body and long tail for tree dwelling lizards). This indicates that populations of *Urosaurus ornatus* are seemingly 'adapted' to the habitat they live in. However, quantification of performance and behaviour are needed to determine the adaptive nature of these observations.

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ADDITIONAL KEY WORDS: lizard – morphometrics – habitat use – locomotion – *Urosaurus*.

INTRODUCTION

Recent ecomorphological studies have shown that the predicted correlations between morphology and ecology on broad taxonomic levels (e.g. comparing forelimb structure across all vertebrates) are often obscured when comparing more closely related groups (e.g. at the family level). Comparisons among closely related species often indicate little support for adaptive radiations into novel habitats (Jacksic, Nuñez & Ojeda, 1980; Wiens & Rotenberry, 1980; Wiens, 1989; Vitt, 1991; Miles, 1994; Vanhooydonck & Van Damme, 1999; Zaaf & Van Damme, 2001). Remarkably, some groups of lizards, such as *Anolis* lizards, rapidly radiate into novel habitats and show clear morphological changes related to their microhabitat use (e.g. Collette, 1961; Moermond, 1979; Irschick *et al.*, 1997; Losos, Warheit & Schoener, 1997).

Despite the enormous body of work devoted to the ecomorphology of lizard locomotion in the past decade, surprisingly few studies have tested ecomorphological paradigms at the lowest taxonomical level (i.e. within species; see Garland & Losos, 1994 for an overview). However, such studies are essential in our understanding of evolutionary patterns and processes, as they reflect the smallest amounts of evolution that can still easily be detected and studied in nature (see Van Damme, Aerts & Vanhooydonck, 1998). Previous studies have documented differences in locomotor performance capacity among populations from different habitats (Crowley, 1985; Huey & Dunham, 1987; Snell *et al.*, 1988; Sinervo & Losos, 1991; Van Damme, Aerts & Vanhooydonck, 1997, 1998; Macrini & Irschick, 1998) which appeared to be consistent across different years (Huey *et al.*, 1990). Some of these studies indicated that simple biomechanical predictions often remained unsupported at the population level. Despite clear differences in performance among populations, these could not be correlated with morphological traits which

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are typically assumed to influence locomotor performance (e.g. leg length). However, as minor morphological changes may have important consequences for performance (Moreno & Carrascal, 1993; Miles, 1994; Van Damme *et al.*, 1998) other, less obvious, morphological traits (e.g. changes in the moment arms, physiology, 3-D muscle architecture) might lie at the basis for the observed differences.

In the present study we compare the morphometrics of body, head and appendicular system among four populations of the phrynosomatid lizard *Urosaurus ornatus* (Baird & Girard, 1852). *U. ornatus* is a common and abundant lizard throughout the south-western USA and occupies a wide variety of habitats such as boulders, rocks, trees, etc., but is rarely found in open habitats with no structural hiding places (Stebbins, 1985; Zucker, 1986; Smith, 1996; Hews *et al.*, 1997). Moreover, previous preliminary analyses have indicated population-level differences in locomotor performance and morphology between saxicolous and tree-dwelling populations (Miles, 1994). We chose to compare four populations from very distinct habitats: trees, low rock faces, boulders and vertical cliffs and canyon walls (Fig. 1). Whereas the tree population lived in a relatively flat, sandy area with large mesquite trees, the other populations typically occupied more rocky areas. The cliff population occupied high, largely smooth and uniform sandstone walls in an otherwise dry, deserty area devoided of much vegetation. The other two populations were respectively associated with medium size boulders in a dry, open riverbed and with low and narrow basaltic rock faces associated with grass and shrubs. Although these habitats differ qualitatively in their overall structure, it is essential to quantify the microhabitat use for each population as lizards might select microhabitats largely differing from the general surrounding structures (see also Vanhooydonck, Van Damme & Aerts, 2000).

The large differences in the superficial physical characteristics of these habitats probably pose very specific demands on the 'bauplan' of the animals (see Table 1). Biomechanical models suggest that lizards occupying smooth, vertical habitats would benefit from a flat body and head to keep the centre of mass close to the substrate (Vanhooydonck & Van Damme, 1999; Zaaf *et al.*, 1999, 2001; Zaaf & Van Damme, 2001). Moreover, short limbs would similarly be beneficial in avoiding the creation of a large backward oriented moment which would cause the lizard to rotate around its centre of mass and thus fall backwards (Cartmill, 1985; Miles, 1994; Vanhooydonck & Van Damme, 1999; Zaaf *et al.*, 1999). Tree-dwellers, in contrast, are expected to show narrow, elongate bodies, long tails and relatively short limbs to keep the centre of mass close to the substrate and to enhance manoeuvrability (Ricklefs, Cochran & Pianka, 1981; Pianka, 1986; Miles, 1994;

Vanhooydonck & Van Damme, 1999). Lizards occupying a boulder habitat typically jump a lot and frequently move between perches on top of boulders (pers. obs.). Consequently, these lizards are expected to show long hind limbs and long distal segments to maximize acceleration time during jumping and running (Bels *et al.*, 1992; Losos 1990a; Van Damme *et al.*, 1998). In addition, as tail and front limbs might interfere with, or even impede rapid accelerations, short tails and forelimbs are also thought to be beneficial for runners and jumpers (Losos, 1990b; see Garland & Losos, 1994 for an overview). The last group, the low-rock dwelling lizards, are expected to show intermediate characteristics including a flat body, to keep the centre of mass close to the substrate when climbing, but also long hindlimbs, as they frequently move on horizontal surfaces.

MATERIAL AND METHODS

MICROHABITAT USE

Microhabitat use was quantified for four populations of *U. ornatus* according to the method described by Vanhooydonck *et al.* (2000). We measured habitat structure (Fig. 1) for ten individuals of a population inhabiting vertical sandstone canyon walls (Vermillion cliffs, Coconino Co., AZ), twelve individuals of a tree-dwelling population near the confluence of the Salt and Verde rivers (Phoenix, Maricopa Co., AZ), ten individuals of a population restricted to low (3–4 m high on average) basaltic cliffs (Flagstaff, Coconino Co., AZ), and eleven individuals of a population living on medium to large boulders in a riparian area (Wet Beaver Creek, Yavapai Co., AZ).

Structural features of the habitat were quantified at four spots: the spot where the lizard was initially observed, and the end-points of three lines at an angle of 120°, and at 150 cm from the initial spot. The direction of these lines was determined haphazardly by throwing a stick on the ground. Habitat structure was determined for a surface area of 1m² with its centre at the focal spot under observation. At the place of sighting, the (1) perch height, (2) distance to nearest cover or hide, (3) distance to nearest vegetative cover, (4) perch type and (5) branch diameter (for lizards observed among vegetation) were recorded. In addition, the percentage cover at ground level of stones/rocks, sand/dirt, grass/herbs, shrubs, leaf litter, dead wood, and trees (6–12) was quantified by visual estimation and the maximal vegetation height (13) was measured at all four spots. We also measured the approach distance (the distance at which the lizard ran from the observer) for all animals (14). To reduce the number of variables, a factor analysis was performed on the mean values of the four spots (variables 6–13) and the values for the central circle only (variables 1–5, 14).
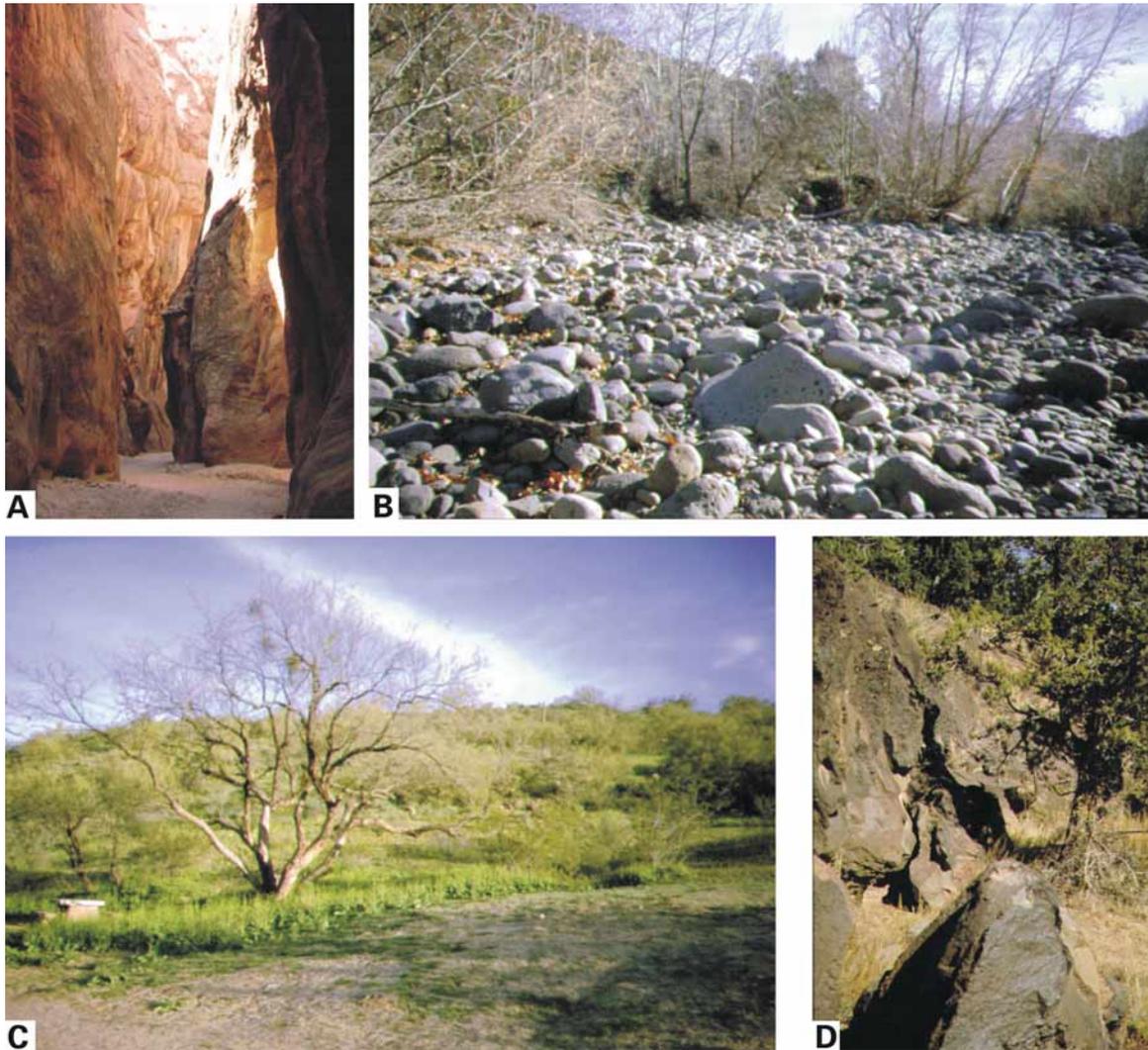
Figure 1. Photographs showing the large-scale structural differences in habitat. A, steep sandstone canyon walls; B, mesquite trees; C, riparian boulder habitat; D, low basaltic rocks.

The broken stick method was used to determine which factors were significant (Jackson, 1993). Factor scores were calculated, and used as input for one-way analyses of variance.

MORPHOMETRY

At least 10 individuals for each population were caught and measured in the field. The following morphological measurements were taken to the nearest 0.01 mm using digital callipers (Mitutoyo CD-15DC; Mitutoyo Ltd., Telford, UK), and for every individual: snout–vent length (SVL), tail length (TL), head length (HL), head width (HW), head height (HH), lower jaw length (LJL), body length (BL), body width (BW), body height (BH), femur length (FL), tibia length (TBL), metatarsus length (MTL), longest toe of the hindfoot (LTL, always the fourth toe), humerus length (HL), radius length (RL), and metacarpus length (MCL). Only animals with all measured segments intact were included into the analysis. All variables were logarithmically transformed ($\log_{10}$) before analysis. Population averages and standard deviations for all measures are represented in Table 2.

Species differences in snout–vent length were tested using a two way ANOVA (population and sex entered as fixed effects). As shape differences were of particular interest, all other measurements were regressed against SVL and the residuals calculated. The residuals were then entered into a principal component analysis and the resulting factor scores compared among habitat types using a two-way analysis of vari-

Table 1. Biomechanical body shape predictions for lizards living in different habitats

	Cliff	Tree	Boulder	Rock	References
Head	Flat	?	?	Flat	Cartmill, 1985; Vanhooydonck & Van Damme, 1999; Zaaf & Van Damme, 2001; Zaaf et al., 1999, 2001
Body	Flat, wide	Long, narrow	?	Flat	Snyder, 1954; Miles, 1994; Van Damme et al., 1997; Vanhooydonck & Van Damme, 1999; Zaaf & Van Damme, 2001; Zaaf et al., 1999, 2001
Forelimb	Short	Short	Short	Short	Snyder, 1962; Jaksic et al., 1980; Pounds, 1988; Losos, 1990b; Sinervo & Losos, 1991
Hindlimb	Short	Short	Long distal segments	Long	Bels et al., 1992; Garland & Losos, 1994
Tail	?	Long	Short	?	Ricklefs et al., 1981; Miles, 1994

Table 2. Morphometric data (in mm) of the four populations of *Urosaurus ornatus*

Variable	Cliff population		Tree population		Rock population		Boulder population	
Sex	Male	Female	Male	Female	Male	Female	Male	Female
N	6	4	7	6	13	2	8	3
SVL	50.13±2.10	44.56±11.20	54.67±0.82	47.83±9.97	47.57±4.56	45.56±2.26	51.05±2.38	48.60±2.34
Tail length	67.35±6.45	38.03±15.24	82.11±16.21	70.24±13.99	60.61±9.45	46.14±18.77	75.05±21.86	71.07±4.08
Head length	11.03±0.35	9.86±1.61	12.35±0.30	10.91±1.62	11.70±0.78	10.84±0.57	11.05±0.55	10.27±0.31
Head width	8.09±0.28	7.28±1.16	9.22±0.37	7.70±1.08	8.03±0.74	7.49±0.41	9.35±0.45	7.80±0.69
Head height	4.91±0.29	4.40±0.74	6.13±0.34	4.92±0.74	4.72±0.57	4.51±0.45	6.01±0.22	5.30±0.26
Lower jaw length	11.94±0.55	10.68±1.92	13.12±0.32	11.34±1.61	12.06±1.06	11.30±0.12	12.29±0.59	11.13±0.40
Body length	39.82±5.82	33.23±8.86	39.68±1.31	34.26±7.14	33.16±3.36	31.75±2.66	32.86±1.70	31.67±1.71
Body width	13.13±1.17	12.36±4.02	13.20±1.08	12.29±3.44	12.50±1.50	13.08±0.27	13.26±1.80	13.90±2.55
Body height	6.22±0.44	5.46±1.37	7.54±0.68	5.80±1.25	5.88±0.66	5.70±0.34	6.76±0.88	7.37±1.52
Femur length	11.10±0.47	9.22±2.26	12.48±0.84	10.97±2.45	11.69±1.40	11.19±0.53	10.93±0.90	10.37±0.55
Tibia length	6.75±0.22	5.83±0.95	8.56±0.85	7.21±1.40	6.97±0.92	6.31±0.30	7.63±1.30	6.60±0.26
Metatarsus length	4.93±0.24	4.08±1.09	6.35±0.74	5.27±1.49	5.20±0.60	5.03±0.35	5.80±0.58	5.20±0.61
Longest toe	8.24±0.52	6.55±0.92	9.67±0.86	7.88±1.21	7.93±0.94	7.31±0.37	9.08±0.51	8.10±0.87
Humerus length	7.99±0.13	6.21±1.93	9.15±0.72	7.83±1.50	8.26±1.00	8.03±0.00	7.00±0.73	5.80±0.87
Radius length	5.59±0.53	4.72±1.36	6.89±0.50	5.92±1.49	5.74±0.71	5.82±0.15	6.38±0.67	5.50±0.36
Metacarpus length	3.35±0.95	2.88±1.35	3.83±0.51	3.09±0.87	2.88±1.35	2.68±0.37	2.73±0.21	2.53±0.12

Table entries are averages ± SD.

Table 3. Eigenvalues, percentage of variation explained, and factor loadings of the analysis based on the field microhabitat data

	Factor 1	Factor 2	Factor 3
Eigenvalue	3.90	2.23	1.48
% variation explained	29.99	17.17	11.37
Perch height	0.05	0.45	−0.22
Approach distance	0.46	0.24	**0.65**
Distance to nearest cover	0.29	−0.09	**0.79**
Distance to nearest vegetative cover	**0.73**	0.02	0.18
Branch diameter	**−0.86**	0.15	0.13
% rocks and stones	**0.87**	0.21	0.24
% sand and dirt	**−0.90**	0.07	−0.10
% leaf litter	0.06	**−0.95**	0.03
% grass and herbs	0.30	0.10	**−0.66**
% shrubs	0.06	0.39	0.06
% trees	**−0.62**	−0.08	−0.12
% dead wood	0.11	−0.10	0.04
Maximal vegetation height	−0.07	**−0.92**	−0.04

Only the first two factors were significant based on a broken stick model.
Factor loadings indicated in bold are strongly correlated with the respective factors.

ance (habitat and sex entered as factors). The broken stick method was used to determine which factors were significant (Jackson, 1993).

RESULTS

HABITAT USE

Urosaurus ornatus from the different populations clearly differed in their respective microhabitat use. The factor analysis performed on the original variables yielded two new significant variables. Jointly, the first two factors explained almost 50% of the total variation. The third factor, although not significant, explained another 11% of the variation and was included in the subsequent analysis.

The first factor was positively correlated with the distance to the nearest vegetative cover, the percentage rocks and stones, and negatively correlated with branch diameter, the percentage of trees and the percentage of sand and dirt (Table 3). Mean factor scores on this axis differed between populations ($F_{3,39} = 30.20$, $P<0.001$). Post-hoc tests indicated that this factor separated the tree population from the others. Whereas the tree population scored negatively on this axis, the cliff, rock and boulder populations scored similarly and positive on this axis (Fig. 2). This indicates that cliff, rock and boulder-dwelling populations were associated with rocky habitats far away from vegetative cover, and the absence of trees.

The second factor was negatively correlated with the percentage of leaf litter and vegetation height (Table 3). Again, mean factor scores differed significantly between populations ($F_{3,39} = 22.17$; $P<0.001$). Post-hoc tests indicated that all populations differed from one another on this factor (with the exception of cliff and rock populations). Whereas the cliff and rock populations scored positively on this axis, the tree population scored slightly negatively and the boulder population strongly negatively on this factor (Fig. 2). This implies that lizards from cliff and rock populations are not associated with high vegetation and the presence of leaf litter. The tree and boulder populations, in contrast, are associated with higher vegetation and lots of leaf litter.

Although not significant, the third factor correlated positively with approach distance and distance to nearest cover, and negatively with the percentage of shrubs (Table 3). Again, populations differed significantly from one another ($F_{3,39} = 5.42$; $P=0.003$). Post-hoc tests showed that this factor discriminated beween rock and boulder populations, and between cliff populations on the one hand, and tree and rock populations on the other hand. The cliff population correlated strongly positively, the boulder population moderately positively, and the tree and rock populations negatively with this factor. This implies that the cliff-dwelling population is characterized by large distances to cover, resulting in large approach distances. Moreover, this factor indicated that tree and rock populations tend to be associated with the presence of shrubs.
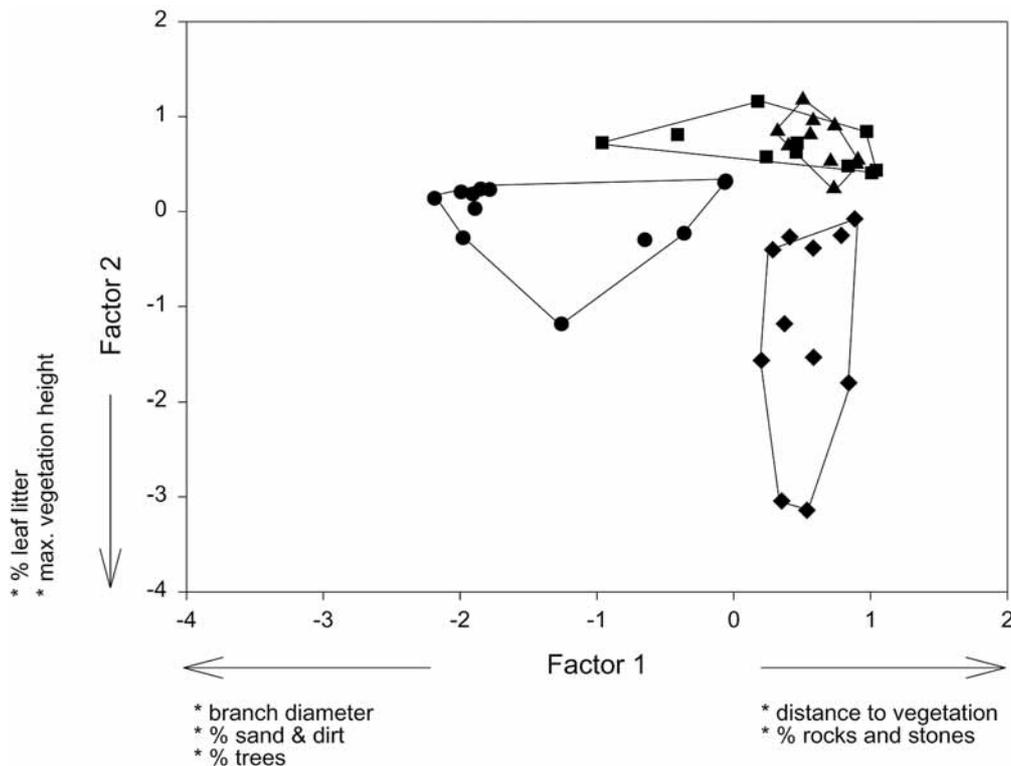
Figure 2. Position of the four populations of *Urosaurus ornatus* in the microhabitat space described by the first two factors. The arrows indicate strong correlations of the factors with distinct habitat variables. (■) Cliff-, (●) tree-, (▲) rock- and (◆) boulder-dwelling lizards.

MORPHOMETRICS

The individuals from the four populations did not differ significantly in snout–vent length ($F_{3,41}=1.03$; $P=0.39$). Sexes did differ from one another ($F_{1,41}=4.74$; $P=0.04$), but interaction effects were not significant ($F_{3,41}=0.49$; $P=0.69$).

The factor analysis on the size-free morphological variables yielded two new significant variables, together explaining 45% of the total variation. As the third factor approached significance, and explained another 11% of the variation, it was also included in the subsequent analysis. A MANOVA on the factor scores revealed significant habitat (Rao's $R_{9,95}=17.93$, $P<0.0001$) and sex (Rao's $R_{3,39}=6.86$, $P<0.0001$) effects. Interaction effects were not significant (Rao's $R_{9,95}=0.79$, $P=0.38$). Subsequent univariate tests showed that habitat effects were significant on all factors (see further), and that sex effects were only significant on the second factor ($F_{1,41}=14.17$, $P<0.01$), with males scoring higher than females.

The first factor showed high positive loadings for residual head width, residual head height, residual body height and residual longest toe length (Table 4). An ANOVA on the factor scores showed significant differences between populations from different habitats ($F_{3,41}=9.02$, $P<0.001$). Post-hoc tests indicated

that this factor discriminated between boulder populations and all others, and between cliff and tree-dwelling populations. Individuals from the boulder population scored strongly positively, those from the tree population slightly negatively, and both the rock and cliff populations strongly negatively on this factor (Fig. 3). This implies that rock and cliff populations are characterized by narrow and flat heads, a flat body and short toes on the hind foot. Lizards from the boulder population, in contrast, are characterized by long hind toes, high bodies, and a wide and high head.

The second factor correlated positively with residual head length, residual lower jaw length, residual femur length, and residual humerus length (Table 4). Again, an analysis of variance indicated that populations differed significantly on this factor ($F_{3,41}=28.49$, $P<0.0001$). Post-hoc tests indicated that all populations differed from one another on this factor. Whereas the rock population scored strongly positive on this factor, the tree population scored only moderately positive. Both the cliff, and boulder populations scored strongly negatively on this factor (Fig. 3). This implies that individuals from the rock population, and those of the tree population to a lesser degree, are characterized by long heads and long proximal limb segments. The *Urosaurus* lizards from the cliff and boulder popu-

Table 4. Eigenvalues, percentage of variation explained, and factor loadings of the analysis based on morphometric data

	Factor 1	Factor 2	Factor 3
Eigenvalue	3.69	3.13	1.71
% variation explained	24.61	20.90	11.37
Residual tail length	0.09	−0.03	**0.77**
Residual head length	−0.08	**0.88**	0.13
Residual head width	**0.85**	0.02	0.09
Residual head height	**0.78**	−0.25	0.14
Residual lower jaw length	0.27	**0.71**	−0.08
Residual body length	−0.45	0.20	−0.42
Residual body width	0.17	0.07	**−0.63**
Residual body height	**0.69**	−0.09	−0.31
Residual femur length	−0.04	**0.83**	0.01
Residual tibia length	0.19	0.13	**0.67**
Residual metatarsus length	**0.32**	0.25	0.46
Residual longest toe length (hind foot)	**0.65**	0.29	0.31
Residual humerus length	−0.19	**0.80**	0.03
Residual radius length	0.36	0.44	0.44
Residual metacarpus length	−0.26	0.31	−0.29

Only the first two factors were significant based on a broken stick model. Factor loadings indicated in bold are strongly correlated with the respective factors. All variables were the residual against snout-vent length.

lation, however, are characterized by short proximal limb segments and a short head.

The third factor, although not significant, correlated positively with residual tail and body length, and negatively with residual body width (Table 4). Again, populations were significantly different on this factor ($F_{3,41} = 4.42$, $P = 0.009$). Post-hoc tests indicated that this factor discriminated between the tree and rock populations, and between the cliff population on one hand, and the tree and boulder populations on the other hand. The individuals of the cliff population scored strongly negative, and those from the rock population moderately negative on this axis. Both the boulder and tree populations scored moderately positive on this axis (tree more than boulder). This indicates that tree and boulder (less so) populations are characterized by long tails, and long but narrow bodies. The cliff and rock (to a lesser degree) populations on the other hand are characterized by short tails, and short, broad bodies.

DISCUSSION

Although populations were chosen to represent structurally differing habitats, the quantification of the microhabitats indicated distinct structural differences in habitat components. The biggest differences were the absence of trees in the cliff and rock habitats, the presence of shrubs in the rock habitat and the presence of leaf litter and higher vegetation in the boulder habitat. An interesting consequence of the habitat structure in the cliff dwelling population is its large average distance to any form of cover. This implies that these animals are more succeptible to predation. Indeed, the analysis showed that the lizards are wary as indicated by the large approach distances. Similar, but less strong trends are observed for the boulder population indicating a largely open habitat with sparsely distributed shelters (note however, that cottonwood trees were abundant in the area, but outside the area of habitat quantification). The importance of locomotor performance, and the underlying morphological traits affecting performance, is thus likely to be significant in these habitats.

The analysis performed on the morphometric data indicated clear differences between populations. The observed morphological trends correspond strikingly well with our a priori predictions based on simple biomechanical considerations (Zaaf & Van Damme, 2001; Zaaf *et al.*, 1999, 2001; Table 1). The cliff population was characterized by a flat, wide body, a flat head, and relatively short limb segments (humerus, femur and longest toe) compared with the other populations. All of these are in accordance with our pre-
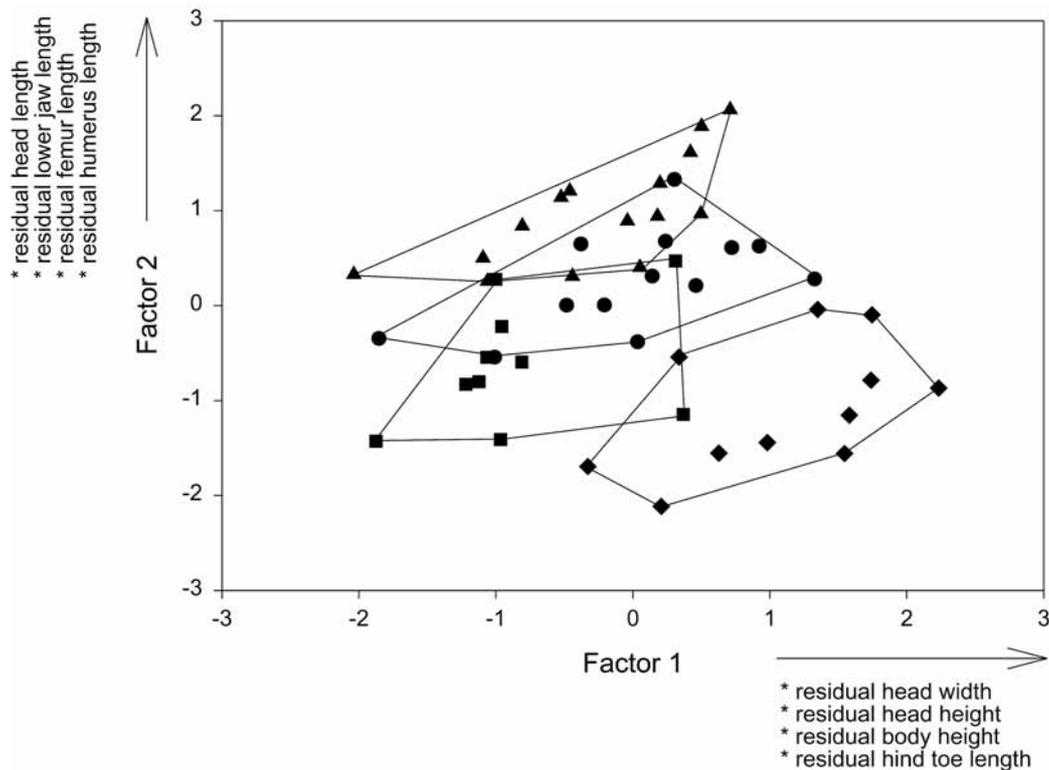
Figure 3. Position of the four populations of *Urosaurus ornatus* in the morphospace described by the first two factors. The arrows indicate strong correlations of the factors with distinct habitat variables. (■) Cliff-, (●) tree-, (▲) rock- and (◆) boulder-dwelling lizards.

dictions, and this population thus seems to be fairly well 'adapted' to its habitat. Lizards from the boulder population also showed a bauplan largely in accordance with our predictions. Most notable are the relatively long toes on the hind limb (which aid in propulsion and acceleration, see Bels *et al.*, 1992; Losos, 1990a; Van Damme *et al.*, 1998), short proximal limb segments (humerus and femur) and long tails. Whereas short forelimbs and long tails are thought to be beneficial for runners (especially for species that run bipedally at high speeds), the short proximal hind limb segments may induce a higher gear ratio which is also beneficial for fast accelerations (see Arnold, 1998; Bonine & Garland, 1999; Vanhooydonck & Van Damme, 2001). The lizards from the tree population are characterized by slender bodies, long tails and long proximal limb segments (humerus and femur). Whereas a slender, elongate body and a long tail will probably improve manoeuverability, surefootedness and balance in arboreal lizards (Losos & Sinervo, 1989; Sinervo & Losos, 1991), the relatively long limbs are not in accordance with biomechanical predictions for climbing lizards. However, this may not be surprising as tree dwelling lizards probably move on horizontal elements within the arboreal habitat. In that case, long proximal segments might ensure a good performance on horizontal

elements without negatively affecting climbing ability as postural changes (i.e. increased sprawling) can potentially circumvent the negative effects of having long limbs while climbing on broad structures. Clearly, the kinematics of climbing, and the time spent climbing versus moving on the horizontal should be quantified before any speculation on the significance of the difference in limb length is possible. The rock-dwelling population of *U. ornatus* generally showed intermediate characteristics with relatively flat, wide bodies and short tails, but with long proximal limb segments. Again, the structural diversity of the habitat (more vegetation and shelters, less extreme surface topology) probably puts conflicting pressures on the morphology of the animals.

The quantification of locomotor behaviour, and performance in relevant locomotor tasks (e.g. jumping, sprinting, climbing, manoeuverability) for the different populations is essential in our understanding of adaptive relationships between morphology and habitat use in these animals (Arnold, 1983). However, as the observed trends clearly follow a priori models (at least for the more extreme environments) we believe that the observed differences between populations are likely the result of adaptive processes (Wainwright, 1994). The large intraspecific differences in habitat use, and

the corresponding large changes in morphology in this phrynosomatid lizard, have clear implications for broad comparative eco-morphological analyses. In such analyses, ecological variables (such as habitat use, prey type, home range) are often taken from the literature, and morphological variables taken from other literature sources or from museum specimens. Given the large population-level variation in ecological and morphological variables, this might confound analysis of large-scale evolutionary patterns among species.

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