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EVOLUTION OF EXTREME BODY SIZE DISPARITY IN MONITOR LIZARDS (*VARANUS*)

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Many features of species' biology, including life history, physiology, morphology, and ecology are tightly linked to body size. Investigation into the causes of size divergence is therefore critical to understanding the factors shaping phenotypic diversity within clades. In this study, we examined size evolution in monitor lizards (*Varanus*), a clade that includes the largest extant lizard species, the Komodo dragon (*V. komodoensis*), as well as diminutive species that are nearly four orders of magnitude smaller in adult body mass. We demonstrate that the remarkable body size disparity of this clade is a consequence of different selective demands imposed by three major habitat use patterns—arboreality, terrestriality, and rock-dwelling. We reconstructed phylogenetic relationships and ancestral habitat use and applied model selection to determine that the best-fitting evolutionary models for species' adult size are those that infer oppositely directed adaptive evolution associated with terrestriality and rock-dwelling, with terrestrial lineages evolving extremely large size and rock-dwellers becoming very small. We also show that habitat use affects the evolution of several ecologically important morphological traits independently of body size divergence. These results suggest that habitat use exerts a strong, multidimensional influence on the evolution of morphological size and shape disparity in monitor lizards.

KEY WORDS: Brownian motion, evolutionary allometry, habitat use, Ornstein–Uhlenbeck process, phylogenetic comparative methods, Varanidae.

Monitor lizards (*Varanus*) have diversified into an exceptional range of body sizes. From the largest extant lizard species, the Komodo dragon, *Varanus komodoensis* (more than 100 kg and 3 m total length), to the pygmy monitors, *V. brevicauda* and *V. primordius* (about 10 g and 20 cm total length), this clade spans four orders of magnitude in adult body mass and more than an order of magnitude in total length (Pianka 1995; Pianka and King 2004)—easily the largest size range among any recognized genus of vertebrates. Monitor lizards, therefore, provide a compelling model for investigation into the causes and consequences of body size evolution.

Understanding how and why body size diverges among species has been an important goal in evolutionary biology because size is correlated with many features of species' biology. Evolutionary changes in size are tightly linked to major alterations in physiological attributes including metabolic rate and locomotor performance (Schmidt-Nielsen 1984, Brown et al. 1993), which in turn are associated with changes in behavioral and life-history traits, such as home range size, generation time, and

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reproductive output (Calder 1984). The degree of similarity in body size among species also typically reflects the strength of resource competition, and size differences often arise in association with ecological differentiation when closely related species occur in sympatry (Schoener 1975; Pacala and Roughgarden 1985). In addition, morphological traits scale with body size, and substantial proportions of morphological diversity can be explained by size differences. Because of the ubiquity of correlated changes, studies of body size evolution are integral to investigation into the origins of phenotypic diversity.

Indeed, widespread interest in body size evolution has brought to light a variety of intriguing patterns. For example, Cope's rule, the tendency for species in a lineage to increase in size relative to the common ancestor, has been documented for many taxa (Stanley 1973; Arnold et al. 1995; Alroy 1998; Laurin 2004; Van Valkenburgh et al. 2004; Hunt and Roy 2006; Chown and Gaston 2010). In addition, recent work has illuminated how body size disparity (i.e., the spread of body sizes among species [Foote 1997]) varies through time during a clade's history (Dommergues et al. 2002; Cooper and Purvis 2010; Harmon et al. 2010; Slater et al. 2010) or accumulates differently among lineages (Monroe and Bokma 2008; Sol and Price 2008; Adams et al. 2009; Cooper and Purvis 2010; Mahler et al. 2010). These studies have been particularly successful at identifying potentially general patterns of size evolution, such as early accumulation of disparity within clades (Dommergues et al. 2002; Cooper and Purvis 2010; Slater et al. 2010), constraints on size diversification (Harmon et al. 2010), and associations between rates of size diversification and geographic or climatic variables (Cooper and Purvis 2010) or ecological opportunity (Mahler et al. 2010). However, the adaptive basis underlying body size divergence among species has received comparatively little attention. Early diversification of size within a clade, for example, may correspond with ecological opportunity at the early stages of radiation, but how size evolves with different aspects of niche divergence remains unclear. In this study, we test whether differential habitat use has contributed to the evolution of the extraordinary body size disparity of monitor lizards.

Habitat use is known to be an important selective factor during diversification in many evolutionary radiations (e.g., tetraodontiform fish (Alfaro et al. 2007), labrid fish (Price et al. 2011), *Enallagma* damselflies (McPeek and Brown 2000), and *Anolis* lizards (Losos et al. 1998; Losos 2009). A shift in habitat leads to a novel set of ecological circumstances and selective demands, which can alter the course of lineage and morphological evolution. Particularly in lizards, divergence among species in their use of structural habitats has been shown to exert strong influence on morphological diversification (Losos et al. 1998; Aerts et al. 2000; Vanhooydonck et al. 2000; Herrel et al. 2002; Schulte et al. 2004). However, these studies have focused on morphological variation that is independent of size differences, such as increases in relative forelimb length with shifts to arboreality (Aerts et al. 2000), and the nature of habitat's effect on size diversification remains unclear.

The 69 recognized species of monitor lizards are generally active predators that occur in a variety of environments, including tropical forests, deserts, and grasslands throughout the Old World, with greatest species and ecological diversity in Australia (Storr et al. 1983; Pianka and King 2004; JCVI/TIGR Reptile Database). Monitors vary in their use of structural habitats; most species are terrestrial and range widely across broad flat surfaces, but some primarily forage and shelter in trees, and others are associated with rocks and seek refuge in crevices (Storr et al. 1983; Bennet 1995; Pianka 1995; Thompson and Withers 1997; Pianka and King 2004). We asked whether body size disparity among monitor species has evolved as a consequence of these three habitat use types—terrestriality, arboreality, and rock-dwelling.

Differences in habitat use may contribute to size disparity in two possible ways. First, habitats differ in their physiological, functional, and ecological demands, and thus may impose selection toward different adaptive peaks (Aerts et al. 2000; Butler and King 2004). In this case, species that differ in habitat use will adapt toward different habitat-specific size optima, resulting in an increase in size disparity within the clade as a whole, although not among species that share the same habitat type. Alternatively, some habitat types may promote diversification because they can be used in many ways and thus facilitate microhabitat specialization or ecological divergence along other niche axes, leading to elevated rates of size diversification and greater within-habitat size disparity (Simpson 1953; Alfaro et al. 2007; Collar et al. 2010). Here we evaluate these hypotheses by comparing the fit of evolutionary models to body size data for monitor species given a phylogeny relating them.

Habitat differences are also likely to contribute to diversification of morphological structures, such as tail and limb lengths (Aerts et al. 2000; Butler and King 2004; Collar et al. 2010). Although monitor lizards have diversified widely in size, the extent of shape evolution and its possible association with ecology remains an open question. Some previous work has found evidence for associations between ecology and morphological variation independent of size in Australian monitors, including an association between habitat and tail shape (Bedford and Christian 1996) and between habitat and a multivariate combination of limb, head, and body dimensions (Thomson and Withers 1997). Other researchers, however, report contradictory evidence regarding such ecomorphological correlations in *Varanus* and, in fact, have suggested that monitor species may exhibit negligible shape variation (Shine 1986; Greer 1989; James et al. 1992; Pianka 1995; King and Green 1999).

In this study, we adopt a phylogenetic comparative approach to examine the effects of habitat on body size diversification and

on the evolutionary allometry of several morphological traits relevant to movement in the environment. We inferred phylogenetic relationships for 37 species based on mtDNA sequences and reconstructed the evolutionary history of habitat use on the resulting phylogeny. We used these reconstructions and data for species' adult body size and morphological trait values to address four questions: (1) Have habitat use differences contributed to the evolution of body size disparity in *Varanus*? (2) Have habitat differences led to variation in evolutionary allometric slopes for morphological traits? (3) Has morphological evolution deviated from isometry? (4) Has habitat affected morphological evolution independently of body size divergence?

Materials and Methods

SPECIES VALUES FOR ADULT BODY SIZE AND MORPHOLOGICAL TRAITS

Data for body size and morphological trait values for 37 *Varanus* species—just over half of the recognized species diversity—were collected by Pepin (2001). Details regarding measurement techniques can be found in that work and are only briefly presented here. The majority of species values were taken as the means of measurements made on the five largest adult specimens sampled from museum collections. For three species (*V. keithhornei*, *V. komodoensis,* and *V. salvadorii*), however, means were taken from fewer than five specimens ($n = 3$, 4, and 4, respectively) because adults were rare in collections. Body size was measured as snout-vent length (SVL), which is the distance between the anterior-most point of the head and the cloaca. To quantify size, we used SVL rather than body mass because SVL is measured with greater accuracy on preserved museum specimens. Although a strong correlation is expected between SVL and body mass, we note that our results and conclusions pertain to size quantified as SVL and results could vary for body mass. In addition, we focused on four morphological traits that are important for various aspects of lizard movement: tail length, forelimb length, hindlimb length, and body circumference. Tail length is the distance from the cloaca to the posterior-most point of the tail. Mid-body circumference is the distance around the abdomen at its widest point. Forelimb and hindlimb lengths are the sums of the upper and lower limb segments. Head-neck length and head width were also measured by Pepin (2001), but analyses of these data do not provide additional insight beyond those based on the other four variables; for this reason, we do not report results for head-neck length or head width. Species values for SVL and morphological traits were log-transformed for use in all subsequent analyses.

PHYLOGENETIC ANALYSIS

We reconstructed phylogenetic relationships based on 2761 base pairs of mtDNA for the same 37 *Varanus* species in the morphological dataset. In addition, we used the following taxa as outgroups based on the analysis of Macey et al. (1999): *Anguis fragilis, Anniella pulchra, Elgaria kingi, Heloderma horridum, Heloderma suspectum, Lanthanotus borneensis, Shinisaurus crocodilurus, Xenosaurus grandis*. The sequenced region of mtDNA contains three protein-coding genes (ND1, ND2, COI), nine transfer RNA genes (tRNALeu, tRNAIle, tRNAGln, tRNAMet, tRNATrp, tRNAAla, tRNAAsn, tRNACys, and tRNATyr), and the origin of light-strand replication (OL). Previously published DNA sequences were obtained from GenBank (Table S1) and originally published in Ast (2001) and Macey et al. (1999). Four additional unpublished sequences are from Pepin (2001) representing *V. albigularis, V. brevicauda, V. caudolineatus,* and *V. rosenbergi*. Alignment and site homology inference were identical to those used in Schulte et al. (2003). Final analyses used the same 2042 unambiguously aligned sites as Schulte et al. (2003). Aligned sequences are available in TreeBase (Study accession number S11554, Matrix accession number M8991).

We used Bayesian methods implemented in the program BEAST 1.5 (Drummond and Rambaut 2007) to simultaneously infer phylogenetic topology and branch lengths proportional to time (Drummond et al. 2006). We applied the general time reversible model of substitution with gamma-distributed rate variation among sites plus invariant sites (Yang 1994) because a previous phylogenetic analysis showed this model provides the best fit for this region of mtDNA for a broadly overlapping set of *Varanus* species (Schulte et al. 2003). Substitution rates were allowed to vary among lineages according to an uncorrelated (among branches) log-normal distribution (Drummond et al. 2006; Drummond and Rambaut 2007), although we used no external calibration for these rates and set the root depth to be 1.0. We performed four runs of BEAST's MCMC algorithm to sample the posterior probability distribution of model parameters and trees. Each run lasted 20 million generations and was sampled every 2000 generations. We used the program Tracer (Drummond et al. 2006) to assess the proportion of each MCMC sample to be discarded as burn-in (the first 10% of generations was sufficient) and to verify convergence of MCMC chains and adequacy of the effective sample sizes for parameter estimates (>200 for all parameters). We retained a subsample of 1000 phylogenies from the complete sample of trees for use in subsequent analyses.

ANCESTRAL HABITAT USE RECONSTRUCTIONS

We assigned habitat use states to each species and used stochastic character mapping to reconstruct the history of habitat use in *Varanus*. Habitat assignments were based on expert accounts compiled in Pianka and King (2004), and some ambiguous species were augmented with knowledge based on our own observations. We note that some species (*V. indicus*, *V. mertensi*, *V. mitchelli*, *V. semiremex*, *V. salvator*) are considered to be aquatic

or semi-aquatic but were categorized here as terrestrial because they move mostly across the ground in areas where they do not encounter water, and the aquatic habitat type was judged to be insufficiently different to justify a separate category for our purposes. In addition, two species that are commonly found on rocky outcrops (*V. glauerti* and *V. glebopalma*) are known to cling to and move about broad vertical or steeply inclined surfaces. Because other rock-dwelling monitors use mostly horizontal rock surfaces embedded in the ground, this type of habitat use more closely resembles arboreality, and these species were categorized as arboreal in our analysis.

To reconstruct the history of habitat use in *Varanus* lineages, we used stochastic character mapping, which is a Bayesian method that applies MCMC to sample the posterior probability distribution of ancestral states and timings of transitions on phylogenetic branches under a Markov process given a phylogeny and observations for species (Nielsen 2002; Huelsenbeck et al. 2003). We used SIMMAP 1.0 (Bollback 2006) to sample one stochastic character map for each of the 1000 trees retained from the phylogenetic analysis in BEAST. The resulting 1000 reconstructions of habitat and phylogeny represent a set of phylogenetic topologies, branch lengths, and habitat histories sampled in proportion to their posterior probabilities given our data for *Varanus* species. This sample of 1000 reconstructions was used in all subsequent analyses as a way of integrating over uncertainty in phylogeny and ancestral states in a manner similar to the method described by Huelsenbeck and Rannala (2003).

MODEL SELECTION FOR BODY SIZE EVOLUTION

We applied recently developed phylogenetic comparative methods to determine the process by which habitat use promotes body size diversification in *Varanus*. Alternative hypotheses—habitats impose selection toward different adaptive peaks versus habitats contribute differently to size diversification—correspond to different models of phenotypic evolution that can be fit to data for species given a phylogenetic tree. Adaptation toward different size optima in lineages that differ in habitat use can be approximated by an Ornstein–Uhlenbeck (OU) process with multiple habitat-specific optima (Hansen 1997; Butler and King 2004). According to this model, the optimum does not correspond to an adaptive peak in the population genetics sense (as in Lande 1979), but rather it is the primary optimum to which species that share a habitat state are attracted and is the average of species-specific optima that deviate from the primary optimum because of unconsidered selective factors or constraints (Hansen 1997). Alternatively, the hypothesis that habitats contribute differently to body size diversification can be modeled as Brownian motion with multiple rates of evolutionary change that are associated with habitats (O'Meara et al. 2006; Thomas et al. 2006; Collar et al. 2009, 2010). Although Brownian motion is commonly used to depict phenotypic evolution in a flat adaptive landscape (Felsenstein 1988; Hansen and Martins 1996), it also describes adaptive evolution under some conditions (Hansen and Martins 1996; Revell et al. 2008), such as when species-specific selective factors or constraints are large relative to selection imposed by the primary selective regime (Hansen 1997). Therefore, if some habitats promote diversification because they can be used in a variety of ways, corresponding to disparate species-specific adaptive peaks within a habitat type, this scenario may more closely resemble Brownian evolution.

For each reconstruction of phylogeny and habitat, we fit both OU and Brownian models that allowed parameters to vary in lineages inferred to use different habitats. In general, OU models describe phenotypic evolution from an ancestral value (θ_0) toward one or more fixed adaptive optima specified for selective regimes ($\theta_{i;}$). Evolution toward these optima is governed by the strength of selection (α) and stochastic effects, which are modeled as a Brownian motion process (determined by the parameter, σ^2; Felsenstein 1988; Hansen 1997; Butler and King 2004). We explored the fit of multiple-peak OU models that allow lineages inferred to use different habitats (as specified by stochastic character maps) to evolve toward different body size optima with the same strength of selection and Brownian rate specified for all habitats (Hansen 1997; Butler and King 2004). The most complex OU model includes three adaptive optima, one for each habitat use type (OU3: θ_{terr}, θ_{arb}, θ_{rock}). We also fit three two-peak OU models that correspond to each combination of an optimum shared between two habitat types and a separate optimum for the other (OU2 arboreal: $\theta_{terr=rock}$, θ_{arb}; OU2 terrestrial: θ_{terr}, $\theta_{arb=rock}$; OU2 rock-dwelling: $\theta_{terr=arb}$, θ_{rock}). The simplest OU model specifies a single optimum for all *Varanus* lineages regardless of habitat state (OU1: $\theta_{terr=arb=rock}$).

In addition, we fit Brownian motion models that allowed the evolutionary rate (i.e., the time independent variance of character change; see Felsenstein 1985) to vary across lineages inferred to use different habitats (see O'Meara et al. 2006; Thomas et al. 2006; Collar et al. 2009, 2010). We specified five Brownian models that describe the effects of habitat on size evolution in a manner parallel to the OU models described above. The three-rate Brownian model specifies separate rates associated with terrestriality, arboreality, and rock-dwelling (BM3: σ^2_{terr}, σ^2_{arb}, σ^2_{rock}), three two-rate models allow for a shared rate in two of the three habitat types (BM2 arboreal: $\sigma^2_{terr=rock}$, σ^2_{arb}; BM2 terrestrial: σ^2_{terr}, $\sigma^2_{arb=rock}$; BM2 rock-dwelling: $\sigma^2_{terr=arb}$, σ^2_{rock}), and a single-rate model specifies one rate of evolution for all *Varanus* lineages. We view the single-peak OU and single-rate Brownian models as null models with respect to the hypothesis that habitat influenced body size diversification.

We used maximum likelihood implemented in the program Brownie 2.1 (O'Meara et al. 2006; O'Meara 2008) to fit OU

and Brownian models to species SVL for each of the 1000 reconstructions of phylogeny and habitat use. To quantify model fit, we used the small sample size corrected Akaike information criterion (AICc; Burnham and Anderson 2002), and we compared AICc among models in two ways. First, we evaluated the mean AICc for each model across reconstructions and compared mean AICc scores as a way of selecting the best model while averaging over uncertainty in phylogeny and habitat reconstructions. Second, we compared AICc among models for each reconstruction. This latter method resulted in a distribution of fit comparisons that allowed us to assess the sensitivity of model selection to alternative phylogenetic and ancestral habitat state reconstructions. To compare fit among models, we evaluated the difference between each model's AICc and the best-fitting model's AICc (ΔAICc) as well as Akaike weight, which is the proportion of support a model receives relative to the total support for all models (Burnham and Anderson 2002).

EVOLUTIONARY ALLOMETRY OF MORPHOLOGICAL TRAITS

One simple explanation for associations between habitat and diversification of morphological traits is that morphological evolution is tightly correlated with changes in size; habitat may affect size evolution but exert no independent influence on morphological shape (Fig. 1A). Alternatively, shifts in habitat use may alter the relationship between evolutionary changes in a trait and body size (i.e., evolutionary allometry) in lineages that use different habitats. A change in evolutionary allometry may take several forms. First, the slope of the evolutionary allometric relationship may change such that increases in size are associated with shallower (or steeper) morphological change in some habitats compared to others (Fig. 1B). In addition, habitats may impose selection for larger (or smaller) morphological structures across all sizes (Fig. 1C). And finally, the strength of the evolutionary allometric relationship may vary among habitat types if some habitats allow for more variability in morphology at any given size (Fig. 1D). Notably, the latter two scenarios correspond to the alternative ways (described above) in which habitat may contribute to disparity—by imposing selection toward different optima or by allowing for more or less variability. Below we describe a detailed investigation into how habitat may have influenced the evolutionary relationship between morphology and size.

TEST FOR VARIATION IN SCALING COEFFICIENTS AMONG HABITAT TYPES

To test whether habitat differences have led to changes in the evolutionary scaling coefficients for morphological traits, we used a numerical simulation approach described by Garland et al. (1993). We first evaluated the F-statistic for the interaction term of an analysis of covariance (ANCOVA) performed on species data,

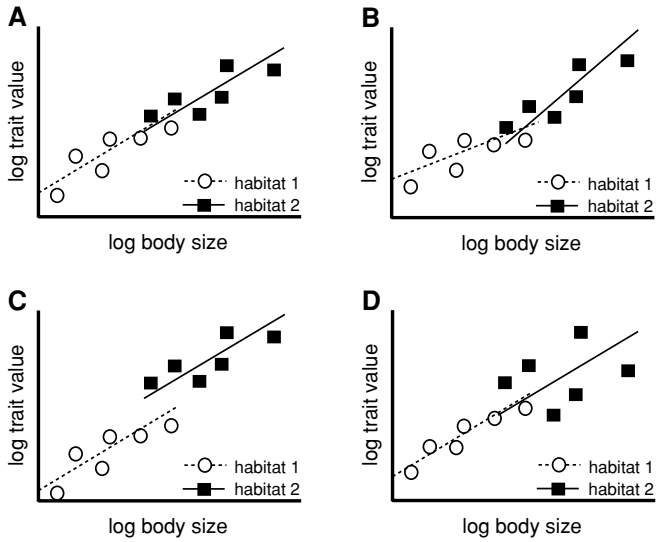

Figure 1. Schematic illustration of the possible effects of habitat on interspecific allometry. In all cases habitat 2 is associated with relatively larger species than habitat 1. (A) There is no difference in allometry between habitats, and differences in trait values between species in habitats 1 and 2 can be explained by the size differences between habitats. (B) Habitat 2 is associated with a greater allometric slope than habitat 1. (C) There is no difference in allometric slopes, but size-corrected trait values for species in habitat 2 are greater than those in habitat 1. (D) There is no difference in allometric slopes or size-corrected trait values, but species in habitat 2 exhibit greater size-independent variation than those in habitat 1.

in which the dependent variable is the morphological trait, SVL is the covariate, and habitat is the independent categorical variable (the interaction term is therefore SVL $\times$ habitat). We tested the significance of the interaction effect against a null distribution generated by simulating bivariate evolution given a constant relationship between the trait and SVL (i.e., homogeneity of allometry among habitat types). For each trait, we estimated a single evolutionary covariance matrix (containing the evolutionary variances for the trait and for SVL on the diagonal and the covariance of evolutionary changes between them elsewhere; Revell et al. 2007a) given all *Varanus* species and a phylogeny. Evolutionary covariance matrix estimation was performed using the function *ic.sigma* in the GEIGER package (Harmon et al. 2008) for R (R Development Core Team 2010). We then applied the empirically estimated evolutionary covariance matrix as a generating condition for 1000 simulations of bivariate Brownian evolution on the phylogeny; this step was carried out using GEIGER's function *sim.char* (Harmon et al. 2008). For each simulation replicate, we evaluated the F-statistic for the interaction term as we did for the observed species data. P-values for interaction effects are therefore the proportion of simulations that provide an F-statistic greater than the F-statistic based on observed species data.

We iterated this process across the sample of phylogenetic reconstructions for *Varanus* and obtained a distribution of *P*-values (evaluated for each tree) for each trait.

TESTS OF EVOLUTIONARY ISOMETRY

After finding little evidence for heterogeneity in allometric slopes among habitats (see Results), we compared slopes estimated for all *Varanus* to the expectation under isometry. Because the four traits we examined are linear measurements, the expected slope under isometric evolutionary change is 1.0. We estimated allometric slopes by performing separate reduced major axis regressions involving standardized independent contrasts for body size against the standardized contrasts for each trait (Felsenstein 1985; Garland et al. 1992). All contrasts were evaluated using the *pic* function for the APE package (Paradis et al. 2004) in R (R Development Core Team 2010). Regressions were forced through the origin (Garland et al. 1992) and carried out using the *line.cis* function for the SMATR package (Warton et al. 2006) in R (R Development Core Team 2010). This procedure was repeated for each of the 1000 phylogenetic reconstructions resulting in a distribution of slope estimates. The overall allometric slope coefficient was taken as the mean of this distribution. We summed error in the estimation of slope coefficients and error associated with alternative phylogenetic reconstructions to obtain 95% confidence intervals for the overall slope estimates. Evolution of a trait was considered to differ from isometry if its 95% confidence interval did not overlap 1.0.

MODEL SELECTION FOR SIZE-CORRECTED MORPHOLOGICAL TRAITS

We assessed the effect of habitat on morphological evolution independently of body size divergence by fitting multiple-peak OU and multiple-rate Brownian models to species' size-corrected trait values. For each phylogeny, we obtained size-corrected trait values for species as the distance (in the Y dimension) between the observed value and its fitted value based on a phylogenetic reduced major axis regression—the line with slope estimated from reduced major axis regression on independent contrasts (see above) that intersects the phylogenetic means for the morphological trait and SVL (Garland and Ives 2000; Revell 2009). We then fit to these size-corrected species trait values the same set of OU and Brownian models that we used to assess habitat's effects on size evolution and compared fit among models using AICc (as described above).

Results

Bayesian phylogenetic analysis in BEAST resulted in a sample of 1000 ultrametric trees that were in a broad agreement with previous reconstructions based on the same region of mtDNA for a largely overlapping set of *Varanus* species (Ast 2001; Schulte et al. 2003). Figure 2 shows the maximum clade credibility tree (i.e., the one with the highest posterior probability summed across nodes) for this sample of trees. We note that phylogenetic topologies across this sample were highly consistent; nearly all nodes of the maximum clade credibility tree had posterior probabilities of at least 0.99.

We found strong support for multiple transitions to each of the three habitat use types. At least 95% of the stochastic habitat maps infer more than one transition into each habitat. This is not surprising given that the groups of species contained within habitat categories are para- or polyphyletic (Fig. 2). In the sample of habitat reconstructions, the modal number of transitions is nine (minimum = 8, maximum = 14); the modal number of transitions to terrestriality is two (minimum = 1 [for 50 out of 1000 trees], maximum = 6), to arboreality is five (minimum = 3, maximum = 7), and to rock-dwelling is two (minimum = 1 [for 3 out of 1000 trees], maximum = 5). Figure 2 shows one stochastic habitat map with the modal number of transitions into each habitat on the maximum clade credibility tree.

The best fitting model for SVL evolution in *Varanus* is the three-peak OU model (Table 1), which infers weak selection toward an optimum for extremely large SVL in terrestrial lineages, extremely small SVL in rock-dwellers, and intermediate SVL for arboreal lineages (Table 2). Comparing mean AICc among models reveals that the three-peak OU model is better supported than seven of the nine other models (ΔAICc for alternative models are greater than 3.0) and receives the most Akaike weight (0.30), although we find nearly equivalent support for the two-peak OU model inferring a shared small-size peak for arboreality and rock-dwelling and a separate large-size peak for terrestriality (OU2 terrestrial; weight = 0.23; ΔAICc = 0.40; see Tables 1, 2). Looking at the distribution of fit comparisons performed on each phylogenetic and habitat reconstruction, the three-peak OU model is preferred most often (in 41% of reconstructions) and the two-peak OU model with a unique optimum for terrestriality is preferred for a substantial proportion (29%). Also receiving support is the two-rate Brownian model estimating a slow rate of SVL evolution that is shared in terrestrial and arboreal lineages and a faster rate associated with rock-dwelling (BM2 rock-dwelling; weight = 0.15; ΔAICc = 1.39; preferred in 18% of reconstructions). The remaining models were preferred in fewer than 5% of reconstructions or not at all (Table 1).

Although the three-peak and two-peak (with shared optimum for arboreality and rock-dwelling) OU models were preferred by comparisons of AICc, they estimated the selection parameter, α, to be very small, implying slow adaptation toward optima (Table 2). These parameter estimates prompted us to investigate the importance of α by comparing the fit of these models to an

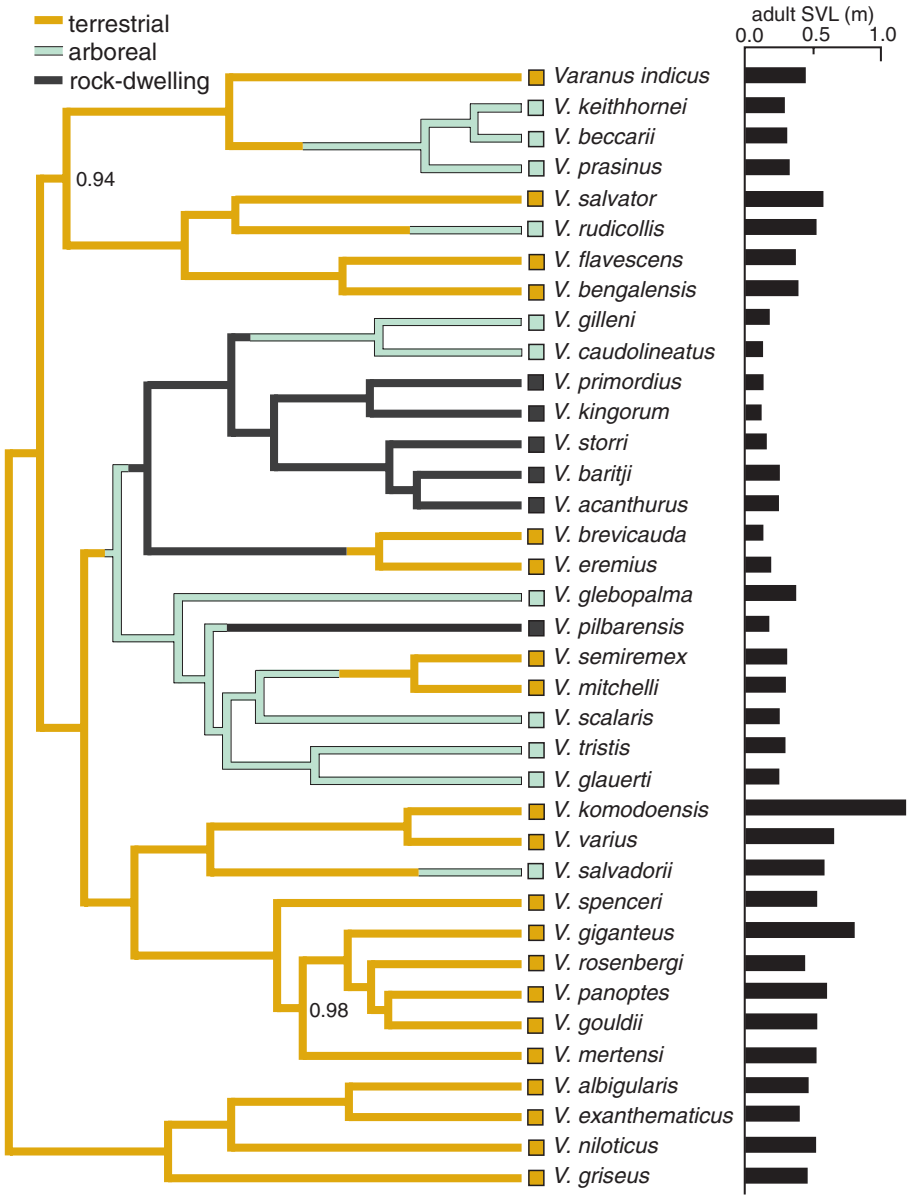

Figure 2. Phylogenetic relationships, habitat reconstruction, and distribution of body size for *Varanus* species. The phylogeny depicted is the maximum clade credibility tree resulting from Bayesian inference on mtDNA sequences for 37 species. Nodes are supported by at least 0.99 posterior probabilities unless otherwise noted. The history of habitat mapped onto this tree is a single stochastic character map given the observed states for species and this phylogeny. Colors on branches indicate inferred habitat state and colored boxes next to species names represent species habitat states; orange is terrestrial, green is arboreal, and dark gray is rock-dwelling. Species values for adult SVL are based on data for measurements on preserved adult specimens (see Materials and Methods for details).

additional set of models that specify multiple Brownian rates as well as separate phylogenetic means associated with the three habitat states (Thomas et al. 2009). These additional models can be interpreted as multiple-peak OU models in which there is no attraction to the mean values per habitat state (i.e., $\alpha = 0$; Thomas et al. 2009). Fitting these models using the function *ML.RatePhylo* for the MOTMOT package (Thomas et al. 2009; we also used the function read.simmap [written by Liam Revell and available at http://anolis.oeb.harvard.edu/~liam/R-phylogenetics] and a custom script to convert stochastic character maps from SIMMAP [Bollback 2006] to the input format required by *ML.RatePhylo*) in R (R Core Development Team 2010), we found that three of the five multiple-rate models with multiple means received little support (ΔAICc $>$ 2.0 on average and for the vast majority of reconstructions; see Table S2). Two of the models—the single-rate model with three means (BM1, 3 means) and the two-rate, three-mean model with an elevated rate for rock-dwelling (BM 2 rock, 3 means; see Tables S2 and S3)—received support,

Table 1. Summary of comparisons of model fit to log SVL given 1000 habitat and phylogeny reconstructions. Names for the two-peak OU and two-rate Brownian models designate the habitat for which a unique peak or rate is specified (e.g., OU2 arb includes a separate peak for arboreality and a shared peak for terrestriality and rock-dwelling).

Model	*k*	AICc	95% ΔAICc	weight	Percent preferred	Percent disfavored
OU3	6	−29.88±3.65	(0.00, 4.55)	0.30±0.20	40.8	25.2
OU2 arb	5	−20.99±2.10	(4.97, 17.32)	0.01±0.01	0.0	100.0
OU2 terr	5	−29.48±2.68	(0.00, 5.32)	0.23±0.15	28.8	32.2
OU2 rock	5	−26.82±3.26	(0.87, 9.69)	0.07±0.06	0.6	86.8
OU1	4	−21.84±1.61	(4.90, 15.81)	0.01±0.01	0.0	100.0
BM3	4	−26.56±2.57	(1.38, 9.78)	0.06±0.05	0.0	85.6
BM2 arb	3	−25.76±1.86	(0.00, 11.37)	0.05±0.07	6.0	88.0
BM2 terr	3	−25.38±1.81	(1.29, 12.32)	0.04±0.04	1.0	95.6
BM2 rock	3	−28.49±2.66	(0.00, 7.76)	0.15±0.12	18.2	51.0
BM1	2	−26.74±1.61	(0.00, 10.91)	0.08±0.07	4.6	75.6

k is the number of parameters in model.
95% ΔAICc is the mid-95% interval of ΔAICc across reconstructions.
Percent preferred is the percent of reconstructions for which the model is chosen as best by comparison of AICc (i.e., lowest AICc).
Percent disfavored is the percent of reconstructions for which the model is disfavored (i.e., ΔAICc is >2.0).

although somewhat less than the preferred three-peak and two-peak OU models on average (ΔAICc [BM1, 3 means] = 1.16, ΔAICc [BM2 rock, 3 means] = 1.07). In addition, these models were preferred for 18.2% and 13.4% of reconstructions, respectively, which were smaller proportions than those for the OU three-peak (33.2%) and OU two-peak (OU2 terr: 20.0%) models.

The multiple-mean, multiple-rate models that received support are similar to the preferred OU models in that the inferred phylogenetic means for habitats have the same relationships to one another; terrestriality has the largest mean body size, rock-dwelling has the smallest mean, and arboreality is intermediate. This overlap suggests that these OU and multiple-mean models receive support because they allow for the tendency of terrestrial species to be large and rock-dwelling species to be small. In fact, the total mean weight for models that allow separate means or optima in terrestrial and rock-dwelling species is 0.77 (i.e., these models account for 77% of the total support available across all models), suggesting that these parameters are important in explaining the data. The multiple-rate, multiple-mean models differ from the OU models in that they do not include selection toward the means. The total mean weight for models that include selection toward separate terrestrial and rock-dwelling optima is 0.41 (accounting for just over half of the support for models that

Table 2. Parameter estimates for models fit to log-transformed SVL (measured in millimeters). Values are means±standard error, where standard error represents variation in the estimate that is due to uncertainty in ancestral habitat and phylogeny reconstruction.

Model	Weight	Ancestral state	OU noise	Phyl half-life	Terr peak/rate	Arb peak/rate	Rock peak/rate
OU3	0.30±0.20	2.37±0.19	0.031±0.004	3083.2±1503.4	1503.45±786.25	2.98±225.55	−1506.31±815.65
OU2 arb	0.01±0.01	2.50±0.03	0.042±0.003	3524.9±504.7	504.74±244.44	−504.73±244.44	504.74±244.44
OU2 terr	0.23±0.15	2.44±0.07	0.033±0.003	3426.6±1103.1	1103.07±402.30	−1103.06±402.35	−1103.06±402.35
OU2 rock	0.07±0.06	2.32±0.04	0.036±0.004	3519.9±1413.8	1413.79±488.11	1413.79±488.11	−1413.78±488.11
OU1	0.01±0.01	2.58±0.01	0.000±0.000	3524.9±0.0	0.00±0.00	0.00±0.00	0.00±0.00
BM3	0.06±0.05	2.60±0.02	—	—	0.032±0.007	0.026±0.017	0.160±0.060
BM2 arb	0.05±0.07	2.57±0.02	—	—	0.051±0.007	0.027±0.015	0.051±0.007
BM2 terr	0.04±0.04	2.60±0.02	—	—	0.033±0.007	0.062±0.013	0.062±0.013
BM2 rock	0.15±0.12	2.61±0.02	—	—	0.030±0.006	0.030±0.006	0.169±0.066
BM1	0.08±0.07	2.58±0.01	—	—	0.044±0.003	0.044±0.003	0.044±0.003

OU noise is the rate parameter, σ^2, for the Brownian process underlying stochastic effects in the OU models.
phyl half-life=ln (2) / α, where α is the strength of selection for the OU process (Hansen 1997) and has the same units as phylogenetic branch lengths, which are in relative time (i.e., the total depth of the tree is 1.0).

Table 3. Results of the phylogenetic ANCOVA testing for heterogeneity among habitat types in the allometric slopes for morphological traits. Sample size for this analysis is the number of sampled species (37).

Trait	$F_{\mathrm{SVL}\times\mathrm{habitat}}$	mean P	95% int for P
Tail length	2.110	0.187	(0.157, 0.217)
Body circumf.	0.972	0.444	(0.409, 0.478)
Forelimb length	1.275	0.349	(0.311, 0.386)
Hindlimb length	0.175	0.857	(0.832, 0.879)

95% int for *P* is the mid-95% interval for *P*-values across reconstructions.

specify different means or optima for terrestriality and rock-dwelling), which suggests that the importance of the selection parameter in explaining the data is somewhat ambiguous. We argue, however, that the biological meaning of the separate phylogenetic means is unclear when there is no selection toward them and multiple transitions into each habitat state have occurred, as seems to be the case for monitor lizards (see Fig. 2). We therefore focus on the preferred OU models in the Discussion because they are more readily interpretable with respect to the effects of transitions between habitats on body size evolution.

We found no evidence that habitat differences have led to shifts in evolutionary allometric slopes for the four morphological traits. A phylogenetic ANCOVA testing for the effect of the interaction between SVL and habitat did not approach significance for any of the reconstructions (Table 3). Because the effect of habitat on evolutionary allometric slopes is weak, we estimated for each trait a single slope coefficient for all *Varanus* and tested whether this estimate differed from isometry. We could not reject isometric evolution for tail length (mean slope = 1.11, 95% CI = [0.88, 1.44]), but we found evidence of positive allometric evolution for body circumference (mean slope = 1.17, 95% CI = [1.052, 1.29]), forelimb length (mean slope = 1.11, 95% CI = [1.01, 1.21]), and hindlimb length (mean slope = 1.20, 95% CI = [1.08, 1.36]; see Fig. 3).

Body size explains a large proportion of variation in morphology among *Varanus* species. Tail length shows the weakest relationship with size ($R^2 = 0.84$), implying the greatest amount of size-independent variability, and the other three traits have very strong associations with size ($R^2 \geq 0.96$; Fig. 3). Figure 4 shows the distribution of residual species trait values in each of the three habitat categories. Although comparisons of medians and variances between these groups are not valid because species are nonindependent observations (Felsenstein 1985; Garland 1992; O'Meara et al. 2006), we present these data for heuristic purposes, as comparisons of these distributions may reflect separate optima (if medians differ substantially) or rates (if variances differ greatly).

Size-corrected tail length evolution has likely proceeded according to a two-peak OU model with a shared optimum for relatively long tails in arboreal and rock-dwelling lineages and a separate optimum for shorter tails in terrestrial lineages (OU2 terrestrial; Table 4). This model receives substantially more support than any other model when comparing mean AICc (weight = 0.74 ± 0.05, mean ΔAICc for all other models >8.0 except OU3 for which mean ΔAICc = 2.64) and is the preferred model in all reconstructions.

A two-rate Brownian model with an elevated evolutionary rate in arboreal lineages best fits body circumference diversification (BM2 arboreal; Table 4). This model provides the best fit based on comparisons of mean AICc and weight ($= 0.24 \pm 0.08$), but substantial support is also found for a two-peak OU model with a shared narrow-bodied peak for terrestrial and arboreal lineages and a wide-bodied peak for rock-dwelling lineages (OU2 rock; weight = 0.22 ± 0.08; mean ΔAICc = 0.69). Additionally, a single-peak OU model also receives support (weight = 0.14 ± 0.04; mean ΔAICc = 1.55). The two-rate model is preferred for the majority of reconstructions (56.6%), the two-peak model is the best fit for a smaller but substantial proportion (40.4%), and the single-peak model is preferred for only a small fraction (2.6%).

The best supported model of forelimb evolution is a two-rate Brownian model inferring a faster rate in arboreal lineages relative to the shared rate for ground- and rock-dwellers (BM2 arboreal; Table 4); however, the single rate Brownian model (BM1) also receives substantial support. The preferred two-rate model provides the best fit based on mean AICc and weight ($= 0.30 \pm 0.09$) and is the most commonly preferred among reconstructions (59.2%), but the single-rate model receives only slightly less support on average (mean ΔAICc = 0.61; weight = 0.27 ± 0.07) and when comparing fit for each reconstruction (preferred in 40.6%).

Hindlimb evolution is best described by the single-peak OU model (OU1), although there is some support for a two-peak model with a peak shared between terrestrial and arboreal lineages (OU2 rock) and for the single-rate Brownian model (BM1; Table 4). The single-peak model is preferred based on mean AICc comparisons and weight ($= 0.32 \pm 0.07$) and receives the lowest AICc score for the vast majority of reconstructions (85.8%). Support for the two-peak OU and single-rate models is lower by both methods of comparing AICc (weight[OU2 rock] = 0.15 ± 0.06; OU2 rock preferred in 5.6% of reconstructions; weight[BM1] = 0.11 ± 0.07; BM1 preferred in 6.2% of reconstructions).

Discussion

The extraordinary body size disparity of monitor lizards has evolved as a consequence of selection associated with different habitat use patterns. Evolutionary model fitting suggests that terrestriality and rock-dwelling represent selective regimes that

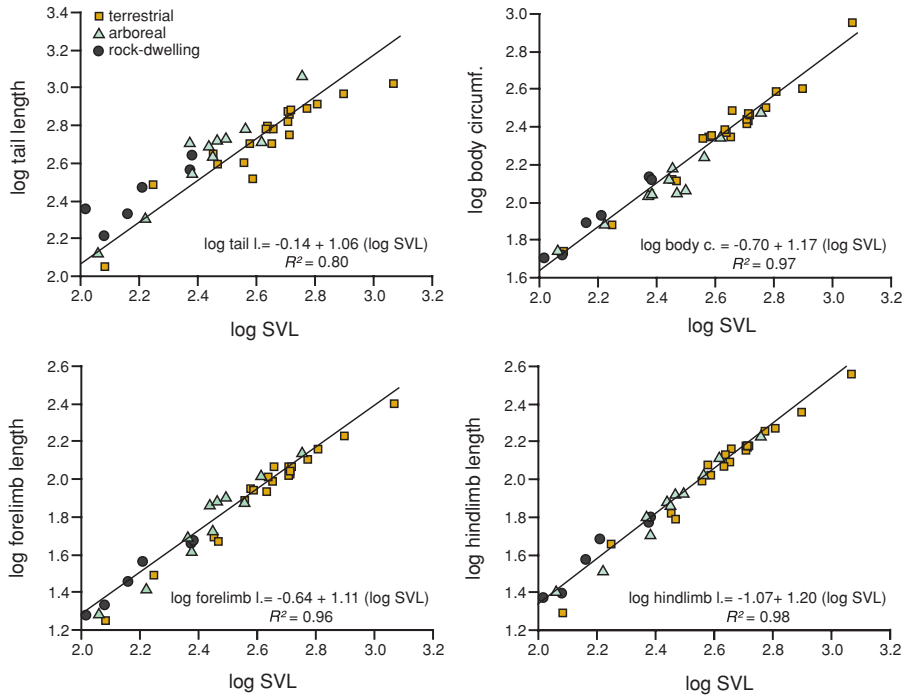

Figure 3. Scaling of morphological traits in *Varanus*. Data are species values for log-transformed morphological traits and SVL, but the scaling relationships depicted are based on phylogenetic reduced major axis regressions of traits on size (see Materials and Methods for details). R^2 is the proportion of variation in species values for a trait that is explained by the regression of that trait on size. Colored symbols denote habitat categories: orange squares are terrestrial, green triangles are arboreal, and gray circles are rock-dwelling species.

have led to oppositely directed size evolution with ground-dwellers evolving toward large body sizes and rock-dwellers evolving small size (Tables 1, 2). Arboreality may represent a separate selective regime with an intermediate size optimum, but support for this scenario is negligible over one in which arboreality and rock-dwelling impose similar selection for small size (Table 1). Nevertheless, these results suggest that selection associated with rock-dwelling is responsible for the evolution of many of the diminutive monitor species, including the pygmy rock monitor (*V. kingorum*) and Northern blunt-spined monitor

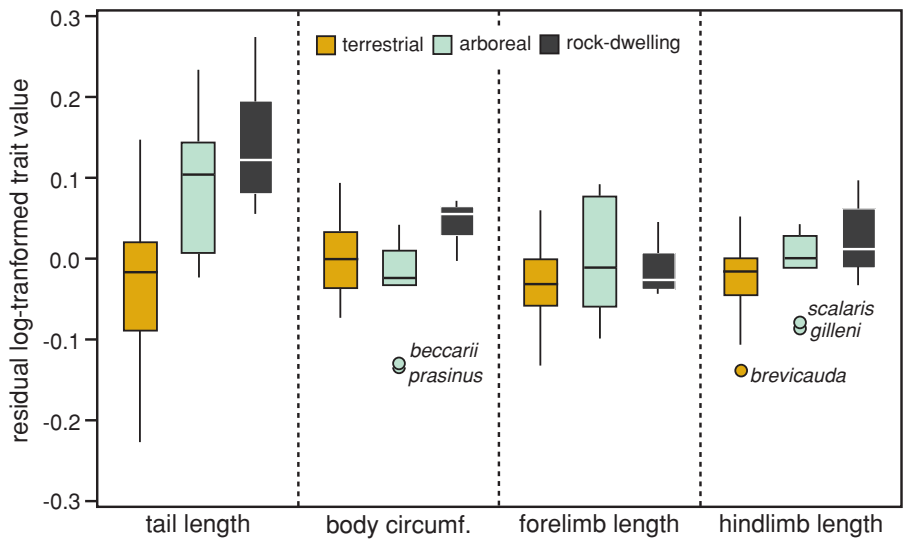

Figure 4. Boxplots for species' size-corrected morphological traits in each of the three habitat categories. Whiskers are standard, extending to the 9th and 91st percentile of the distributions. Labeled points are species values falling outside of this range. Colors correspond to habitat states: orange is terrestrial, green is arboreal, and gray is rock-dwelling.

Table 4. Summary of fit and parameter estimation for the three best-fit models for each size-corrected morphological trait.

Trait	Model	95% ΔAICc	Weight	Percent pref	Anc state	OU noise	Phyl half-life	Terr peak/rate	Arb peak/rate	Rock peak/rate
Tail Length	OU2 terr	0.00±0.00	0.74±0.05	100.0	0.0031±0.0038	0.0535±0.0109	0.1885±0.0462	−0.0377±0.0079	0.1320±0.0133	0.1320±0.0133
	OU3	2.01±2.86	0.20±0.02	0.0	0.0075±0.0089	0.0532±0.0109	0.1884±0.0463	−0.0376±0.0082	0.1233±0.0149	0.1468±0.0163
	BM1	3.94±13.70	0.02±0.02	0.0	0.0000±0.0000	—	—	0.0183±0.0016	0.0183±0.0016	0.0183±0.0016
Body Circumf.	BM2 arb	0.00±2.77	0.24±0.08	56.6	0.0050±0.0015	—	—	0.0028±0.0002	0.0109±0.0020	0.0028±0.0002
	OU2 rock	0.00±2.86	0.22±0.08	40.4	0.0023±0.0023	0.0150±0.0033	0.2114±0.0500	−0.0062±0.0015	−0.0062±0.0015	0.0537±0.0072
	OU1	0.00±3.21	0.14±0.04	2.6	0.0001±0.0001	0.0136±0.0027	0.2603±0.0527	0.0014±0.0009	0.0014±0.0009	0.0014±0.0009
Forelimb Length	BM2 arb	0.00±2.19	0.30±0.09	59.2	−0.0015±0.0026	—	—	0.0017±0.0002	0.0060±0.0010	0.0017±0.0002
	BM1	0.00±2.54	0.27±0.07	40.6	0.0000±0.0000	—	—	0.0027±0.0002	0.0027±0.0002	0.0027±0.0002
	BM2 terr	0.84±3.31	0.12±0.03	0.2	−0.0008±0.0016	—	—	0.0020±0.0003	0.0037±0.0005	0.0037±0.0005
Hindlimb Length	OU1	0.00±1.06	0.32±0.07	85.8	−0.0003±0.0002	0.0144±0.0028	0.2092±0.0456	−0.0066±0.0011	−0.0066±0.0011	−0.0066±0.0011
	OU2 rock	0.00±2.67	0.15±0.06	5.6	0.0010±0.0022	0.0134±0.0034	0.2262±0.0629	−0.0099±0.0018	−0.0099±0.0018	0.0200±0.0144
	BM1	0.00±7.12	0.11±0.07	6.2	0.0000±0.0000	—	—	0.0043±0.0004	0.0043±0.0004	0.0043±0.0004

95% ΔAICc is the mid-95% interval of ΔAICc across reconstructions.
Percent pref is the percent of reconstructions for which the model is preferred by comparison of AICc (i.e., lowest AICc).
OU noise is the rate parameter, σ^2, for the Brownian process underlying stochastic effects in the OU models.
phyl half-life = ln (2) / α, where α is the strength of selection for the OU process (Hansen 1997).

(*V. primordius*), whereas selection for large size in terrestrial lineages has contributed to the evolution of the largest extant lizard species, the Komodo dragon (*V. komodoensis*) and perentie (*V. giganteus*; see Fig. 2).

Although the OU models inferring separate selective regimes for rock-dwelling and terrestriality receive the most support based on comparisons of mean AICc and are preferred for a majority of habitat reconstructions (Table 1), these models infer weak selection toward size optima that are beyond the range of observed species values (Table 2). As we discuss in a subsequent section (see section "Interpreting parameter estimates for preferred OU models of size evolution"), these parameter estimates are biologically unrealistic and may be a consequence of specifying models that are simpler than the true underlying process of size evolution, perhaps because the strength of selection varies among habitat types. Nevertheless, we interpret the preference for habitat-associated multiple-peak OU models, particularly over null models in which the evolutionary process is uniform among lineages (i.e., the single-peak OU and single-rate Brownian models; see Table 1), as evidence that habitat has driven body size divergence, although additional factors also may have played a role.

The ecological and functional demands imposed by arboreality, rock-dwelling, and terrestriality have likely led to differential selection on body size in *Varanus*. Selection for small size in arboreal species and rock-dwellers likely has a functional basis. Effective climbing and clinging to trees may impose constraints on how large and heavy arboreal monitors can become. Although even the largest monitors are known to climb trees occasionally (Pianka and King 2004), these species are likely restricted to parts of trees that can support their large body mass. In contrast, smaller, primarily arboreal monitors are able to use more of the available habitat, although we note that the arboreal Papuan crocodile monitor (*V. salvadorii*) is quite large and yet reportedly moves within the tree canopy with remarkable agility (Pianka and King 2004). Size selection in rock-dwellers is likely imposed by the crevices in which these species seek refuge from predators. Indeed many species of rock-dwelling lizards from other taxa have evolved small size for seemingly similar reasons (Revell et al. 2007b; Goodman et al. 2008). The mechanistic basis for size selection in terrestrial species is probably more complex. Nearly all monitor lizards are active predators and terrestrial species tend to range widely during foraging (Pianka and King 2004). Selection for large size may thus be related to locomotor efficiency, as larger monitors may be able to forage over larger areas. In addition, large size may be an adaptation for capturing and subduing the large prey that monitor lizards are known to take (Losos and Greene 1988; Pianka 1994). Also, widely foraging, ground-dwelling lizards are highly conspicuous in the environment and large size may deter potential predators.

In addition to divergence among monitor species that use different habitats, the best fitting multiple-peak models also describe size variation among species that use the same habitat as a consequence of weak selection and variation in the amount of time species have spent in alternative selective regimes (Hansen 1997; Butler and King 2004). Even though extant species share the same habitat state, they may have experienced different histories of habitat-imposed selection and thus may differ in the amount of time they have had to evolve toward body size optima. For example, according to the habitat reconstruction in Figure 2, two types of histories lead to terrestrial species. The majority of ground-dwellers have experienced the terrestrial selective regime since at least the first lineage-splitting event within *Varanus*, but an alternative habitat history has led to the terrestrial species, *V. brevicauda* and *V. eremius*, which spent about half of their time since the first split within *Varanus* under arboreal or rock-dwelling selective regimes. Because these habitats imposed selection in the opposite direction of selection associated with terrestriality, the small size of these species relative to other ground-dwellers seems to be partly a result of time spent using arboreal or rocky habitats. Although the history of selective regimes explains some of the size variation among terrestrial species, the weakness of selection is also a contributing factor. Following the reversion to ground-dwelling, *V. brevicauda* and *V. eremius* have experienced the terrestrial regime for a length of time equal to about a quarter of the total history of *Varanus* but have not increased in size relative to closely related rock-dwelling and arboreal species. This slowness of adaptation within the terrestrial regime is reflected in the small value for the selection parameter, α, and suggests that attraction to the terrestrial optimum is weak relative to unconsidered selective factors or constraints shared by these species. A similar account explains large body sizes in the arboreal species, *V. rudicollis* and *V. salvadorii*, which spent their early evolutionary histories in the terrestrial selective regime before transitioning to arboreality on terminal phylogenetic branches (Fig. 2).

MORPHOLOGICAL EVOLUTION IN *VARANUS*

Habitat use also has contributed to morphological evolution independently of its effects on body size. We found little evidence that evolutionary scaling coefficients differ among habitats (Table 3), but body circumference, forelimb length, and hindlimb length increase with positive allometry, indicating that *Varanus* species change shape with evolutionary changes in body size. Because terrestrial species tend to be largest, positively allometric evolution implies that increasing size associated with terrestriality is associated with a tendency to become stouter bodied and longer limbed. In addition, model comparisons of size-corrected trait values reveal that habitat has influenced evolution of tail length, forelimb length, and body circumference. Altogether our results suggest a multidimensional effect of habitat on the evolution of morphological disparity in monitor lizards. Habitat contributed to the evolution of disparate sizes and size-correlated morphological variation but also led to additional morphological diversification independent of size divergence.

Tail length showed the most size-independent variation among *Varanus* species (Fig. 4), and we found that habitat differences have been important in the evolution of this diversity. Tail length evolution has not deviated from isometry in the *Varanus* radiation, but size-corrected tail length has evolved toward different adaptive optima in lineages that use different habitats (Table 4 and Fig. 4). The best fitting evolutionary model for size-corrected tail length is a two-peak OU model that infers strong selection toward a long-tail optimum associated with arboreality and rock-dwelling and a short-tail optimum in ground-dwellers (Table 4). These results are generally consistent with associations between tail length and habitat use observed in previous studies on *Varanus* that documented relatively long tails in rock-dwelling species (Bedford and Christian 1996) and in species that climb trees or move about on rocks (Thompson and Withers 1997). This ecomorphological relationship makes functional sense because arboreal and rock-dwelling species may use their longer tails for balance during climbing or scrambling on steeply inclined or uneven surfaces, as has been shown in other lizard species that frequently climb steep inclines (Ballinger 1973). In contrast, shorter tails weigh less and may allow for more efficient movement during long forays along flatter ground surfaces. Furthermore, tails are used to maintain body orientation during jumping in other groups of lizards (Higham et al. 2001; Gillis et al. 2009), and the longer tails of arboreal and rock-dwelling species may be related to selection for jumping performance if these habitats require moving between surfaces that are displaced vertically. The frequency with which varanid species jump is unknown, however, and selection due to jumping performance may be of only secondary importance.

The evolution of body circumference has been positively allometric, indicating that monitor lizards have become somewhat stouter bodied at larger sizes. Size-corrected body circumference is best fit by a two-rate Brownian model with a rate in arboreal lineages that is about fourfold higher than the rate in rock-dwelling and terrestrial lineages. But we also found substantial support for a two-peak OU model with strong selection toward a narrow-body optimum for arboreality and terrestriality and a wide-body optimum for rock-dwellers. The ambiguity in model selection may be a result of two arboreal species that possess exceptionally narrow bodies, *V. beccarii* and *V. prasinus*. Although arboreal species mostly possess negative body circumference residuals, these species are extreme (Fig. 4). Together with *V. keithhornei*, which possesses the third most negative body circumference residual, these species form a clade of Australian arboreal monitors that are relatively distantly related to other arboreal species (Fig. 2). The evolution of more extreme body narrowing in this

clade compared to other tree-dwellers is reflected in the elevated rate of evolution among arboreal species in the two-rate Brownian model. Aside from this clade, arboreal species exhibit a distribution of size-corrected body circumferences that is similar to ground-dwellers (Fig. 4), and this pattern likely contributes to the support of the two-peak OU model. Nevertheless, the tendency for arboreal species to evolve relatively narrow bodies may be related to selection for gracile and light-weight bodies that are more effective at climbing steep inclines and moving along narrow branches, as has been documented for other lizard species that use this type of habitat (Sinervo and Losos 1991; Losos and Irschick 1996).

Forelimb length has evolved with slight positive allometry, but deviation from isometry is marginal. The best supported model for size-corrected forelimb length is a two-rate Brownian model with a fourfold elevated rate in arboreal lineages. These parameter estimates are consistent with the result that arboreal species appear to be more variable than species in the other habitats (Fig. 4). Among the monitors with the longest size-corrected forelimbs are the species, *V. beccarii*, *V. prasinus*, and *V. keithhornei*, which comprise the narrow-bodied, arboreal *Varanus* clade (discussed above). Because long forelimbs have been identified as an adaptation for clinging and climbing in other lizard groups (Aerts et al. 2000), this observation suggests that these species are the most morphologically specialized for arboreality of all monitor lizards. Some arboreal species, such as *V. gilleni* and *V. scalaris*, possess relatively short forelimbs, though, suggesting that in *Varanus* a variety of forelimb lengths may be effective for moving about in trees. As a caveat to this conclusion, however, we note that the two-rate model is only slightly preferred over the single-rate model (Table 4), which receives substantial support on average and across reconstructions (preferred in 40% and disfavored in only 7%). Therefore, the effect of arboreality on rate of forelimb evolution is somewhat ambiguous.

Evolutionary change in hindlimb length has been positively allometric. As *Varanus* species have increased in size during evolution, their hindlimbs have lengthened disproportionately. Although habitat had no apparent effect on the evolutionary relationship between hindlimb and size (Table 4 and Fig. 3), the largest species are generally terrestrial. Therefore, ground-dwellers tend to have longer hindlimbs than species in other habitats. A proportionate increase in hindlimb length with increasing body size may have enhanced locomotor efficiency in large species that move over greater expanses (Dodson 1975), although endurance seems to be unrelated to body size in Australian monitor lizards (Clemente et al. 2009a). In addition, increased relative hindlimb length in large-bodied terrestrial monitors may have conferred greater sprint speed. Indeed, this idea is supported by Clemente et al.'s (2009b) result that sprint speed increases with positive allometry in Australian monitors. Such increases in speed may be related to increases in foraging efficiency or evasion of predators in open habitats, as has been shown for other lizard groups (Pounds 1988; Losos 1990; Melville and Swain 2000; Herrel et al. 2002; Vanhooydonck et al. 2006). Alternatively, positive allometric evolution of the hindlimb may have led to no increase in locomotor performance with increasing size, but rather increases in relative hindlimb length may have simply maintained locomotor performance as body size increased (Pounds et al. 1983).

INTERPRETING PARAMETER ESTIMATES FOR PREFERRED OU MODELS OF SIZE EVOLUTION

The preferred OU models of body size evolution infer an optimum for extremely large size in terrestrial lineages and another for very small size associated with rock-dwelling (or with both rock-dwelling and arboreality). However, these size optima are well outside the range of observed species values, and selection is estimated to be very weak (Table 2). We report the estimated strength of selection as the phylogenetic half-life ($= \ln(2)/\alpha$, where α is the selection parameter of the OU model; Hansen 1997), which is the time required to evolve half the distance from the ancestral value to the optimum. Because we set the root depth of the phylogeny equal to 1.0, our estimates of phylogenetic half-life for SVL ($\sim 3 \times 10^3$) imply selection so weak that *Varanus* lineages are unlikely to reach the optima. Indeed, these half-life estimates are consistent with optima that are beyond biologically realistic body sizes (Table 2).

Taken at face value, the parameter estimates for the preferred OU models suggest that *Varanus* lineages have been evolving slowly toward optima that they are unlikely to reach. Hansen (1997) describes this scenario as opposing evolutionary trends in different selective regimes, where phenotypes tend to increase relative to the ancestral value in one regime and decrease in the other. One interpretation of these results, therefore, is that habitats have contributed to oppositely directed adaptive size evolution in *Varanus*. Although this model may be somewhat biologically unrealistic given that body size cannot increase or decrease without limit, it will be appropriate if species are not nearing those boundaries. According to this interpretation, our results imply that any effect of approaching size limits is not apparent given the observations for species and the reconstructions of phylogeny and habitat.

Alternatively, the extreme parameter estimates may be a result of specifying models that are simpler than the true process underlying body size evolution. One way in which our OU models may be under-parameterized is that a single strength of selection, α, is specified for all *Varanus* lineages (i.e., α is the same for all habitat-imposed selective regimes). If some habitats impose stronger selection than others (i.e., the steepness of adaptive peaks varies), then the estimated global α will be a compromise among habitat-specific α's. In fact, inspection of the body size distribution

among species and inferred habitat use histories suggests that this may be the case for *Varanus*. Rock-dwelling species exhibit less variation in SVL than either arboreal or terrestrial species (see Fig. 2), which suggests that selection associated with rock-dwelling may be relatively strong. On the other hand, selection associated with terrestriality may be particularly weak considering that size is variable among species that have been terrestrial since the *Varanus* common ancestor and that the terrestrial species *V. brevicauda* and *V. eremius* have remained small since their reversion to terrestriality. Species that use ground surfaces may experience relaxed constraints on size relative to rock- or tree-dwellers that hide in crevices or move about on thin branches. It seems plausible that the multiple-peak OU models we fit would accommodate underlying variation in α by inferring weak selection toward extremely distant optima, which could reasonably produce both relatively rapid evolution toward small sizes in rock-dwellers as well as variability associated with terrestriality.

Another possible reason for variation in the strength of selection is that species-specific background selective factors may be more pronounced for some habitat types, such as terrestriality, resulting in species-specific optima that are more dispersed around the primary habitat-imposed optimum. Variation in the magnitude of species-specific effects may arise because some habitats are associated with greater heterogeneity in genetics or environmental circumstances (Hansen 1997). These effects may be particularly pronounced in ground-dwelling monitor lizards. The largest *Varanus* species, *V. giganteus* and *V. komodoensis*, are over a meter in SVL and belong to a clade of similarly large-bodied species found in Australia and neighboring islands, whereas smaller terrestrial species, such as *V. flavescens* and *V. bengalensis* (about 0.5 m SVL), are included in a clade of Southeast Asian monitors. A third clade of African monitors (*V. albigularis*, *V. exanthematicus*, *V. griseus*, *V. niloticus*) includes ground-dwellers with intermediate body sizes. Even though these species use the same habitat, the effect of terrestriality on size has likely occurred in very different selective backgrounds in species occupying different geographic areas. For example, monitors found in Australian deserts are subjected to different environmental demands, predators, and resource competitors than species found in the tropical forests of Southeast Asia. These differences in selective demands across continents may correspond to disparate geographically associated adaptive peaks for terrestriality. Nevertheless, our model comparisons reveal support for habitat-imposed selection on body size even though varied biological circumstances in *Varanus* lineages may have contributed to a more complex process of size evolution than described by our multiple-peak OU models.

Although the OU models discussed above provide the best fit to monitor body size evolution, an alternative two-rate Brownian model also receives support (Table1). According to this model, rock-dwelling is associated with an elevated rate of size evolution relative to the shared rate for arboreal and terrestrial lineages (Table 2). Support for this model is reduced when it is compared to multiple-rate models with separate habitat-associated phylogenetic means (Table S2); the two-rate model with a single phylogenetic mean receives less support than the single-rate model with multiple means or the parallel two-rate model with multiple means. But the combined support for the two two-rate models that infer an elevated rate of size evolution in rock-dwellers is moderate (combined mean weight = 0.20; these models together are preferred for 22% of reconstructions). This is somewhat surprising, however, because a relatively high Brownian rate is expected to lead to elevated variability among species (O'Meara et al. 2006), and extant rock-dwellers are consistently small bodied, exhibiting little variation in body size relative to the other habitat types (Fig. 2). We suspect that the high rate estimate for rock-dwellers is a consequence of relatively recent transitions to rock-dwelling for extant *Varanus* species. Although rock-dwellers do not differ much in size, this variation has arisen over a relatively short amount of time, resulting in a high rate estimate. Support for these models appears to be sensitive to variation in habitat reconstructions, which differ in exactly when and on what branches transitions to rock-dwelling occurred. Additional information on the timing of these transitions would help to evaluate the importance of an elevated rate in rock-dwellers for explaining body size disparity in monitor lizards.

Conclusions

In this study, we identify habitat use as a determinant of the extreme body size disparity for which monitor lizards are exemplary. The preference for OU models with multiple habitat-associated adaptive peaks to describe the distribution of size among monitor species provides evidence that the differential selective demands of habitats have contributed to size evolution in spite of the many confounding factors that also influence divergence of this important phenotypic trait. We emphasize that our model selection results do not exclude other possible contributing factors because our approach is limited to detecting the best model from those we specified a priori. In fact, the extreme and unrealistic parameter estimates of the preferred OU models imply that the process underlying size evolution is more complex than our specified models. Future work may better capture the complexity in the evolutionary process by implementing OU models that allow for more kinds of variation in the adaptive landscape, perhaps by allowing the strength of selection to vary in different selective regimes.

We also detect substantial diversification in morphological traits independent of body size in *Varanus* and implicate habitat use differences as a factor in the evolution of morphological shape

disparity. The relationships we document between habitat use and the evolution of tail, forelimb, and body circumference are similar to ecomorphological associations that are well established in other lizard groups. These results suggest that although size is the primary axis of phenotypic divergence in monitor lizards, additional morphological diversification has been important during this radiation's evolutionary history.

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Supporting Information

The following supporting information is available for this article:

Table S1. GenBank accession numbers for all sequences used in this study.
Table S2. Summary of fit for Brownian motion models specifying multiple rates and multiple phylogenetic means for habitat categories and comparisons to multiple-peak OU models and multiple-rate Brownian models with a single mean.
Table S3. Parameter estimates for Brownian motion models with multiple rates and multiple means fit to log SVL.

Supporting Information may be found in the online version of this article.

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