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Concordance between locomotor morphology and foraging mode in lacertid lizards

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Abstract

Foraging behaviors exist along a continuum from highly sedentary, ambush foraging, to more continuous searching, or active foraging. Foraging strategies, or modes, are defined based upon locomotor behaviors (e.g. percent time moving, moves per minute). In lizards, traits correlated with ambush and active foraging have been of interest for some time; however, general patterns of correlated evolution between locomotor morphology and locomotor behavior have only recently begun to be quantified. In this study, variation in hindlimb morphology is investigated in a model group of lizard species that vary between active foraging and more sedentary (or mixed) foraging mode. Canonical variates analysis reveals that the two active foraging species occupy similar regions of the morphospace, while the two more sedentary species occupy different regions. The active foraging species have a narrow pelvis with shorter tibia and femora. The more sedentary species have a wide pelvis, long tibia and femora, and slightly longer metatarsals. Phylogenetic patterns of trait variation were examined through ancestral character state reconstruction and show morphological shifts in concert with foraging mode in these species. The observed shifts in locomotor morphology are discussed in light of published data on sprint speed and endurance in these species. Together, the data show that linking morphological variation to variation in stride length and stride frequency is critical to understanding the evolution of locomotor performance. Much more stride length and frequency data are needed among ambush, mixed, and active foraging species because these parameters, and their morphological components, are likely correlated with variation in food acquisition mode.

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Keywords: Lacertidae; Lizards; Locomotion; Hindlimb morphology; Eco-morphology

Introduction

Foraging patterns are described along a continuum from ambush or sit-and-wait (SW) foragers that use short, rapid bursts of locomotion to ambush prey, to wide or active foragers (AF) that exhibit longer, more continuous locomotion while in search of patches of food resources. Mixed (= intermediate or saltatory) foragers exist between the ends of this continuum. The continuum in foraging mode was formalized as a major pattern in lizard biology more than twenty years ago (Huey and Pianka, 1981). Since then, numerous studies have related foraging modes (SW/AF) to many aspects of lizard ecology, morphology and behavior and it is now clear that foraging mode permeates many aspects of lizard biology (Reilly et al., 2007).

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Locomotion is particularly relevant to foraging mode. The SW to AF continuum is defined based on two principal locomotor variables, moves per minute (MPM) and percent time moving (PTM). Given this variation in behavior, foraging mode should also be tightly correlated with locomotor morphology and performance. In lizards, morphological variables related to the locomotor apparatus (principally the hindlimb and pelvis) are often predictors of sprint speed and endurance (Garland and Losos, 1994; Miles, 1994; Bonine and Garland, 1999; Aerts et al., 2000; Vanhooydonck et al., 2007). Sprint speed has been shown to coevolve with foraging behavior and depending on the taxa studied or methodology used, endurance may, too (see below). To effectively capture the elusive prey that they eat (Huey and Pianka, 1981; Vanhooydonck et al., 2007), more sedentary SW and mixed species likely use high sprint capacity and/or acceleration to ambush passing prey, while AF species employ continuous walking (high endurance) in search of hidden prey. In fact, Miles et al. (2007) found that in six out of seven evolutionary transitions from an AF ancestor to a SW species sprint speed increased (Table 2.2 in Miles et al., 2007). McElroy et al. (2008) also demonstrated the correlated evolution of foraging mode with speed and running mechanics; SW species use only higher speeds and running mechanics (bouncing gaits), while AF species use lower speeds and walking mechanics. Therefore, if natural selection optimizes both the search and capture phases of foraging along the SW–AF continuum, then morphological attributes that enhance locomotor style (e.g. speed vs. endurance) should be correlated with each foraging mode.

The SW–AF paradigm in lizards is known to be closely tied to phylogenetic history. Foraging mode is fixed in most lizard families and thus correlations between other traits and foraging mode are often confounded unless the proper phylogenetic approach is taken (Cooper, 1995; Perry, 1999). Three families of lizards (Cordylidae, Lacertidae, and Scincidae) contain species that exhibit substantial variation in foraging mode (Cooper and Whiting, 2000) including some members that exhibit intermediate, or mixed, foraging styles. The lacertid lizards of southern Africa are an ideal system to test hypotheses regarding the evolution of foraging mode and associated traits. This clade is a well-supported lineage that contains species with a wide range of foraging behaviors (highly sedentary to highly active). Four closely related species (AF = *Heliobolus lugubris*, *Pedioplanis namaquensis*; mixed = *Pedioplanis lineoocellata*, *Meroles suborbitalis*) are widely cited as varying in foraging mode and, in fact, are the original model species used to describe the tradeoffs inherent to the ambush and active foraging strategies (Huey and Pianka, 1981). These species are similar in body size, broadly sympatric, and found in similar habitats (deserts) on similar sandy substrates (Huey and Pianka, 1981; Pianka, 1986). These species are part of a single (southern African) radiation of the Lacertidae (Arnold, 1989, 1991; Lamb and Bauer, 2003) and the phylogenetic relationships are known for these genera (Fig. 1). Furthermore, various aspects of these species' ecology have been well studied (e.g. Pianka et al., 1979; Huey, 1982; Pianka, 1986) and as a result, they are available in large series of museum specimens, including the original voucher specimens used to describe their diets and movement rates. Finally, several aspects of the physiology of these species have been studied in the context of their varied foraging modes and thus, these four species are an apt model system to test hypotheses regarding the correlated evolution of traits that enhance foraging success.

Recent analyses have used lizards as a model to investigate how morphology responds to evolutionary shifts in foraging behavior. An analysis of 250 species from 20 families shows that SW species have longer distal limb elements than proximal ones (Miles et al., 2007). Longer distal elements (e.g. metatarsals) are likely to increase maximal sprint speed by increasing stride

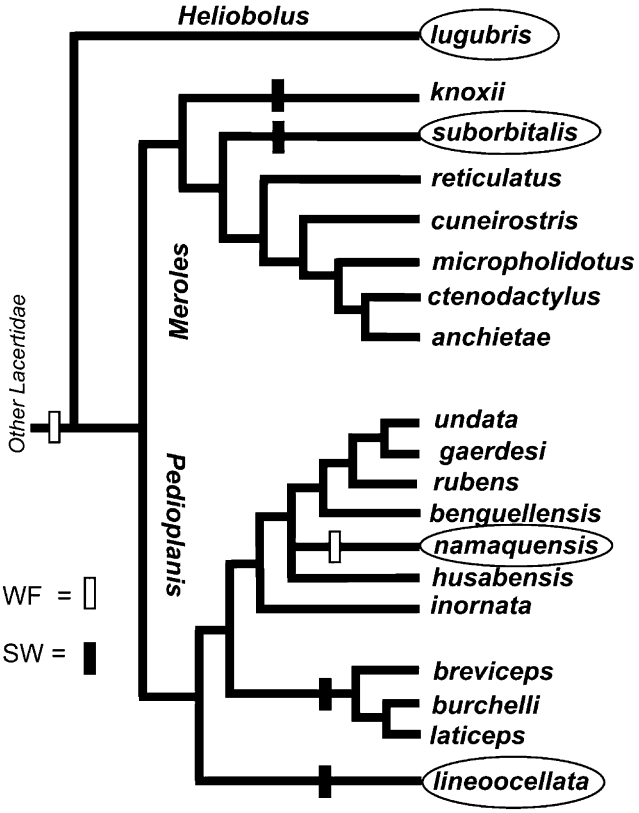

Fig. 1. Evolution of foraging mode among three genera of lacertid lizards. Circled species are included in this study. The mixed mode evolved once at the *Pedioplanis–Meroles* node and *P. namaquensis* has secondarily derived active foraging (see justification in McBrayer, 2004). Phylogeny after Arnold (1991) and Lamb and Bauer (2003).

length; longer strides (and higher speeds) should allow a sprinting ambush forager a greater range of attack distances for prey capture. In fact, SW lizards have higher sprint speeds. However, the converse is not necessarily true; AF species have shorter limbs and greater endurance than SW species, but this difference in endurance is related to phylogenetic history rather than foraging mode alone (Miles et al., 2007). Another recent study tested the hypothesis that AF, not mixed or SW, would have longer limbs; however, this hypothesis was rejected (Verwaijen and Van Damme, 2007). Given the need for rapid acceleration and high maximal speed, SW or mixed foraging species would likely benefit more from having longer limbs. This hypothesis is supported by the findings of Verwaijen and Van Damme (2007). Moreover, both of these studies found evidence for divergent morphological evolution among SW and AF taxa when analyzed at both a higher taxonomical level (Miles et al., 2007) or a lower one (29 species of Lacertidae; Verwaijen and Van Damme, 2007).

In this study, hind limb morphology was compared among the 'original' four lacertid species used to describe the foraging mode paradigm by Huey and Pianka (1981). The present study purposefully used this reduced subset of the sub-Saharan radiation of the Lacertidae. Including only species from this radiation ensures a very close phylogenetic separation of the study taxa and thus any covariance among foraging mode and morphology observed is likely recent evolutionary events and probably attributable to ecological (e.g. foraging mode) differences. Furthermore, locomotor morphology is known to vary with substrate type (Garland and Losos, 1994; Miles, 1994). Although other studies have included more species for added phylogenetic resolution, doing so has resulted in the inclusion of species that span a wide range of substrate types (e.g. Miles et al., 2007) as well as from different radiations within a particular clade (Verwaijen and Van Damme, 2007). The species included here occur on similar sandy soils, thereby decreasing this important source of variation.

Detailed morphological analyses of the locomotor apparatus of these four lacertid species have not heretofore been conducted and doing so will generate hypotheses for understanding how their morphological variation may lead to performance variation, and in turn, shape the evolution of their foraging behavior (or vice versa). Here, the two more sedentary, mixed foraging species are predicted to have longer hindlimb elements than the AF species because these would enhance sprint speed and ambush foraging success. Furthermore, we predict that morphology will vary across the four study species in a predictable manner, i.e. hindlimb elements will increase in the transition to the mixed foraging strategy (*M. suborbitalis*, *P. lineoocellata*) and will decrease in length with the re-emergence of AF in *P. namaquensis*. These predications were examined by comparing multivariate and univariate patterns of morphological evolution.

Methods

To quantify morphological differences among the four study species, alcohol-preserved specimens were obtained from the Los Angeles County Museum of Natural History (*H. lugubris*, $n = 20$; *Meroles suborbitalis*, $n = 20$; *Pedioplanis lineoocellata*, $n = 20$; *Pedioplanis namaquensis*, $n = 20$; LAMNH specimen numbers are available from the corresponding author). Snout-vent-length (SVL, mm) was recorded for each specimen, and each specimen was radiographed following the procedure in McBrayer (2004). Skeletal variables were measured by digitizing landmarks on each radiograph (tpsDig v. 2.10; Rohlf, 1998, 2006). A single individual digitized all measurements two times and the average of the two measurements was retained for statistical analysis. The following linear measurements were taken from each skeletal image: femur length, femoral head width, ilium length, metatarsal length, pelvis width, pubis length, tibia length, and toe length. These linear measurements were chosen because they are biomechanically informative and have been shown to be related to locomotor performance (e.g. Snyder, 1954).

Because the four species differ in body size (SVL), all statistical analyses were performed on size-corrected data. The effect of body size was removed by regressing each of the eight variables on SVL. The residuals from these regressions were collected and used in all subsequent analyses. All data were normally distributed.

A combination of multivariate and univariate analyses was performed. Canonical variate analysis (CVA) was used to find the combination of the eight morphological variables that would best discriminate the four species based upon their assigned foraging modes. ANOVA and Tukey–Kramer post-hoc tests were used to test for differences in femur length, pelvis width, tibia length, metatarsal length, and toe length. Femur length, tibia length, metatarsal length, and toe length were summed to estimate total limb length. These variables were identified by the CVA as contributing heavily to one or more of the three CV axes, and this subset of morphological variables was used because they are frequently found to be directly correlated with greater sprint speed (e.g. Garland and Losos, 1994; Miles et al., 2007), which is likely to be important to mixed foraging lizards because their diet contains a higher number of mobile, elusive prey items than that of AF lizards (Huey and Pianka, 1981). All statistical analyses were performed using NCSS^{TM} statistical software (NCSS, Kaysville, UT, USA).

To visualize correlated changes in multivariate morphology and foraging mode, ancestral character states were reconstructed in Mesquite v. 2.5 (Maddison and Maddison, 2008). Ancestral character states were calculated using maximum parsimony for each species' mean score on each of the three canonical variate axes and published data on percent time moving and moves per minute for each species.

Results

The canonical variate analysis of the eight morphological variables revealed that each species occupied a significantly different region of the morphospace (Wilks $\Lambda_{\mathrm{CV1}} = 0.31$, $F_{24,195} = 4.0$, $P<0.0001$; Wilks $\Lambda_{\mathrm{CV2}} = 0.54$, $F_{14,136} = 3.6$, $P<0.0001$; Wilks $\Lambda_{\mathrm{CV3}} = 0.83$, $F_{6,69} = 2.4$, $P<0.0352$; Fig. 2). Eigenvalues for each of the three significant canonical variate axes were 0.73, 0.54, and 0.21, respectively. The first canonical axis explained 49.3% of the variance in locomotor morphology. Pelvis width and toe length had the highest loadings along this axis (Table 1). Individuals with wide pelves loaded heavily on the negative end of the axis, while individuals with longer toes loaded heavily on the positive end. The second canonical axis explained 36.5% of the variance and loaded with metatarsal length (+ loadings; *M. suborbitalis*) and pubis length (− loadings). The third canonical axis explained 14.2% of the variance; it loaded with tibia length (+ loadings; *P. lineoocellata*) and ilium length (− loadings).

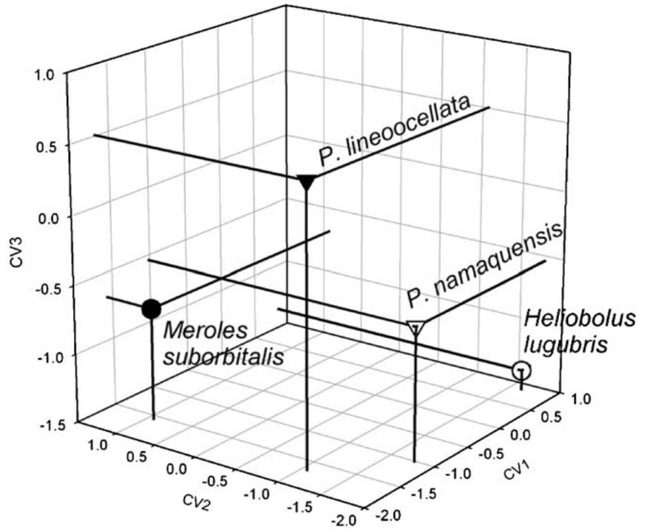

Fig. 2. Three-dimensional plot of mean canonical scores of each species. All species are significantly different from each other, and active foragers are significantly different from mixed foragers. Variable–variate correlations are presented in Table 1. Filled = mixed foragers; open = active foragers.

Table 1. Canonical variate (CV) loadings (variable–variate correlations) for species (CV1–CV3) and foraging mode alone (one CV, mode; far right).

	CV1	CV2	CV3	Mode
Pelvis width	−0.62	0.38	0.16	−0.61
Pubis length	0.12	−0.03	0.11	0.09
Ilium length	0.01	0.21	−0.05	0.03
Femoral head width	−0.14	0.43	0.43	−0.22
Femur length	−0.22	−0.02	0.74	−0.38
Tibia length	−0.12	0.20	0.90	−0.30
Metatarsal length	0.11	0.55	0.62	−0.02
Toe length	0.30	0.20	0.50	0.18
Eigenvalue	0.73**	0.54**	0.21**	0.62**
% variance	49.3	36.5	14.2	100

All axes were significant (**$P<0.01$).

Data were re-coded by foraging mode alone (mixed: *M. suborbitalis*, *P. lineooccellata*; AF: *H. lugubris*, *P. namaquensis*) and the CVA was re-run to explore how foraging modes projected into the morphological space. The mixed foragers occupied a region of the morphospace significantly different from that of the active foragers (Wilks $\Lambda = 0.62$, $F_{8,69} = 5.4$, $P<0.0001$; Fig. 2 open vs. filled symbols). The AF species grouped closer together on CV2 indicating similarities in morphology on that axis. A parallel trend was observed for the mixed foraging species on CV1. The congeneric species (*P. lineoocellata*, *P. namaquensis*) grouped together as expected, but were separated along CV3 and CV2. Inspection of the loadings revealed that pelvis width (−) and toe length (+) were again the most important variables in separating mixed from active foraging (Table 1, mode).

In addition to an ordination, CVA performs a classification procedure to reveal how well the data can be used to assign individuals to their proper category. The data were classified in two ways, by species and by foraging mode, to reveal if the phylogenetic (species) or ecological (foraging mode) group was a better discriminator of the morphological data. Both analyses (species and foraging mode) showed low rates of misclassification (Table 2).

Table 3 shows both mean and size-corrected values for each morphological variable. Univariate ANOVA with post-hoc tests were used to test for specific, size-corrected morphological differences among the variables with the highest loadings in the CVA. Compared to its mixed foraging congener *P. lineoocellata*, *P. namaquensis* had shorter total limb length ($F_{3,74} = 15.92$, $P<0.0001$), femur length ($F_{3,74} = 26.51$, $P<0.0001$), and tibia length ($F_{3,74} = 21.64$, $P<0.0001$). *Pedioplanis namaquensis* had shorter tibia and toes than

Table 2. CVA classification matrix.

Species Foraging mode	*H. lugubris* Active	*M. suborbitalis* Mixed	*P. lineoocellata* Mixed	*P. namaquensis* Active
H. lugubris	16	2	0	2
M. suborbitalis	2	14	2	1
P. lineoocellata	1	0	15	4
P. namaquensis	3	1	4	11
Active foraging	34	5	N/A	N/A
Mixed foraging	8	31	N/A	N/A

The numbers in each cell represent the number of observations correctly classified to species, or when pooled, to foraging mode (bottom).

H. lugubris, despite both being AF (toe: $F_{3,74} = 3.64$, $P = 0.016$; Table 3). Mixed foragers had significantly wider pelves than AF species and genera ($F_{3,74} = 29.6$, $P < 0.0001$; Table 3). When viewed in light of the species' phylogeny and foraging modes (Fig. 1), five of the six locomotor variables (femur length, tibia length, pelvis width, toe length, total limb length) show evolutionary transitions to longer limbs between *H. lugubris* (AF) and *Meroles suborbitalis* (mixed) and the ancestor of the *Pedioplanis* species (likely a mixed forager). When more active foraging appears again in *Pedioplanis namaquensis*, there is a shift to shorter limbs.

Mixed foragers clustered toward the negative end of CV1 (smaller values; wide pelves), while active foragers were toward the positive end of CV1 (larger values; narrow pelves, long toes; see Fig. 2, Table 1). The phylogenetic reconstructions of trait values for percent time moving mirrored these transitions in morphology (compare shading on left and right, Fig. 3A–C). Similar patterns of separation were observed for CV2 (Fig. 3B), where mixed foragers (*M. suborbitalis*, *P. lineoocellata*) had longer metatarsals. The reconstruction showed a shift away from the ancestral morphology of *H. lugubris* (AF) to more positive values of the mixed foraging

Table 3. Mean values (mm ± 1 S.E.) of hindlimb traits in active and mixed foraging lacertid lizards.

	H. lugubris $N = 20$ Active	*M. suborbitalis* $N = 19$ Mixed	*P. lineoocellata* $N = 20$ Mixed	*P. namaquensis* $N = 19$ Active
Femoral head width	1.50 ± 0.04 (-0.03 ± 0.03)	1.50 ± 0.02 (0.05 ± 0.03)	1.49 ± 0.04 (0.06 ± 0.04)	1.21 ± 0.02 (-0.07 ± 0.02)
Femur length	11.05 ± 0.15 $(-0.49 \pm 0.09)^{A}$	11.03 ± 0.10 $(0.03 \pm 0.08)^{B}$	11.63 ± 0.18 $(0.75 \pm 0.12)^{C}$	9.58 ± 0.13 $(-0.31 \pm 0.13)^{AB}$
Ilium length	2.41 ± 0.10 (-0.04 ± 0.09)	2.38 ± 0.08 (0.06 ± 0.09)	2.33 ± 0.10 (0.04 ± 0.10)	1.99 ± 0.06 (-0.06 ± 0.06)
Metatarsal length	6.91 ± 0.10 $(-0.07 \pm 0.10)^{AB}$	6.58 ± 0.09 $(0.04 \pm 0.10)^{AB}$	6.68 ± 0.12 $(0.24 \pm 0.09)^{B}$	5.40 ± 0.10 $(-0.21 \pm 0.09)^{A}$
Pelvis width	6.49 ± 0.08 $(-0.30 \pm 0.06)^{A}$	6.74 ± 0.08 $(0.25 \pm 0.07)^{B}$	6.71 ± 0.07 $(0.26 \pm 0.05)^{B}$	5.73 ± 0.04 $(-0.21 \pm 0.03)^{A}$
Pubis length	3.84 ± 0.11 (-0.08 ± 0.10)	3.70 ± 0.06 (-0.05 ± 0.06)	3.86 ± 0.07 (0.12 ± 0.06)	3.46 ± 0.05 (0.01 ± 0.06)
Tibia length	9.78 ± 0.15 $(-0.37 \pm 0.11)^{AD}$	9.58 ± 0.11 $(0.03 \pm 0.10)^{BD}$	10.13 ± 0.19 $(0.74 \pm 0.14)^{C}$	7.82 ± 0.11 $(-0.42 \pm 0.11)^{A}$
Toe length	11.76 ± 0.17 $(-0.09 \pm 0.10)^{AB}$	10.98 ± 0.14 $(-0.29 \pm 0.14)^{A}$	11.47 ± 0.24 $(0.33 \pm 0.16)^{B}$	10.10 ± 0.15 $(0.04 \pm 0.13)^{AB}$
Total limb length	39.46 ± 0.52 $(-1.02 \pm 0.30)^{A}$	38.16 ± 0.39 $(-0.19 \pm 0.36)^{A}$	39.90 ± 0.67 $(2.06 \pm 0.40)^{B}$	32.90 ± 0.41 $(-0.90 \pm 0.37)^{A}$

The species differed significantly in SVL; thus, values in parentheses below the raw data are size-corrected (±1 S.E.). All analyses were conducted on size-corrected values. Lettering indicates the results of Tukey–Kramer multiple comparison tests among five important morphological variables. Shared letters indicate no significant difference between the species.

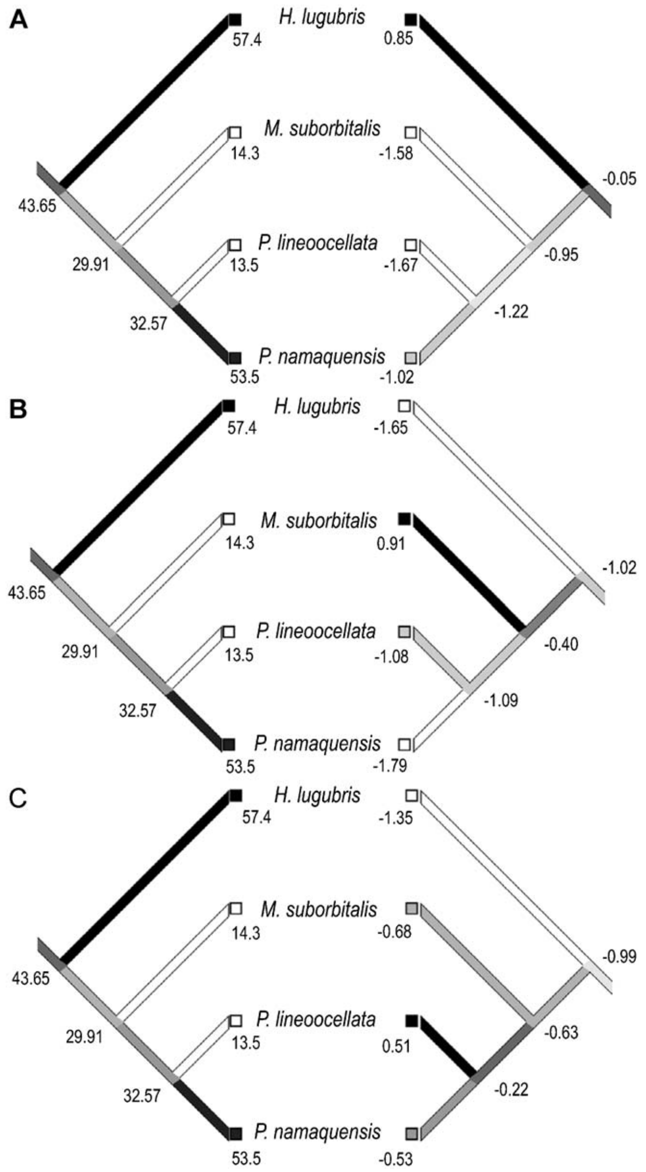

Fig. 3. Reconstruction of ancestral character states along the phylogeny of the four lacertid species. Percent time moving is mapped on each phylogeny on the left (A–C). On the right, the mean canonical variate score for each species is mapped at the tip. Ancestral values are found at the nodes. (A) = CV1, (B) = CV2, and (C) = CV3. Different shades of grey indicate relative changes in values among nodes. See text for explanation.

species, and then back to the more negative values of *P. namaquensis*, an active forager. The reconstruction for CV3 showed the congeneric species (*P. namaquensis*, *P. lineoocellata*) were different; *P. lineoocellata* (AF) had a high positive value (i.e. long tibia and femur, short ilia length), while *P. namaquensis* resembled the other species (Fig. 3C). Reconstructions were performed for moves per minute and each canonical axis; these showed the same patterns as depicted in Fig. 3, hence they are not presented.

Discussion

This study supports the hypothesis that locomotor morphology changes in a predictable manner with foraging mode. These results broadly agree with other work, (Miles et al., 2007; Verwaijen and Van Damme, 2007), yet are novel because this study includes closely related members of mixed and active foraging species. Moreover, these results provide evidence that locomotor morphology and cranial morphology (McBrayer, 2004) both change readily as foraging mode evolves. Here, various hindlimb elements changed with shifts in foraging mode (Fig. 3, Table 3). This and other studies draw attention to the degree to which repeated and predictable patterns of morphological evolution are present among closely related species that vary in foraging mode (Verwaijen and Van Damme, 2007) and across all lizards (Miles et al., 2007).

The canonical variate analysis indicated that distinct morphological solutions exist for the mixed and AF behaviors (Tables 1 and 2; Fig. 2), yet the classification procedure reliably assigned observations to the proper foraging mode (Table 2, bottom). The species were distributed along a continuum of morphological variation with AF species loading the positive (+) end of CV1 (open symbols) and the mixed species loading the opposite (−) end (Fig. 2). The order of these species along CV1 mirrors their variation in percent time moving, and variation of moves per minute is very similar (*H. lugubris* = 2.97, *P. namaquensis* = 2.78, *M. suborbitalis* = 1.83, *P. lineoocellata* = 1.54). This observation and the results in Table 3 and Fig. 3 lend support to the hypothesis that variation in hindlimb morphology is correlated with the movement patterns that define foraging modes.

The loadings of the CV analysis showed that mixed foraging species have wider pelves, longer femora, and longer metatarsals (Table 1, Fig. 2). In contrast, AF species have narrow pelves, long pubes, slightly longer toes and shorter metatarsals and femora. Numerous studies show that hindlimb length, especially femur length and long distal limb elements, are correlated with high sprint speeds (Garland and Losos, 1994; Aerts et al., 2000; Vanhooydonck et al., 2002). The longer femora and metatarsals of the mixed foraging species likely enhance maximal running speed. It is less clear what the implications are for variation in the pelvic girdle. A wider pelvis could increase agility or maneuverability (especially at high speeds) and a combination of speed and maneuverability would be of use to mixed foragers in capturing mobile prey (Huey and Pianka, 1981; Pianka, 1986). Unfortunately, how morphology affects maneuverability over a range of speeds has never been tested in terrestrial lizards (but see Higham et al., 2001 for arboreal lizards), yet it has begun to be explored in fish (Higham, 2007a, b; Collar et al., 2008).

The variations observed in toe length, metatarsal length, tibia length, and femur length can each affect locomotor performance by altering muscle moment arms and stride length. Locomotor performance was studied by Huey and colleagues in three of the four species studied here. The *Pedioplanis* species were similar in maximal sprint speed (*P. lineoocellata* = 2.63 m/s; *P. namaquensis* = 2.68 m/s) and were each faster than *H. lugubris* (1.58 m/s) (Huey, 1982; Huey et al., 1984). Unfortunately, no data on endurance were collected for *P. namaquensis*, but as expected, *P. lineoocellata* had significantly less endurance than the active foraging *H. lugubris*. The similar maximal speeds of the congeners could be due to the subtle nature of the morphological differences observed here (toe vs. metatarsal length), or physiological differences. The morphological differences between *P. lineoocellata* and *P. namaquensis* shown in Fig. 2 might offset differences in muscle mass, fiber type, moment arm, muscle physiology, or combinations of these to result in similar speeds. However, it is important to note that these two species have taken alternative routes to achieve high speeds. *P. lineoocellata* has long tibia and metatarsals, but short toes, while *P. namaquensis* has short tibia and metatarsals, but long toes. These species must achieve similar speeds by altering leg length via different limb segments because muscle physiology appears to be very similar (see below). Therefore, this system likely possesses multiple functional pathways (sensu Alfaro et al., 2005) to achieve high sprint speed. In turn, the presence of multiple functional pathways is likely an important component of the evolution of novel locomotor performance and/or foraging modes and warrants further investigation.

An alternative hypothesis might be that physiological, not morphological differences generate behavioral differences in locomotor performance and foraging mode. Bennett et al. (1984) showed no significant differences in muscle physiology between *H. lugubris* and *P. lineoocellata*. (No data were available for *P. namaquensis*.) Differences were apparent in aerobic scope, heart mass, and hematocrit; hence, physiological processes associated with overall aerobic capacity may drive differences in performance. However, if muscle physiology does not differ between these close relatives, then morphological differences observed in the present study would contribute to variation in running performance by changing muscle mechanical advantage and power.

Some support for this hypothesis exists. Huey (1982) showed that the mixed foraging *P. lineoocellata* had longer stride lengths (0.151 m) and lower stride frequency (16.8 Hz) compared to its congener *P. namaquensis* (stride length = 0.130 m, stride frequency = 19.6 Hz). This difference is likely tied to the longer hindlimb length of *P. lineoocellata*, which is mostly the result of its longer metatarsals and tibia compared to those of *P. namaquensis*. *H. lugubris* is similar to *P. namaquensis* in stride length (0.136 m) but not stride frequency (12.3 Hz); these species were also similar in all limb dimensions except tibia and toe length (Table 3). Therefore, the morphological differences observed in this study likely have distinct effects on salient aspects of locomotor performance.

To facilitate our understanding of how locomotor traits might evolve to shape foraging modes, future studies should tease apart the complex relationships between limb morphology, sprint speed, and endurance and their relationship to foraging mode. Assuming equal muscle masses, sprint speed increases via increases in stride length, or stride frequency, or both (Avery et al., 1987; Vanhooydonck et al., 2002). Current evidence suggests that ambush and mixed foragers have longer limbs (via total length, or segments like the femur and/or tibia; this study; Miles et al., 2007). If true, then ambush and mixed species should increase sprint speed by increasing stride length (again, assuming equal muscle mass). How lizards run faster has been examined in many lizards (e.g. Reilly and Delancey, 1997a, b; Fieler and Jayne, 1998; Jayne and Irschick, 1999; Vanhooydonck et al., 2006). This study and others suggest that ambush and mixed species have long legs and run faster, but the stride parameters (length, frequency) have not been rigorously compared among foraging modes outside of the species studied here. Actively foraging lizards are predicted to have longer, thinner bodies, and in many cases shorter limbs (Miles et al., 2007). To increase speed, AFs could rely more on an increase of stride frequency (Vanhooydonck et al., 2002), or retain key morphological element(s) to increase maximum burst speed (e.g. long toes, or greater distal muscle masses). Active foragers would benefit from long toes and long strides to decrease the cost of transport during foraging (walking), and may likely increase stride frequency, more than stride length, as they run maximally (see above). Although energetically costly (Van Damme et al., 1998; Vanhooydonck et al., 2002), increasing stride frequency for predator escape would be an intermittent energetic cost. Since AF species take in more energy per unit time (Anderson and Karasov, 1981), they may be able to offset these costs for the greater benefit of lighter, longer limbs that minimize the cost of transport during foraging. Future work should strive to understand the interplay among these variables and limb morphology in the context of varying foraging modes. Because foraging mode variation is an integral part of the evolutionary history of modern lizards (Reilly et al., 2007), doing so has the potential to reveal how selection on functional traits like limb length and/or sprint speed, led to divergences in foraging behavior or vice versa.

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References

Aerts, P., Van Damme, R., Vanhooydonck, B., Zaaf, A., Herrel, A., 2000. Lizard locomotion: how morphology meets ecology. Neth. J. Zool. 50, 261–277.

Alfaro, M.E., Bolnick, D.I., Wainwright, P.C., 2005. Evolutionary consequences of many-to-one mapping of faw morphology to mechanics in labrid fishes. Am. Nat., E140–E154.

Anderson, R.A., Karasov, W., 1981. Contrasts in energy intake and expenditure in sit-and-wait and widely foraging lizards. Oecologia 49, 67–72.

Arnold, E.N., 1989. Towards a phylogeny and biogeography of the *Lacertidae*: relationships within an old-world family of lizards derived from morphology. Bull. Br. Mus. (Nat. Hist.) Zool. 55, 209–257.

Arnold, E.N., 1991. Relationships of the South African lizards assigned to *Aporosaura*, *Meroles*, and *Pedioplanis* (Reptilia: Lacertidae). J. Nat. Hist. 25, 783–807.

Avery, R.A., Mueller, C.F., Smith, J.A., Bond, D.J., 1987. The movement patterns of lacertid lizards: speed, gait and pauses in *Lacerta vivipara*. J. Zool. London 211, 47–63.

Bennett, A.F., Huey, R.B., John-Alder, H., 1984. Physiological correlates of natural activity and locomotor capacity in two species of lacertid lizards. J. Comp. Physiol. B 154, 113–118.

Bonine, K.E., Garland, T., 1999. Sprint performance of phrynosomatid lizards, measured on a high-speed treadmill, correlates with hindlimb length. J. Zool. 248, 255–265.

Collar, D.C., Wainwright, P.C., Alfaro, M.E., 2008. Integrated diversification of locomotion and feeding in labrid fishes. Biol. Lett. 4, 84–86.

Cooper, W.E., 1995. Foraging mode, prey chemical discrimination, and phylogeny in lizards. Anim. Behav. 504, 973–985.

Cooper Jr., W.E., Whiting, M.J., 2000. Ambush and active foraging modes both occur in the scincid genus *Mabuya*. Copeia 2000, 112–118.

Fieler, C.L., Jayne, B.C., 1998. Effects of speed on the hindlimb kinematics of the lizard *Dipsosaurus dorsalis*. J. Exp. Biol. 201, 609–622.

Garland, T.J., Losos, J.B., 1994. Ecological morphology of locomotor performance in squamate reptiles. In: Wainwright, P.C., Reilly, S.M. (Eds.), Ecological Morphology: Integrative Organismal Biology. University of Chicago Press, Chicago, pp. 240–302.

Higham, T.E., 2007a. Feeding, fins and braking maneuvers: locomotion during prey capture in centrarchid fishes. J. Exp. Biol. 210, 107–117.

Higham, T.E., 2007b. The integration of locomotion and prey capture in vertebrates: morphology, behavior, and performance. Integr. Comp. Biol. 47, 82–95.

Higham, T.E., Davenport, M.S., Jayne, B.C., 2001. Maneuvering in an arboreal habitat: the effects of turning angle on the locomotion of three sympatric ecomorphs of *Anolis* lizards. J. Exp. Biol. 204, 4141–4155.

Huey, R.B., 1982. Phylogenetic and ontogenetic determinants of sprint performance in some diurnal Kalahari lizards. Koedoe 25, 43–48.

Huey, R.B., Pianka, E.R., 1981. Ecological consequences of foraging mode. Ecology 62, 991–999.

Huey, R.B., Bennett, A.F., John-Alder, H.B., Nagy, K.A., 1984. Locomotor capacity and foraging behaviour of Kalahari lacertid lizards. Anim. Behav. 32, 41–50.

Jayne, B.C., Irschick, D.J., 1999. Effects of incline and speed on the three-dimensional hindlimb kinematics of a generalized iguanian lizard (*Dipsosaurus dorsalis*). J. Exp. Biol. 202, 143–159.

Lamb, T., Bauer, A.M., 2003. *Meroles* revisited: complementary systematic inference from additional mitochondrial genes and complete taxon sampling of southern Africa's desert lizards. Mol. Phylogenet. Evol. 29, 360–364.

Maddison, W.P., Maddison, D.R., 2008. Mesquite: a modular system for evolutionary analysis. Version 2.5. Available at 〈http://mesquiteproject.org〉.

McBrayer, L.D., 2004. The relationship between skull morphology, biting performance and foraging mode in Kalahari lacertid lizards. Zool. J. Linn. Soc. 140, 403–416.

McElroy, E.J., Hickey, K.L., Reilly, S.M., 2008. The correlated evolution of biomechanics, gait and foraging mode in lizards. J. Exp. Biol. 211, 1029–1040.

Miles, D.B., 1994. Covariation between morphology and locomotory performance in sceloporine lizards. In: Vitt, L.J., Pianka, E.R. (Eds.), Lizard Ecology: Historical and Experimental Perspectives. Princeton University Press, Princeton, pp. 207–235.

Miles, D.B., Losos, J.B., Irschick, D., 2007. Morphology, performance, and foraging mode. In: Reilly, S.M., McBrayer, L.D., Miles, D.B. (Eds.), Lizard Ecology: The Evolutionary Consequences of Foraging Mode. Cambridge University Press, Cambridge, pp. 49–93.

Perry, G., 1999. The evolution of search modes: ecological versus phylogenetic perspectives. Am. Nat. 153, 98–109.

Pianka, E.R., 1986. Ecology and Natural History of Desert Lizards: Analyses of the Ecological Niche and Community Structure. Princeton University Press, Princeton.

Pianka, E., Huey, R., Lawlor, L., 1979. Niche segregation in desert lizards. In: Horn, D., Stairs, G., Mitchell, R. (Eds.), Analysis of Ecological Systems. Ohio State University Press, Columbus, pp. 67–115.

Reilly, S.M., Delancey, M.J., 1997a. Sprawling locomotion in the lizard *Sceloporus clarkii*: the effects of speed on gait, hindlimb kinematics, and axial bending during walking. J. Zool. London 243, 417–433.

Reilly, S.M., Delancey, M.J., 1997b. Sprawling locomotion in the lizard *Sceloporus clarkii*: quantitative kinematics of a walking trot. J. Exp. Biol. 200, 753–765.

Reilly, S.M., McBrayer, L.D., Miles, D.B., 2007. Lizard Ecology: The Evolutionary Consequences of Foraging Mode. Cambridge University Press, Cambridge.

Rohlf, F.J., 1998. On applications of geometric morphometrics to studies of ontogeny and phylogeny. Syst. Biol. 47, 147–158.

Rohlf, F.J., 2006. tpsDig, version 2.10. Department of Ecology and Evolution, State University of New York, Stony Brook.

Snyder, R.C., 1954. The anatomy and function of the pelvic girdle and hindlimb in lizard locomotion. Am. J. Anat. 95, 1–14.

Van Damme, R., Aerts, P., Vanhooydonck, B., 1998. Variation in morphology, gait characteristics and speed of locomotion in two populations of lizards. Biol. J. Linn. Soc. 63, 409–427.

Vanhooydonck, B., Van Damme, R., Aerts, P., 2002. Variation in speed, gait characteristics and microhabitat use in lacertid lizards. J. Exp. Biol. 205, 1037–1046.

Vanhooydonck, B., Herrel, A., Van Damme, R., Irschick, D.J., 2006. The quick and the fast: the evolution of acceleration capacity in *Anolis* lizards. Evolution 60, 2137–2147.

Vanhooydonck, B., Herrel, A., Van Damme, R., 2007. Interactions between habitat use, behavior, and the trophic niche of lacertid lizards. In: Reilly, S.M., McBrayer, L.D., Miles, D.B. (Eds.), Lizard Ecology: The Evolutionary Consequences of Foraging Mode. Cambridge University Press, Cambridge, pp. 427–449.

Verwaijen, D., Van Damme, R., 2007. Does foraging mode mould morphology in lacertid lizards? J. Evol. Biol. 20, 1950–1961.