

## Article

# Functional diversity of small-mammal postcrania is linked to both substrate preference and body size

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## Abstract

Selective pressures favor morphologies that are adapted to distinct ecologies, resulting in trait partitioning among ecomorphotypes. However, the effects of these selective pressures vary across taxa, especially because morphology is also influenced by factors such as phylogeny, body size, and functional trade-offs. In this study, we examine how these factors impact functional diversification in mammals. It has been proposed that trait partitioning among mammalian ecomorphotypes is less pronounced at small body sizes due to biomechanical, energetic, and environmental factors that favor a “generalist” body plan, whereas larger taxa exhibit more substantial functional adaptations. We title this the Divergence Hypothesis (DH) because it predicts greater morphological divergence among ecomorphotypes at larger body sizes. We test DH by using phylogenetic comparative methods to examine the postcranial skeletons of 129 species of taxonomically diverse, small-to-medium-sized (<15 kg) mammals, which we categorize as either “tree-dwellers” or “ground-dwellers.” In some analyses, the morphologies of ground-dwellers and tree-dwellers suggest greater between-group differentiation at larger sizes, providing some evidence for DH. However, this trend is neither particularly strong nor supported by all analyses. Instead, a more pronounced pattern emerges that is distinct from the predictions of DH: within-group phenotypic disparity increases with body size in both ground-dwellers and tree-dwellers, driven by morphological outliers among “medium”-sized mammals. Thus, evolutionary increases in body size are more closely linked to increases in within-locomotor-group disparity than to increases in between-group disparity. We discuss biomechanical and ecological factors that may drive these evolutionary patterns, and we emphasize the significant evolutionary influences of ecology and body size on phenotypic diversity.

**Key words:** adaptive landscapes, ecomorphology, morphometrics, phenotypic diversity, phylogenetic comparative methods, trait partitioning

Phenotypic diversity is unevenly distributed across many axes, including time, geography, phylogeny, and environment (Sepkoski et al. 1981; Schluter 2000; Hillebrand 2004; Alfaro et al. 2009).

Although this unevenness is influenced by extrinsic factors, such as climate change and mass extinction events, many intrinsic factors play central roles in catalyzing or constraining phenotypic diversity.

Ecological traits in particular are key drivers of phenotypic diversification, because they trigger adaptive changes that result in trait partitioning among ecomorphotypes. For instance, arborealists exhibit elongate digits adapted for climbing (Kirk et al. 2008), and fossorialists exhibit stout limbs adapted for digging (Hildebrand 1985a). Nevertheless, the morphological separation between species of different ecomorphotypes is almost always imperfect. That is, the range of morphologies in one ecomorphotype often overlaps with the range of morphologies in other ecomorphotypes. This is because morphology is influenced by numerous additional factors, such as phylogeny, body size, and functional tradeoffs (e.g., Polly et al. 2016; Polly 2020). These factors confound efforts to examine how ecological traits drive phenotypic diversification.

Body size is one of the most conspicuous aspects of phenotypic diversity, and the relationship between body size and ecology in vertebrates has been the focus of extensive study (Peters 1986; Brown and Maurer, 1989; Yom-Tov and Geffen 2011). Among mammals, in particular, body size may be the most useful single predictor in understanding a species' ecological adaptations (Damuth and MacFadden 1990), because body size is correlated with ecological traits such as diet (Kay 1984; Kay and Covert 1984; Price and Hopkins 2015; Pineda-Munoz et al. 2016; Grossnickle 2020), physiology (McNab 1983, 1990), and life history (Case 1978; Tomiya 2013). The same holds for locomotion, where body size can influence limb shape (Biewener 1983; Kilbourne and Hoffman 2013, 2015), posture (Jenkins 1971; Biewener 1989), and gait (Hildebrand 1985b; Biewener 1990, 2005; Lovegrove and Haines 2004). Nevertheless, biomechanical, energetic, and environmental demands on the postcranial skeleton differ with body size; so, although body size is correlated with locomotor traits, it can also act as a confounding variable that affects the magnitude of trait partitioning among taxa of different locomotor modes.

The complicating influence of body size on mammalian locomotor adaptations was articulated by Jenkins (1974) in his study of the tree shrew *Tupaia glis*. He argued that among small mammals, differentiating between "arboreal" and "terrestrial" species on the basis of postcranial morphology is nearly impossible because even small ground-dwellers require postcranial adaptations for climbing (e.g., inversion–eversion of the hind feet, pronation–supination of the forefeet) to contend with uneven and disordered substrates (e.g., tree roots, woody debris; Jenkins 1974). Jenkins (1974) therefore proposed that "arborealism" and "terrestrialism" are not discrete phenomena among small mammals, and that only at larger body sizes would the postcranial skeleton reflect a canalization of one locomotor mode or the other. This hypothesis was elaborated upon by Jenkins and Parrington (1976) in their analysis of Late Triassic mammaliaforms, wherein they concluded that the postcranial skeletons of early mammals, which were small in size, were adapted for traversing spatially complex and uneven surfaces, whether that be in the trees or on the ground. Thus, they codified the idea that primarily ground-dwelling species would require the same locomotor repertoire as primarily tree-dwelling species.

Jenkins' hypothesis implies that the postcranial skeletons of arborealists and terrestrialists should be nearly indistinguishable in small mammals (Jenkins 1974; Jenkins and Parrington 1976), but this hypothesis has been critiqued in the years since it was first proposed. Detailed studies on the functional morphology of small-bodied metatherians (Szalay 1984; Argot 2001, 2002; Szalay and Sargis 2001) and eutherians (Sargis 2002a, 2002b; Salton and Sargis 2008, 2009) have demonstrated that tree-dwellers and ground-dwellers do show distinct locomotor adaptations. Further,

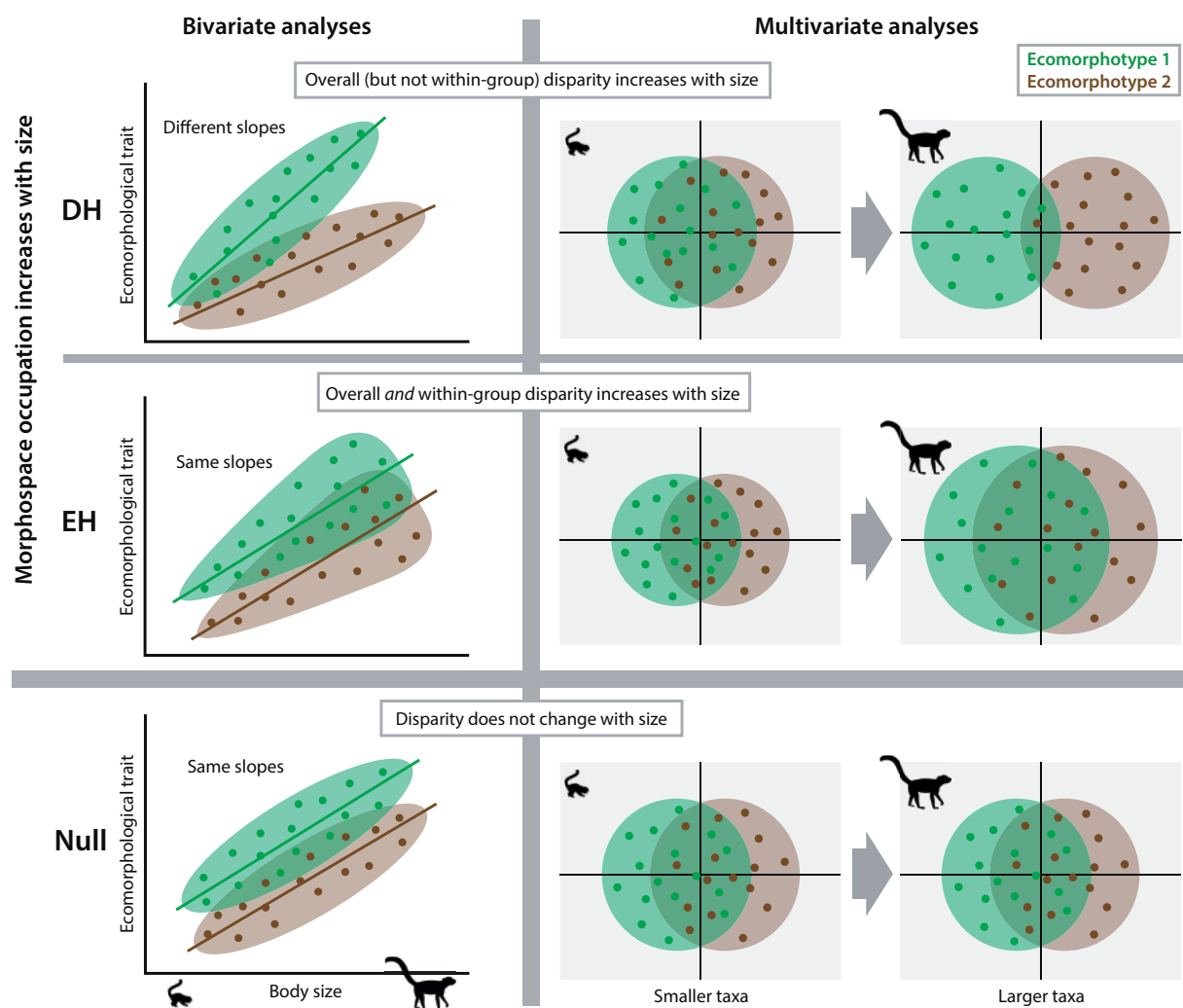
multivariate analyses based on linear measurements taken from mammalian postcranial skeletons have successfully differentiated small mammals on the basis of their locomotor modes (Samuels and Van Valkenburgh 2008; Hopkins and Davis 2009; Samuels et al. 2013; Chen and Wilson 2015; Meng et al. 2017; Caledo et al. 2019; Nations et al. 2019; Grossnickle et al. 2020; Weaver et al. 2020). These studies have therefore cast doubt on Jenkins' hypothesis.

Although previous studies have challenged Jenkins' prediction that small-mammal tree-dwellers and ground-dwellers are morphologically indistinct, there are two additional implications of his hypothesis that have not been explored in detail. First, if postcranial adaptations of tree-dwellers and ground-dwellers are less distinct in smaller species, then it follows that postcranial adaptations are more pronounced in larger species. This prediction can be assessed by comparing interspecific allometric patterns of functional traits for the two locomotor guilds (i.e., tree-dwellers and ground-dwellers). Second, if there is greater differentiation in the postcranial morphologies of larger-bodied tree-dwellers and ground-dwellers, then overall morphospace occupation among species should also increase with body size. This prediction can be tested by measuring morphological disparity in mammals of different size categories. Assessing these two factors—differentiation and disparity—in relation to body size can inform how body size influences the diversity of locomotor ecomorphologies among tree-dwelling and ground-dwelling mammals.

We term these two implications of Jenkins' hypothesis the "Divergence Hypothesis" (DH) because it predicts greater morphological divergence and, in turn, greater overall disparity among ecomorphotypes at larger body sizes. Beyond Jenkins (1974) and Jenkins and Parrington (1976), a number of studies have found support for DH. For example, skeletal adaptations for gliding are much more pronounced in larger mammals than in smaller mammals (Runestad and Ruff 1995; Grossnickle et al. 2020), thus demonstrating interspecific allometric scaling differences between gliding and nongliding ecomorphotypes. Further, proximal limb morphology has been shown to be indistinct among some small rodents with different locomotor modes (Hedrick et al. 2020). DH is conceptualized in Figure 1, demonstrating that the allometric trends of ecomorphological traits should show greater divergence between tree-dwellers and ground-dwellers at larger body sizes. In multivariate space this can be conceptualized as a greater separation between tree-dwellers and ground-dwellers in morphospace, resulting in greater overall and between-group disparity (Figure 1).

An alternative to DH is that the postcranial morphologies of tree-dwellers versus ground-dwellers are distinct at all body sizes, but within-locomotor-group morphological disparity increases with body size (Figure 1). We term this the "Expansion Hypothesis" (EH) because it predicts that larger mammalian species will occupy greater regions of morphospace, but this pattern will be driven by an expansion of within-group diversity, not between-group diversification. As highlighted in Figure 1, this hypothesis is supported by parallel regression slopes of specific ecomorphological traits (regressed against body size) and an increase in overall and within-group morphospace occupation (and morphological disparity) with greater body size.

A third possibility is that postcranial morphologies of tree-dwellers versus ground-dwellers are distinct at all body sizes, but morphological disparity does not increase with body size. We term this the Null Hypothesis because it predicts neither greater differentiation between ecomorphotypes nor an increase in disparity. Importantly, the Null Hypothesis does not predict that body size has



**Figure 1.** Conceptual framework for testing hypotheses on the association of functional diversity and body size in mammals, with predictions for bivariate allometric trends (left) and multivariate plots of different size categories (right). Mammals are categorized into two hypothetical ecomorphotypes (e.g., “tree-dwellers” and “ground-dwellers”). The Divergence Hypothesis (DH) and Expansion Hypothesis (EH) both predict greater morphological disparity and morphospace occupation among larger species, whereas the Null Hypothesis predicts that morphological disparity is unaffected by body size. See the text for additional details. Silhouettes are by Yan Wong (not copyrighted) and Smokeybjb (CC BY-SA 3.0, <https://creativecommons.org/licenses/by-sa/3.0/>), and available at <http://phylopic.org>.

no influence on locomotor ecomorphotypes, but rather the effect is uniform across both tree-dwelling and ground-dwelling ecomorphotypes at all body sizes (Figure 1).

In this article, we test DH and EH by examining the postcranial skeletons of 129 species of taxonomically diverse, extant, small-to-medium-sized mammals (ranging from 0.005 to 12.8 kg) of known locomotor modes. We use linear measurements taken on postcranial skeletons to test the predictions of DH and EH (Figure 1) in bivariate and multivariate analyses; many of these measurements capture skeletal traits that are highly correlated with locomotor mode (e.g., Samuels and Van Valkenburgh 2008; Chen and Wilson 2015). Further, we fit evolutionary models to the morphological data to examine the influence of body size on ecomorphologies, allowing us to assess the tempo and mode of postcranial ecomorphological evolution in both small- and medium-sized mammals. These analyses provide novel insight on the macroevolutionary patterns that generate phenotypic patterns in mammals of different body sizes.

Although previous studies have used large morphometric datasets to differentiate locomotor modes among mammals (e.g., Samuels and Van Valkenburgh 2008; Chen and Wilson 2015), our study is unique in examining how body size influences the magnitude of postcranial trait partitioning and morphological disparity in mammals of different locomotor classifications. Further, our dataset is taxonomically diverse, and therefore offers the opportunity to put these postcranial morphological variants in a broader phylogenetic and macroevolutionary context (*contra* Samuels and Van Valkenburgh 2008; Nations et al. 2019; Hedrick et al. 2020).

In addition to assessing DH and EH, our study contributes broadly to our understanding of factors that catalyze and constrain phenotypic diversity in mammals. In particular, our results suggest that body mass plays a major role in shaping morphological disparity and macroevolutionary patterns in mammals. Thus, our analyses may provide a framework for future studies that further examine how factors such as body mass and substrate preference influence functional diversity in mammals.

## Materials and Methods

### Morphometric and phylogenetic data

Our morphological dataset is derived from [Chen and Wilson \(2015\)](#), but it includes skeletal measurements for 25 additional species that were obtained from specimen collections at the Burke Museum of Natural History & Culture (UWBM) and the Field Museum of Natural History (FMNH). For each species, we sampled one adult individual (identified by tooth eruption pattern and/or epiphyseal fusion) and, when possible, we chose field-collected rather than captive specimens. When multiple specimens were available, we examined other individuals to confirm that the postcranial morphology of our measured specimen was representative of the species. Further, we removed measurements that are especially subjective or show evidence of considerable measurement error due to factors such as small size (e.g., distal phalanx width). This resulted in 29 total linear measurements ([Supplementary Figure S1](#)), and data for these measurements are provided in [Supplementary Table S1](#). Measurements were collected using calipers (*sensu* [Chen and Wilson 2015](#)). See [Chen and Wilson \(2015\)](#) for descriptions of the osteological measurements. Our sample is taxonomically diverse; it includes 129 species that represent 19 orders and 50 families ([Supplementary Figure S2](#); [Supplementary Table S1](#)).

We classified mammals in our dataset as either “small” (0.005–0.47 kg) or “medium” (0.47–12.8 kg) based on the median body mass (0.47 kg) in our sample. Although our size cutoff is arbitrary, it may have some biological relevance because it closely aligns with Kay’s Threshold (0.5 kg), the body mass that typically defines the upper and lower body size limits of mammalian insectivores and herbivores, respectively ([Kay 1984](#); [Kay and Covert 1984](#)). We also categorized each species as either a “tree-dweller” or “ground-dweller” on the basis of their substrate preference ([Nowak 1999](#); [Chen and Wilson 2015](#)). Thus, our dataset includes four subcategories (e.g., small ground-dweller), each with a sample size between 28 and 37 species ([Supplementary Table S1](#)). Tree-dwellers include species classified as scansorial, arboreal, or gliding. Ground-dwellers include species classified as terrestrial, saltatorial, semifossorial, semiaquatic, or fossorial. We excluded locomotor “specialists” that are not represented in both size categories, thus ensuring comparable overlap in locomotor behaviors. For instance, we excluded cursorial, graviportal, and fully aquatic mammals because they are all large, and fully subterranean fossorial taxa (e.g., mole rats) because they are all small ([Chen et al. 2019](#)). Larger-bodied taxa were also excluded from our dataset to maintain consistency in the type and number of measurements taken on each specimen; for example, we would be unable to take comparable phalangeal measurements for neither cetaceans nor perissodactyls, compared with rodents. Further, the limbs of large-bodied mammals (>20 kg) have been shown to scale differently than those of smaller mammals because they are subject to greater static deformation by gravity ([Economos 1983](#); [Bertram and Biewener 1990](#)). As such, we contend that our current sample is most appropriate to address the hypotheses presented herein.

The rationale for simplifying locomotor modes into tree-dwelling and ground-dwelling categories is two-fold. First, Jenkins’ hypothesis was proposed to address distinctions between arboreal (i.e., tree-dwelling) and terrestrial (i.e., ground-dwelling) mammals ([Jenkins 1974](#)); thus, using these broad categories is more applicable to testing the implications of that hypothesis explicitly. Second, locomotor classifications among extant mammals can be subjective. For example, classifying a mammal as scansorial versus arboreal

depends on the proportion of time the animal spends on the ground versus in the trees, and classifying a mammal as semifossorial versus fossorial depends, in part, on the proportion of time the animal spends in a burrow versus on the surface (along with other behavioral factors). These distinctions often require extensive behavioral field data that are only sporadically available and can be inconsistent across species ([Nowak 1999](#)). By adopting the terminology “tree-dwelling” versus “ground-dwelling,” we aimed to mollify these terminological issues and maintain consistency between locomotor categories.

Nonetheless, we recognize that our choices to include or exclude some taxa, and our binning of multiple locomotor modes into only two tree-dwelling and ground-dwelling groups, are subjective. Therefore, we tested the effect of our choices through supplemental sensitivity analyses where we modulated our sampling strategy ([Supplementary Tables S2–S4](#)). These sensitivity analyses consisted of: 1) including subterranean fossorialists among our small ground-dwellers group, 2) comparing only “non-specialists” (i.e., removing gliders from the tree-dwellers group and fossorialists from the ground-dwellers group), 3) comparing only arboreal and terrestrial taxa, and 4) classifying scansorialists as ground-dwellers. See the [Supplementary Methods](#) for additional information.

Adult body mass estimates are primarily from the PanTHERIA database ([Jones et al. 2009](#)). However, when available, we used mass information provided by museums for the specific specimens we measured ([Supplementary Table S1](#)). To convert the data to a linear scale, we natural-log transformed the cube roots of the body mass estimates (e.g., [Harmon et al. 2010](#); [Slater and Friscia 2019](#)). To account for differences in body size among species, we scaled and standardized trait measurements by transforming them into log-shape ratios ([Mosimann 1970](#)). Log-shape ratios are calculated by dividing measurements by geometric means of all 29 measurements (as a proxy for overall body size) and then  $\log_{10}$ -transforming the resulting ratio ([Claude 2013](#); [Price et al. 2019](#); [Grossnickle 2020](#)). A benefit of this size-correction method is that it preserves variance associated with allometry.

For comparative analyses that incorporate phylogeny, we used a sample of 50 phylogenetic trees from [Upham et al. \(2019\)](#). The trees were randomly chosen from the posterior distribution, and each was pruned to the species in our sample. We repeated comparative analyses for each tree, and the reported statistical results are means of the 50 iterations.

### Ecomorphological analyses

To test for differences between skeletal traits (as log-shape ratios) of tree-dwellers and ground-dwellers, we performed phylogenetic analyses of variance (pANOVAs) by regressing the 29 traits in our dataset against substrate preference (treated as a discrete trait) using phylogenetic generalized least squares (PGLSs). Analyses were performed via the *pgls* function in the *caper* package ([Orme 2018](#)) for R software ([R Core Team 2020](#)). Hereafter, we often refer to the measurements as “ecomorphological traits” because many of the metrics are strongly correlated with locomotor mode.

For bivariate examinations of the individual ecomorphological traits, we used PGLS to regress log-transformed trait data for tree-dwellers and ground-dwellers against transformed body mass. To illustrate allometric trends, we plotted the PGLS regressions (and log-shape ratio regressions) for the 10 traits that were found to most strongly differentiate tree-dwellers and ground-dwellers via pANOVAs. To test for differences in regression slopes between tree-dweller and ground-dweller datasets (as predicted by DH), we



performed phylogenetic analyses of covariance (pANCOVAs) in which substrate preference (i.e., tree-dwelling versus ground-dwelling) is the categorical factor and log-transformed linear measurements are the dependent variable. The pANCOVAs were performed using the *gls.ancova* function in the *evomap* R package (Smaers and Mongle 2016), and we adjusted *p*-values to reduce the false discovery rate associated with multiple testing using the Benjamini–Hochberg procedure (Benjamini and Hochberg 1995). A significant interaction term indicates that slopes are different between the two groups. Confidence intervals for PGLS regressions were produced using the *gls.ci* function in *evomap*. Further, we regressed the size-corrected log-shape ratios against body mass, which better illustrates allometric trends of the locomotor groups (but does not incorporate phylogeny).

In addition to the bivariate analyses, we performed four multivariate analyses, each using the size-corrected measurements for the 29 morphological traits. First, we reduced the dimensionality of the data using a principal component analysis (PCA). We opted not to use a phylogenetic PCA because the benefits of this method have been challenged, especially for disparity calculations like those performed in our study (Polly et al. 2013). Second, we measured the morphological disparity (i.e., phenotypic dissimilarity) of tree-dwellers and ground-dwellers as the sum of variances of the 29 traits (Ciampaglio et al. 2001). The final two multivariate analyses are linear discriminant analyses (LDAs) and phylogenetic multivariate ANOVAs (pMANOVAs). These analyses allow us to test a prediction of DH that ecomorphotypes of larger taxa are more easily distinguished from one another. The LDAs were performed using the *lda* function of the *MASS* R package (Ripley 2020). The pMANOVAs were performed using the *aov.phyl* function of the *geiger* R package (Pennell et al. 2014), using 1,000 simulations for *p*-value calculations. To examine whether differentiation between small tree-dwellers and ground-dwellers was influenced by habitat openness, we also performed a supplemental LDA on small tree-dwellers and ground-dwellers from well-forested environments (*n* = 18 species; Supplementary Table S1) via leave-one-out cross-validation.

### Evolutionary model-fitting

To further examine the ecomorphological evolution of mammals, we fit six evolutionary models to the postcranial data using the *geiger* (Pennell et al. 2014) and *OUwie* (Beaulieu and O'Meara 2016) R packages. For our primary analyses, we chose to fit models to scores of the first two principal components (i.e., PC1 and PC2). Although fitting models to individual PCs have been shown to bias model-fitting results (Clavel et al. 2015; Uyeda et al. 2015), we decided to use PC1 and PC2 scores for several reasons. First, tree-dwellers and ground-dwellers separate out well in both size categories along PC1 (and to a lesser extent, PC2), and ecomorphological separation between locomotor modes is an assumption of all three hypotheses (Figure 1). Second, PC1 and PC2 together capture a considerable amount (49%) of the variation in the dataset. Third, Uyeda et al. (2015) found PC1 to bias results toward an early burst (EB) model, but we find the EB model to be an especially poor fit to our data, suggesting that this PC1-related bias is not significantly influencing our results. Finally, accessible multivariate modeling options (e.g., the *mvMORPH* package from Clavel et al. 2015) do not include models that allow evolutionary rates to vary between selective regimes (in this case, substrate preferences), in contrast to univariate models in *OUwie*.

To explore whether our choice of analyzing PC1 and PC2 biased our results, we repeated our model-fitting analyses on four individual traits that most strongly differentiate tree- and ground-dwellers (proximal-phalanx length, intermediate-phalanx length, femur distal width, and olecranon-process length). We also performed a PCA on the 10 traits that were found to most strongly differentiate tree-dwellers and ground-dwellers via pANOVAs, then we repeated our model-fitting analyses on the PC1 and PC2 scores from the 10-trait dataset. The results from these supplemental analyses remain consistent with our results for PC1 from the 29-trait dataset (Supplementary Table S5).

To test for evolutionary differences between taxa of different body sizes, the model-fitting analyses were performed for subsamples consisting of only “small-sized” taxa and only “medium-sized” taxa, allowing us to determine whether the same model(s) best fits these two groups individually. For instance, DH predicts that mammalian tree-dwellers and ground-dwellers are morphologically similar at smaller body sizes (Figure 1; Jenkins 1974), and therefore the models that treat tree-dwellers and ground-dwellers uniformly (i.e., BM, OU, and EB) are expected to fit more strongly to the small-sized-mammal dataset than to the medium-sized-mammal dataset. Conversely, EH and the Null Hypothesis predict that ecomorphotypes are distinct even at small body sizes, and therefore these hypotheses are supported if two-regime (i.e., “multi-peak”) models best fit the data, as these models allow for parameters (e.g., trait optima, or location of “peaks”) to vary between tree-dwellers and ground-dwellers. If two-regime models best fit the data, we can distinguish between levels of support for EH and the Null Hypothesis by considering the nuances of the modeling results. For example, under the Null Hypothesis, we expect stationary variance ( $\sigma^2/2\alpha$ )—which represents the expected variance if the OU process of lineages reached equilibrium (i.e., current lineages were given enough time to evolve to their respective trait optima)—to be similar among our small- and medium-sized-mammal subsamples; whereas under EH we expect stationary variance (like morphological disparity) to be greater in the medium-sized-mammal subsample (Figure 1).

The EB model predicts greater morphological diversification early in the history of a clade, and it was fit to PC1 scores using the *fitcontinuous* function within *geiger*. The five additional models were fit using *OUwie*. The *fitcontinuous* and *OUwie* functions return identical log-likelihood values for uniform (i.e., single-regime) Brownian Motion (BM1) and Ornstein–Uhlenbeck (OU1; Hansen 1997, Butler and King 2004) models, indicating that it is appropriate to use the two different R packages for model-fitting comparisons. BM1 includes two parameters: the phylogenetic mean and a constant evolutionary rate ( $\sigma^2$ ) under the assumption of stochastic evolutionary change from a central tendency. OU1 includes an additional parameter,  $\alpha$ , which represents the strength of attraction toward a trait optimum ( $\theta$ ). Support for BM1 or OU1 would indicate that substrate preference (i.e., tree-dwelling versus ground-dwelling) does not strongly influence evolutionary changes in skeletal morphology.

Three additional models test the presence of distinct selective regimes for tree-dwellers and ground-dwellers by allowing parameters to vary between these two groups. Support for these models would provide evidence for adaptive zones (Simpson 1944) or adaptive peaks of a fitness landscape (Wright 1932) that are associated with each regime. The *OUwie* function requires the classification of ancestral nodes into selective regimes (i.e., tree-dweller or ground-dweller). The discrete ancestral states were inferred with the *ace* function of the *ape* package (Paradis et al. 2004), using an equal

**Table 1.** Summary statistics for comparative analyses of 29 skeletal measurements of 129 mammalian species

Trait	pANOVA			PCA loading		pANCOVA		Regression slope	
	<i>F</i> stat.	<i>p</i> -value	Adj. $r^2$	PC1	PC2	<i>F</i> stat.	<i>p</i> -value	“Tree”	“Ground”
Astragalus length	0.166	0.830	0.000	−0.060	0.014	3.880	0.142	0.446	0.399
Calcaneus length	1.092	0.492	0.001	−0.155	−0.103	1.088	0.393	0.439	0.409
Fibula length	0.019	0.930	0.000	0.169	−0.098	2.251	0.243	0.434	0.366
<b>Femur distal width</b>	<b>13.657</b>	<b>0.003</b>	<b>0.090</b>	<b>−0.069</b>	<b>−0.244</b>	<b>0.900</b>	<b>0.445</b>	<b>0.466</b>	<b>0.447</b>
Femur head depth	2.413	0.294	0.011	−0.140	−0.325	6.698	0.066	0.470	0.428
<b>Femur length</b>	<b>4.452</b>	<b>0.110</b>	<b>0.026</b>	<b>−0.145</b>	<b>−0.181</b>	<b>7.190</b>	<b>0.063</b>	<b>0.434</b>	<b>0.366</b>
Femur mid-shaft width	0.544	0.643	0.000	−0.056	−0.188	2.033	0.249	0.447	0.456
Humerus distal width	0.662	0.606	0.000	0.008	−0.127	3.387	0.166	0.450	0.445
Humerus head length	0.729	0.605	0.000	−0.378	−0.081	2.416	0.243	0.445	0.419
Humerus head width	0.170	0.830	0.000	0.139	0.010	2.225	0.243	0.476	0.476
<b>Humerus length</b>	<b>11.363</b>	<b>0.006</b>	<b>0.075</b>	<b>0.228</b>	<b>0.077</b>	<b>8.993</b>	<b>0.063</b>	<b>0.444</b>	<b>0.406</b>
Humerus proximal width	2.313	0.294	0.010	−0.114	0.214	1.386	0.346	0.460	0.452
Humerus mid-shaft width	1.376	0.417	0.003	−0.071	0.186	3.993	0.142	0.467	0.472
Ilium length	0.228	0.830	0.000	−0.180	0.278	5.822	0.074	0.445	0.389
<b>Ischium length</b>	<b>7.376</b>	<b>0.034</b>	<b>0.047</b>	<b>0.142</b>	<b>0.170</b>	<b>0.116</b>	<b>0.063</b>	<b>0.459</b>	<b>0.402</b>
Manus inter. phalanx length	20.554	0.000	0.133	−0.039	−0.007	<b>7.466</b>	<b>0.782</b>	<b>0.393</b>	<b>0.392</b>
<b>Manus proximal phalanx length</b>	<b>15.154</b>	<b>0.003</b>	<b>0.100</b>	<b>−0.197</b>	<b>0.064</b>	<b>13.548</b>	<b>0.014</b>	<b>0.406</b>	<b>0.340</b>
Metacarpal length	0.010	0.930	0.000	−0.102	0.008	1.664	0.296	0.415	0.382
Metacarpal width	1.850	0.349	0.007	−0.095	0.059	0.152	0.762	0.470	0.519
Pelvis length	0.044	0.924	0.000	0.161	0.341	5.191	0.093	0.444	0.386
<b>Radius length</b>	<b>7.450</b>	<b>0.034</b>	<b>0.048</b>	<b>−0.094</b>	<b>0.201</b>	<b>7.555</b>	<b>0.063</b>	<b>0.430</b>	<b>0.370</b>
Scapula height	0.113	0.865	0.000	−0.074	−0.022	2.855	0.203	0.453	0.464
Scapula length	3.150	0.215	0.017	0.169	0.348	4.000	0.142	0.417	0.403
<b>Tibia distal width</b>	<b>5.147</b>	<b>0.081</b>	<b>0.031</b>	<b>−0.011</b>	<b>0.218</b>	<b>0.694</b>	<b>0.469</b>	<b>0.455</b>	<b>0.471</b>
Tibia length	0.053	0.924	0.000	0.087	0.034	2.210	0.243	0.388	0.314
Tibia mid-shaft width	1.835	0.349	0.006	0.201	−0.120	0.982	0.405	0.438	0.400
Tibia proximal width	1.715	0.361	0.006	−0.205	−0.282	1.453	0.346	0.444	0.444
<b>Ulna length</b>	<b>6.623</b>	<b>0.042</b>	<b>0.042</b>	<b>0.475</b>	<b>−0.184</b>	<b>5.916</b>	<b>0.074</b>	<b>0.430</b>	<b>0.397</b>
<b>Ulna olecranon length</b>	<b>12.815</b>	<b>0.004</b>	<b>0.084</b>	<b>0.407</b>	<b>−0.263</b>	<b>3.630</b>	<b>0.142</b>	<b>0.414</b>	<b>0.474</b>

In bold are the 10 metrics that best differentiate “ground-dwellers” ( $n = 70$ ) from “tree-dwellers” ( $n = 59$ ) using phylogenetic analyses of variance (pANOVAs), and regressions for these traits are shown in Figure 2A. The first two PCs are plotted in Figure 2B, and their loadings are provided here. The phylogenetic analyses of covariance (pANCOVAs) test for differences in slopes of PGLS regressions. Regression slopes are provided for tree-dwellers (“tree”) and ground-dwellers (“ground”). For both pANOVAs and pANCOVAs, the  $p$ -values are adjusted for multiple testing (Benjamini and Hochberg 1995) for 29 independent tests., adj, adjusted; inter., intermediate; stat., statistic.

rates model, which was preferred by a likelihood ratio test. For each of the 50 phylogenetic trees, we assigned discrete states (tree-dweller or ground-dweller) to each node based on the greatest marginal likelihood at that node.

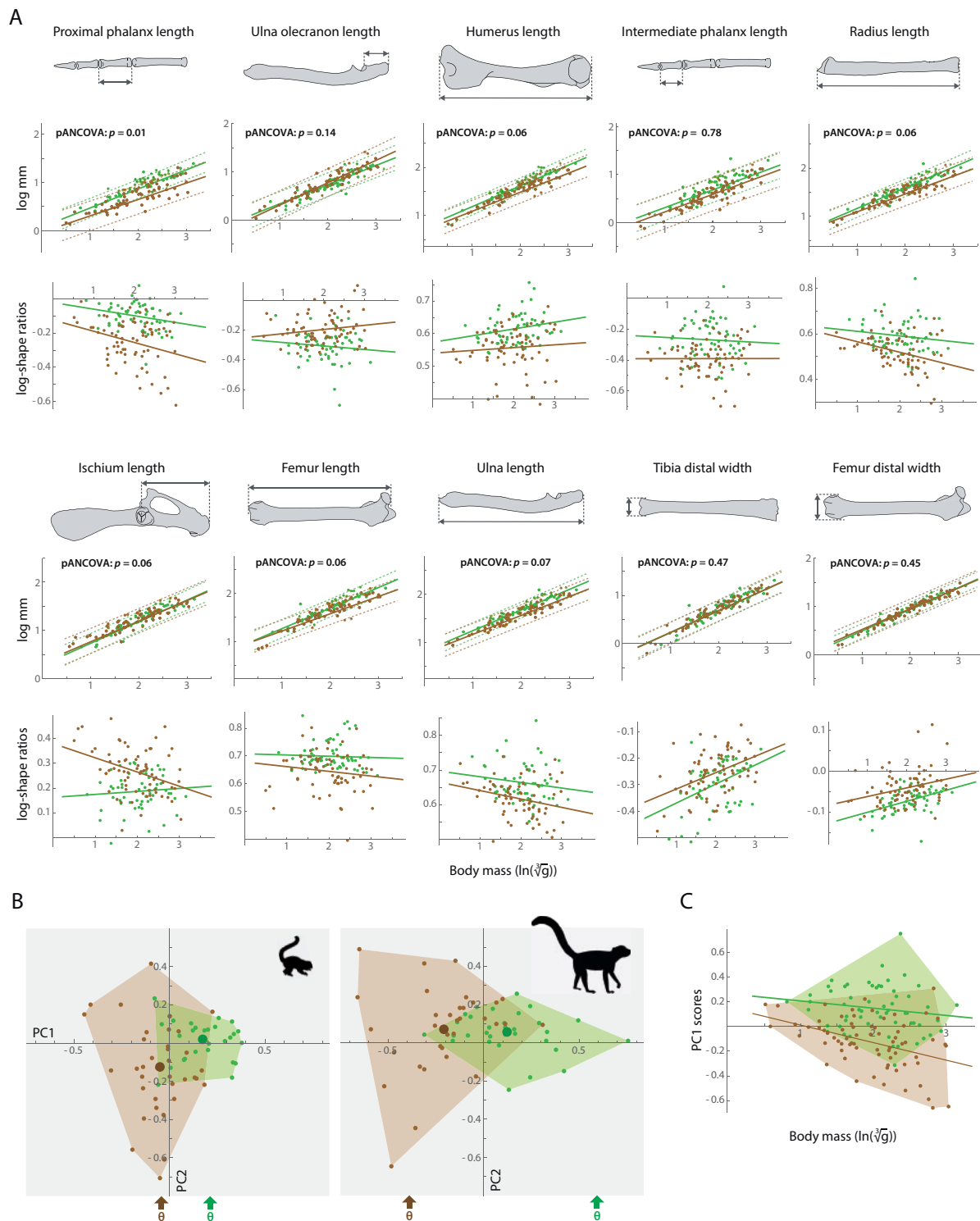
Two-regime BM models (BMS) allow the evolutionary rates ( $\sigma^2$ ) to vary between tree-dwellers and ground-dwellers, but the phylogenetic means ( $\theta$ ) are kept constant between groups (i.e., root.station = TRUE). Further, we fit two two-regime OU models (OUM and OUMV), which allow  $\theta$  to vary between tree-dwellers and ground-dwellers. For OUM,  $\alpha$  and  $\sigma^2$  are kept constant across regimes, but  $\sigma^2$  can vary between locomotor modes for OUMV. Support for the two-regime OU models would suggest the presence of selection for specific trait optima.

Goodness-of-fit for the six models was evaluated using small-sample corrected Akaike information criterion (AICc) values (Akaike 1974, Hurvich and Tsai 1989) and relative Akaike weights. AICc calculations are based on maximum likelihood values and penalize increased model complexity. Phylogenetic half-lives ( $\ln(2)/\alpha$ ) and stationary variance ( $\sigma^2/2\alpha$ ) were calculated to further examine macroevolutionary dynamics in mammals (Cooper et al. 2016; Gearty et al. 2018), and for these calculations we used parameter results from the best-fitting model (i.e., OUM for PC1 scores).

## Results

Our bivariate analyses (i.e., pANCOVAs) reveal that for 28 of the 29 traits regressed against body mass, the slopes are statistically indistinguishable ( $\alpha = 0.05$ ) between tree-dwelling and ground-dwelling species (Table 1; Figure 2A). However, for nine of the 29 traits, the  $p$ -values of the interaction terms are  $< 0.1$ , and slopes for some of these regressions (e.g., proximal phalanx length) indicate that tree-dwellers and ground-dwellers are diverging with greater size (Figure 2A). Thus, there is limited evidence for ecomorphological traits being more distinct at larger body sizes (the pattern predicted by DH), but the statistical support is tenuous.

Our PCA reveals that both small- and medium-sized tree-dwellers and ground-dwellers plot in distinct areas of morphospace (Figure 2B). Likewise, LDAs demonstrate that the percent-correct classification (via leave-one-out cross-validation) of locomotor mode is similar when using the small-mammal-only dataset and the medium-mammal-only dataset, with the small-mammal-only dataset actually outperforming the medium-mammal-only dataset by  $\sim 10\%$  (Table 2). The pMANOVAs further demonstrate considerable differences between tree- and ground-dwellers at both body sizes, with differentiation being statistically significant for both small- and medium-sized mammals (Table 2).



**Figure 2.** (A) Relationships between osteological measurements and body mass in small-to-medium-sized mammalian species, which are classified as either “ground-dwelling” (brown) or “tree-dwelling” (green). The 10 measurements are those that most strongly differentiate “ground-dwellers” and “tree-dwellers” (Table 1). For each measurement, there are two regressions against body mass: logged measurements (top) using PGLSs, and size-corrected log-shape ratios (bottom). To test regression slope predictions of DH, EH, and the Null Hypothesis (Figure 1), we performed phylogenetic analyses of covariance (pANCOVAs) using the PGLS regressions (Table 1). The pANCOVAs were repeated for 50 phylogenetic trees, but the PGLS plots in this figure utilize one randomly chosen tree. (B) A PCA of the 29 skeletal measurements, showing PC1 (29% of variance) and PC2 (20% of variance). The 2 plots are from the same analysis, but only the small-sized species (<0.47 kg) are shown in the left plot, and only the medium-sized species (>0.47 kg) are in the right plot. The large dots represent the mean phenotypes (or centroids) for tree-dweller and ground-dweller. The arrows mark PC1 optima ( $\theta$ ) that are predicted by the evolutionary model-fitting results (specifically, the OUM model). See Supplementary Figure S3 for versions of the PCA plot with labeled genera. (C) PC1 scores of all taxa regressed against body mass. Silhouette sources are provided in Figure 1 caption.

Overall and within-group disparity (measured as the sum of trait variances) both increase at larger body sizes (Figures 2B and 3A). The disparity level of medium-sized mammals is ~35% greater than that of small mammals (Figure 3A). This is highlighted by the

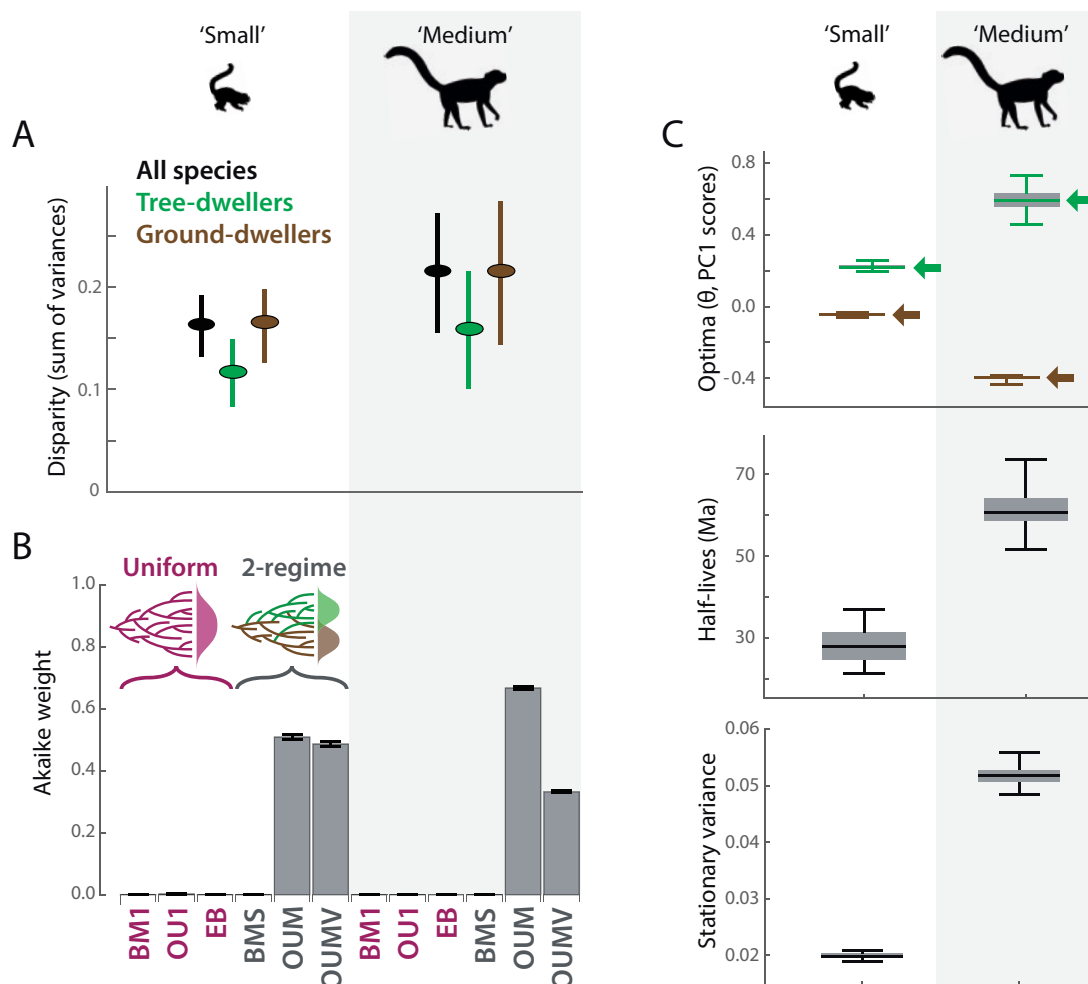
**Table 2.** The pMANOVAs and LDAs that test the differentiation between tree-dwellers and ground-dwellers at different body sizes

	pMANOVA		LDA % correctly classified		
	F stat.	p-value	All	"Tree"	"Ground"
"Small" mammals	4.723	0.010	84.62	82.14	86.49
"Medium" mammals	3.080	0.020	75.00	77.42	72.72

The analyses use all 29 traits of this study (Table 1). The pMANOVA F-statistic is the "approximated F statistic" reported by the *anova.phylo* function in the *geiger* R package (Pennell et al. 2014). The percentage of correctly classified species by the LDA is based on leave-one-out cross-validation, with results reported for all taxa, tree-dwellers-only ("tree") and ground-dwellers-only ("ground").

convex hulls of the ecomorphotypes in Figure 2B, which show that larger species occupy a greater area of morphospace. Further, when PC1 scores were regressed against body mass, the tree-dweller versus ground-dweller slopes remain close to parallel, but the range of PC1 scores for both groups is greater at larger body sizes (Figure 2C).

To test whether the pMANOVAs, LDAs, and disparity calculations were influenced by our choice of sampled taxa, we performed sensitivity analyses in which we varied our sampling strategy (Supplementary Tables S2–S4). For instance, in one sample, we removed locomotor specialists (i.e., gliding, semiaquatic, fossorial, and saltatorial species), leaving a sample of 95 species. In some of these supplemental analyses, the magnitudes of disparity difference between small- and medium-sized mammals were less substantial (Supplementary Table S3) than those in our primary results (Table 1, Figure 3A), and the general pattern of greater disparity among medium-sized taxa does not always hold (Supplementary Table S3). However, when analyzing only the 10 most functionally relevant traits (Figure 2A) medium-sized-mammal disparity is greater than small-sized-mammal disparity in all analyses



**Figure 3.** (A) Morphological disparity of small- and medium-sized mammals, calculated as the sum of trait variances. Vertical lines are 95% confidence intervals generated by bootstrap, using 1,000 replicates. (B) Relative goodness-of-fit (Akaike weights) of evolutionary models fit to PC1 scores. Uniform models (maroon) do not differentiate between "tree-dwellers" and "ground-dwellers", whereas two-regime models (gray) allow certain parameters to vary between these two groups. Values are means of the analyses for 50 phylogenetic trees, and standard errors (whiskers) are calculated from these results. (C) Trait optima, phylogenetic half-lives ( $\ln(2)/\lambda$ ), and stationary variance ( $\sigma^2/2\lambda$ ), calculated using parameter results of the OUM model (Table 3), which is the best-fitting model for each of the two samples examined. The trait optima arrows correspond to the arrows in Figure 2B. Silhouette sources are provided in Figure 1 caption.



(Supplementary Table S3). Further, the slopes of regressions remain statistically indistinguishable between tree-dwellers and ground-dwellers for most of the 29 traits when using additional sampling schemes (Supplementary Table S2). See the Supplementary Results for additional discussion.

In our evolutionary model-fitting analyses, two-regime models—particularly multiple-peak OU models—vastly outperform uniform models (BM1, OU1, and EB) regardless of the body-size category examined (Figure 3B; Table 3; Supplementary Table S5). Model support for two-regime models is equally strong for small-sized and medium-sized mammals. Further, stationary variance of PC1 scores is considerably greater in medium-sized mammals than in small-sized mammals (Figure 3C) via the OUM model, which is the best-fitting model for both size categories (Table 3; Figure 3B).

Parameter results from the model-fitting analyses also informed the differences between small- and medium-sized mammals. Tree-dwelling versus ground-dwelling trait optima for PC1 are substantially closer together in small mammals compared with medium-sized species (Table 3; Figure 3C; see Supplementary Results for discussion of PC2 results). Further, whereas the trait optimum (or adaptive peak) for small-sized mammals lies close to the observed ecomorphological trait mean in the PCA, the trait optimum for medium-sized mammals is far from the observed ecomorphological trait mean in the PCA (Figure 2B). Small-sized species also have greater  $\alpha$  values than medium-sized species ( $\alpha = 0.025$  and  $0.011$ , respectively, for PC1 OUM models; Table 3);  $\alpha$  represents the strength of attraction toward a trait optimum or adaptive peak. The greater  $\alpha$  value is reflected by the phylogenetic half-lives ( $\ln(2)/\alpha$ ; Figure 3C),

which are much shorter for small-sized mammals (ca. 30 Ma) than medium-sized mammals (ca. 60 Ma). In contrast, evolutionary rates ( $\sigma^2$ ) are similar for the two size groups.

## Discussion

### Tree-dweller and ground-dweller ecomorphotypes are distinct at all body sizes

The results of our bivariate and multivariate analyses (Tables 1 and 2; Figures 2 and 3; Supplementary Tables S2–S4) generally contradict the DH. DH predicts that small tree-dwelling and small ground-dwelling species are morphologically very similar, or even undifferentiable, and that ecomorphological traits in those two groups diverge with increasing body size (Figure 1; Jenkins 1974; Jenkins and Parrington 1976). In contrast to this prediction, the allometric slopes of ecomorphological traits are similar between tree-dwellers and ground-dwellers (Figure 2A and C; Table 1). Although these results are more consistent with predictions of EH and the Null Hypothesis (Figure 1), the PGLS regressions and pANCOVAs do suggest there is some slight divergence between the ecomorphologies of tree-dwellers and ground-dwellers at larger body sizes (Figure 2A; Table 1). Nonetheless, in visually evaluating the bivariate plots (Figure 2A), it is apparent that the amount of divergence is subtle (see regression slopes reported in Table 1) and the allometric scaling trends among tree-dwellers and ground-dwellers are not substantially different.

**Table 3.** Fits of evolutionary models to morphological data of tree-dwellers and ground-dwellers, assessed via small-sample AICc values

	Sample	Model	$\sigma^2$ (1)	$\sigma^2$ (2)	$\alpha$	$\theta$ (1)	$\theta$ (2)	SE (1)	SE (2)	LogLik	$\Delta$ AICc
PC1	“Small” mammals	BM1	0.0005	—	—	0.066	—	0.158	—	34.727	13.839
		OU1	0.0008	—	0.013	0.058	—	0.083	—	37.343	10.806
		EB	0.0005	—	0.000	0.066	—	—	—	34.726	16.039
		BMS	0.0003	0.0007	—	0.086	—	0.000	0.162	35.889	13.713
		OUM	<b>0.0010</b>	—	<b>0.025</b>	<b>0.218</b>	<b>−0.046</b>	<b>0.050</b>	<b>0.037</b>	<b>43.831</b>	<b>0.103</b>
		OUMV	0.0005	0.0011	0.020	0.239	−0.058	0.052	0.049	44.961	0.194
	“Medium” mammals	BM1	0.0011	—	—	−0.252	—	0.238	—	12.141	21.869
		OU1	0.0012	—	0.002	−0.238	—	0.211	—	12.292	23.772
		EB	0.0011	—	0.000	−0.252	—	—	—	12.141	24.072
		BMS	0.0011	0.0012	—	−0.179	—	0.000	0.247	12.624	23.108
		OUM	<b>0.0012</b>	—	<b>0.011</b>	<b>0.590</b>	<b>−0.397</b>	<b>0.146</b>	<b>0.082</b>	<b>25.317</b>	<b>0.000</b>
		OUMV	0.0009	0.0014	0.011	0.621	−0.410	0.144	0.090	25.796	1.397
PC2	“Small” mammals	BM1	0.0006	—	—	−0.044	—	0.167	—	31.187	9.738
		OU1	0.0007	—	0.005	−0.049	—	0.124	—	31.568	11.175
		EB	0.0006	—	0.000	−0.044	—	—	—	31.187	11.938
		BMS	0.0003	0.0008	—	−0.016	—	0.000	0.170	35.061	4.190
		OUM	0.0008	—	0.007	0.260	−0.145	0.204	0.106	32.950	10.686
		OUMV	<b>0.0003</b>	<b>0.0016</b>	<b>0.017</b>	<b>0.082</b>	<b>−0.131</b>	<b>0.056</b>	<b>0.069</b>	<b>39.468</b>	<b>0.000</b>
	“Medium” mammals	BM1	0.0006	—	—	0.153	—	0.182	—	29.522	11.166
		OU1	0.0010	—	0.012	0.088	—	0.135	—	32.400	7.613
		EB	0.0006	—	0.000	0.153	—	—	—	29.522	13.370
		BMS	0.0003	0.0010	—	0.156	—	0.000	0.222	31.033	10.348
		OUM	0.0010	—	0.013	0.002	0.111	0.117	0.069	32.732	9.228
		OUMV	<b>0.0006</b>	<b>0.0037</b>	<b>0.039</b>	<b>0.025</b>	<b>0.075</b>	<b>0.026</b>	<b>0.050</b>	<b>38.524</b>	<b>0.000</b>

Models were fit to the scores of the first and second PCs (PC1 and PC2, respectively) of a PCA of 29 skeletal traits (Table 1). Analyses were repeated for 50 phylogenetic trees, and results are means of these analyses. Reported model parameters include the trait optimum ( $\theta$ ), evolutionary rate ( $\sigma^2$ ), and the strength of attraction to the trait optima ( $\alpha$ ), which is also the EB rate decay parameter. For simplicity, the phylogenetic means of BM models are reported in the trait optimum ( $\theta$ ) column. See Figure 3B for Akaike weights (i.e., relative goodness-of-fit) of the PC1 models. For two-regime models that permit parameters to vary between tree-dwellers and ground-dwellers (i.e., BMS, OUM, and OUMV), the numbers after parameters represent the results for tree-dwellers (1) and ground-dwellers (2). Results are provided in the tree-dweller (1) columns for models in which species were not classified into different locomotor modes (i.e., BM1, OU1, and EB). The best-fitting models are in bold, LogLik, log-likelihood; SE, standard error.

Our multivariate analyses also demonstrate that the postcranial morphologies of tree-dwellers and ground-dwellers are distinct at all body sizes. In the PCAs for small- and medium-sized mammals, tree-dwellers and ground-dwellers are differentiated in morphospace (Figure 2B). Further, LDAs reveal that small-sized-mammal datasets outperformed medium-sized-mammal datasets in differentiating tree-dwellers from ground-dwellers, and pMANOVAs show that for both small- and medium-sized mammals the ecomorphological traits of tree- and ground-dwellers are significantly different (Tables 2 and S4). Taken together, these analyses provide strong evidence that small ground-dwellers can be distinguished from small tree-dwellers on the basis of linear measurements taken on the appendicular skeleton; a result that conflicts with the predictions of DH (Figure 1) and conclusions of Jenkins (1974). Thus, despite small mammals encountering spatially complex and uneven substrates both on the ground and in the trees, ecomorphological specializations for specific substrates are reflected in appendicular skeletal morphology, regardless of body size.

An important caveat to our rebuttal of DH, however, is that Jenkins (1974) was specifically referring to mammals in forested habitats in his discussion of “arborealists” versus “terrestrialists.” Many of the small specimens used in our analyses were collected from more open environments in temperate regions of the United States (i.e., not heavily forested); for example, many of the voles and mice. Small ground-dwellers living in open habitats likely have to contend with fewer spatial obstacles than small ground-dwellers living in, for example, closed-canopy forests. Thus, the differentiation we see at small body sizes among tree-dwellers and ground-dwellers may, in part, reflect postcranial adaptations to closed versus open habitats. Nonetheless, our supplemental LDA on small tree-dwellers and ground-dwellers from well-forested environments ( $n = 18$  species; Supplementary Table S1) correctly classified 16 species (89%) via leave-one-out cross-validation. This result supports our refutation of DH and suggests that even forest-dwelling mammals have postcranial skeletal morphologies that are strongly influenced by substrate preference. Further, this result is consistent with functional morphological analyses on small-bodied mammals from closed-canopy forests that have shown that tree-dwellers and ground-dwellers exhibit distinct postcranial morphologies (e.g., Sargis 2002a, 2002b). Therefore, we predict that these patterns will hold even in more spatially complex environments, but this topic requires further investigation.

### Ecomorphological disparity increases with body size

The results of our multivariate analyses conflict with the Null Hypothesis, which predicts that morphological disparity among species does not increase with body size (Figure 1). Instead, the postcranial morphological disparity of medium-sized mammals is greater than that of small mammals (Figures 2B, 3A, and 3C). This pattern is also revealed when PC1 scores are regressed against body mass (Figure 2C); as body mass increases, the spread of ecomorphological trait values relative to the regression lines is greater for both tree-dwellers and ground-dwellers. Although both DH and EH predict an increase in morphological disparity with increased size, we see that the increase in disparity among medium-sized mammals is driven by an increase in within-group morphological disparity rather than an increase in between-group morphological disparity (Figures 2B and 3A). In other words, the increase in disparity is not the result of tree-dwelling and ground-dwelling ecomorphotypes diverging at larger body sizes (as predicted by DH), but rather by medium-sized mammals expanding within their respective

ecomorphospaces. As such, the results of our disparity analyses are most consistent with EH (Figure 1).

Sampling factors likely have a large influence on the morphological disparity results. For instance, the disparity differences between small- and medium-sized species are reversed for ground-dwellers when subterranean fossorialists are included in the “small” sample (Supplementary Table S3; but note that there are no medium-sized subterranean fossorialists), and the results for tree-dwellers might be further altered if bats (which are generally small) were included in our sample. However, in additional supplemental disparity analyses, including analyses of only the 10 most functionally relevant traits (Table 1; Figure 2A), medium-sized species are consistently more disparate than small species (Supplementary Table S3). Further, stationary variance of PC1 scores is calculated from the best-fitting OUM models, and it shows considerably greater variance in medium-sized mammals than in small-sized mammals (Figure 3C). This pattern in stationary variance also holds for the four traits that are most strongly linked to substrate preference (Supplementary Table S5). Thus, we propose that, among non-volant mammals, medium-sized taxa are ecomorphologically diverse relative to small-sized taxa, and this pattern is amplified when examining functionally informative traits.

The observed increase in interspecific disparity with body size is a relatively novel result. Countless studies have demonstrated that body size plays an important role in structuring vertebrate phenotypic diversity (e.g., Collar et al. 2011; Dosik and Stayton 2016; Reynolds et al. 2016; Zelditch et al. 2017; Law et al. 2019), but few (if any) have shown that phenotypic diversity is greater among larger taxa. In fact, some studies support the opposite pattern, that phenotypic diversity is greater among smaller species (e.g., Reynolds et al. 2016).

In sum, the results from our ecomorphological analyses are most consistent with EH. They demonstrate that the postcrania of tree-dwelling and ground-dwelling mammals are distinct at any body size. Thus, substrate preference drives morphological differentiation in both small- and medium-sized mammals. Nonetheless, the morphological disparity of mammal postcrania increases with larger size, suggesting that an evolutionary increase in body size may serve as a catalyst for greater phenotypic diversification.

### Allometric scaling of limbs

That allometric regression slopes of most ecomorphological traits are statistically similar is consistent with previous studies that demonstrated the limbs of smaller-bodied mammals tend to scale close to geometric similarity (Alexander et al. 1979; Biewener 1983; Bertram and Biewener 1990). However, that there is some (albeit weak) statistical support for the ecomorphological traits of tree-dwellers versus ground-dwellers diverging at larger sizes lends some support to the hypothesis that locomotor specializations have a strong influence on postcranial scaling patterns in small mammals (Bou et al. 1987; Bertram and Biewener 1990; Christiansen 1999). These mixed results suggest that, when combined into broad tree-dwelling and ground-dwelling locomotor bins, ecomorphological traits scale close to geometric similarity, but specialized locomotor guilds (e.g., gliders, fossorialists) may have different allometric scaling relationships that manifest as weak support for divergence among tree-dweller and ground-dweller slopes.

Although tree-dwellers and ground-dwellers exhibit similar scale effects, they often differ in their absolute trait values (i.e., intercepts differ for tree-dweller versus ground-dweller regressions, most apparent in the log-shape ratio regressions, Figure 2A). A similar

pattern has also been found in the limbs of scansorial versus cursorial mammals (Kilbourne and Hoffman 2013, 2015). Tree-dwellers tend to have longer and more gracile appendicular skeletons, whereas those of ground-dwellers are stouter and more robust. For example, tree-dwellers have consistently longer ulnae relative to ground-dwellers, whereas ground-dwellers have consistently longer olecranon processes relative to tree-dwellers (Figure 2A). These results are in line with well-established relationships between postcranial morphology and locomotion (e.g., Hildebrand 1985a, 1985b; Cartmill 1985).

### Body size influences tree-dweller and ground-dweller adaptive zones

In congruence with our ecomorphological analyses (Figures 2 and 3A), our evolutionary model-fitting analyses generally support EH. That multiple-peak OU models (OUM and OUMV) outperformed uniform models regardless of the size category examined (Figure 3B; Table 3) is consistent with our finding that tree-dweller and ground-dweller ecomorphologies are distinct at all body sizes (Figure 2). Further, support for multiple-regime models was equally strong for small- and medium-sized mammals (Figure 3B), indicating that there is significant trait partitioning among ecomorphotypes at all body sizes, which conflicts with DH. This suggests that tree-dwellers and ground-dwellers occupy unique adaptive zones (Simpson 1944) or adaptive peaks on a fitness landscape (Wright 1932), even at small body sizes. Further, the Null Hypothesis is refuted because stationary variance of PC1 scores is considerably greater in medium-sized mammals than in small-sized mammals (Figure 3C) via the OUM model, which is the best-fitting model for both size categories (Table 3; Figure 3B). This result is broadly congruent with the morphological disparity results (Figure 3A; Supplementary Table S3), providing strong evidence of increased phenotypic diversity at larger body sizes, which is consistent with EH.

Nevertheless, the position of the tree- and ground-dwelling PC1 trait optima (or adaptive peaks) for small- versus medium-sized mammals more closely match the predictions of DH, not EH (Figure 1). That the medium-sized mammal trait optima lie at more positive (for tree-dwellers) and negative (for ground-dwellers) ends of the PC1 spectrum relative to those of small mammals (Figure 2B) implies greater morphological divergence between ecomorphotypes at larger body sizes. Thus, this result appears to be in conflict with our ecomorphological analyses (Figures 2 and 3A).

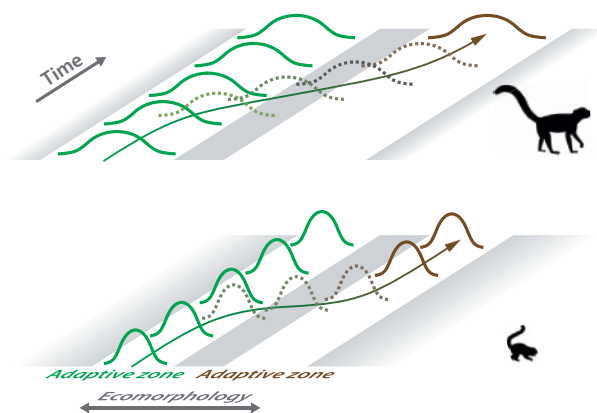
This paradox between trait optima (supporting DH) and ecomorphological results (supporting EH) may be explained by additional parameter results from the model-fitting analyses. Most notably, small-sized species have greater  $\alpha$  values relative to medium-sized species, yet the evolutionary rates ( $\sigma^2$ ) are approximately equal for the two size groups (Table 3). Further, given the greater  $\alpha$  values for small-sized mammals, their phylogenetic half-lives ( $\ln(2)/\alpha$ ; Figure 3C) are much shorter (ca. 30 Ma) relative to medium-sized mammals (ca. 60 Ma). This indicates that small mammals evolve more rapidly toward trait optima, possibly due to stronger selection pressures. This suggests that, among our extant sample, many small-sized mammals have evolved to their adaptive zone, whereas many medium-sized mammals are farther from their adaptive zone. For medium-sized mammals, this may be due to weaker selection (reflected by lower  $\alpha$  values) and the greater separation between optima (Figure 3C) that requires greater evolutionary change (Butler and King 2004). The greater  $\alpha$  value in small-sized mammals is also reflected in their reduced stationary variance relative to medium-sized mammals (Figure 3C), as  $\alpha$  is a component of this

metric. This suggests that, at equilibrium, the adaptive zones of ground-dwellers and tree-dwellers are wider for medium-sized species (Butler and King 2004, Gearty et al. 2018). We conceptualize these macroevolutionary differences between mammals of different sizes in Figure 4, highlighting the wider and more separated adaptive zones in medium-sized mammals.

Taken together, these evolutionary model-fitting results suggest that DH would be supported if medium-sized mammals ceased transitions between adaptive zones, if those adaptive zones remained fixed, and if evolution within their respective adaptive zones continued unperturbed (i.e., the system was permitted to reach equilibrium); such a scenario is ecologically and evolutionarily unrealistic. Any sample of extant taxa represents a snapshot in evolutionary time and, in our case, that snapshot captures a sample of small-to-medium-sized mammals at various points along the ecomorphological continuum between tree-dwelling and ground-dwelling. Those medium-sized taxa that are products of an evolutionary lineage long-committed to a particular substrate may be quite morphologically divergent from smaller taxa in the same locomotor environment, whereas others may be newcomers to their current substrate and therefore overlap considerably with the taxa in the other locomotor mode. Further, adaptive zones themselves can change through time (Simpson 1944), driving ecomorphological shifts in one direction or another. Thus, the EH pattern we observe in our ecomorphological analyses may be the real-world manifestation of an underlying, theoretical DH pattern.

### Drivers of functional diversification in mammalian postcrania

The pattern revealed by our analyses, which is most consistent with EH, consists of two parts: 1) postcranial morphologies among tree-dwellers and ground-dwellers are distinct regardless of body size (Figure 2; Table 2), and 2) within-group morphological disparity increases as a function of body size (Figure 3A and C). That the postcranial morphologies of tree-dwellers versus ground-dwellers are distinct, even at small body sizes, has been argued by numerous



**Figure 4.** Conceptualization of the differences in macroevolutionary patterns between medium-sized mammals (top) and small mammals (bottom), based on the evolutionary model-fitting results (Figure 3; Table 3) and inspired by illustrations in Simpson (1944). Smaller mammals have “narrower” adaptive zones that are closer together (Figure 3C), and they show less within-group morphological disparity (Figures 2B and 3A) and stationary variance (Figure 3C). They may evolve more rapidly into new adaptive zones due to both greater selection pressures (Table 3) and adaptive zones being closer together. The choice of arboreality as the ancestral state is arbitrary. Silhouette sources are provided in Figure 1 caption.

authors (e.g., Szalay 1984; Szalay and Sargis 2001; Sargis 2002a, 2002b; Flores and Mónica Díaz 2009; Chen and Wilson 2015; Nations et al. 2019; Woodman and Wilken 2019), yet the idea persists that small body size obscures the recognition of locomotor adaptations in mammals (e.g., Hedrick et al. 2020). Although some of our bivariate and model-fitting analyses lend tentative support to DH, the majority of our results are consistent with predictions of EH and the Null Hypothesis that changes in body size do not substantially alter the degree of trait partitioning among tree-dwellers and ground-dwellers (Figure 1).

Nevertheless, the logic behind Jenkins' hypothesis is sound; small mammals (especially those in forested environments) exhibit considerable locomotor plasticity, often incorporating a mix of climbing, walking, running, and digging behaviors (Nice et al. 1956; Hauser 1964; August 1984; Nitikman and Mares 1987; da Fonseca and Kierulff 1989; Granatosky 2018). Further, the vertical dimensionality of landscapes is more pronounced at small body sizes, and many small mammals make use of that increased habitat complexity (August 1983; August and Fleming 1984; Stallings 1989; Malcolm 1995). That we observe substantial ecomorphological trait partitioning among small-bodied mammals (<0.5 kg) is therefore at odds with these behavioral data, which imply that small mammals should exhibit more generalized postcranial morphologies.

One possible explanation for why small tree-dwelling and ground-dwelling mammals exhibit considerable behavioral overlap but remain morphologically distinct is that their postcranial skeletons are adapted to avoid the most dangerous aspects of their locomotor environments, rather than to perfect a generalized locomotor repertoire. In other words, their skeletons are not specialized for the locomotor behaviors they engage in most frequently but rather for those rarer behaviors that prevent severe fitness consequences. In arboreal environments, this could be falling, resulting in specializations for maintaining stability on tall, discontinuous substrates that vary in size and angulation (Cartmill 1985). In terrestrial environments, this could be strong predation pressures (Bourlière 1975; Eisenberg 1990; Merritt 2010; Shattuck and Williams 2010), resulting in behavioral and morphological modifications for hiding (e.g., under leaf litter, in a burrow; Bourlière 1975; Hildebrand 1985a, 1985b; Merritt 2010) or fleeing and evasion (e.g., jerboas; Moore et al. 2017). This is somewhat analogous to "Liem's paradox," wherein animals that are typically dietary generalists exhibit specialized feeding apparatuses to exploit fallback foods during periods of environmental stress (Robinson and Wilson 1998; Ungar 2010). Although this topic requires further study, that we find distinct postcranial morphologies among small-bodied tree-dwellers and ground-dwellers nevertheless suggests there are unique adaptive morphological pathways that give rise to these different locomotor strategies.

Compared with medium-sized mammals, small mammals transition relatively quickly from one adaptive zone to the other (Figure 3C), but the adaptive zones themselves are fairly narrow and close together in morphospace (Figures 3C and 4). This supports the evolutionary scenario that small mammals experience strong selective pressures (e.g., related to falling or predation) to evolve ecomorphological adaptations for either ground-dwelling or tree-dwelling and that "intermediate," generalist ecomorphologies are evolutionarily labile. This is evidenced by the greater  $\alpha$  values for small-sized mammals versus medium-sized mammals (Table 3). A second possibility could be related to life histories of small mammals. Small mammals have high rates of fecundity and have relatively short life-spans (on average small mammals live less than a year in the wild;

Merritt 2010). As such, small mammal populations can adapt rapidly when there are sudden changes to their local environments (Bourlière 1975). Thus, selective forces may manifest as phenotypic changes more rapidly given the accelerated pace of small mammalian life histories. Our evolutionary model-fitting analyses do not support the latter hypothesis, however, because the evolutionary rate ( $\sigma^2$ ) of small-sized mammals is less than that of medium-sized mammals via the multipeak OU models, for both PC1 and PC2 (Table 3). Thus, these results suggest that the propensity of small-sized mammals to evolve to new adaptive zones more quickly than medium-sized mammals is likely driven by extrinsic, selective pressures, rather than intrinsic, elevated evolutionary rates.

The second prediction of the EH pattern is that within-group morphological disparity increases as a function of body size (Figure 1). In examining the results of our PCA for medium-sized mammals (Figure 2B), we see that this increased disparity is driven by locomotor specialists; for example, fossorial species cluster at the far negative end of PC1 whereas gliding species cluster at the far positive end of PC1 (Supplementary Figure S3). That greater morphological divergence among specialists is driving the greater disparity among medium-sized taxa is supported by the supplementary disparity results; when all specialists are removed from analyses, disparity is approximately equal for small- and medium-sized groups (see results for "non-specialists" and "arboreal vs. terrestrial" sampling schemes in Supplementary Table S3). The implication of these results is that locomotor specialization requires greater modification of postcranial morphology at larger body sizes. This pattern fits what is known about body size and locomotor adaptations in mammals.

The energetic costs of locomotion scale with body size (Garland 1983; McNab 1990; Biewener 2005); thus, larger-bodied mammals likely experience stronger selective pressures to minimize these energetic costs. Indeed, the mechanical advantage of the major appendicular muscle groups increases significantly with body size, and the mass-specific force exerted by the muscles of a large mammal are substantially lower than a small mammal (Biewener 1989, 1990). Further, as body mass increases, the absolute force experienced by the postcranial skeleton increases significantly (Biewener, 1982), such that larger mammals must modify their long bone architecture (Biewener 1983; Bertram and Biewener 1990; Kilbourne and Hoffman 2013, 2015) and posture (Biewener 1989) to maintain similar levels of peak stress on the skeleton and avoid bone fracture or deformation. As such, larger mammals face greater biomechanical challenges when adopting a new locomotor strategy when compared with small mammals (Biewener 2005, 2015), a concept that holds for climbing (Cartmill 1985), gliding (Runestad and Ruff 1995; Grossnickle et al. 2020), digging (Hildebrand 1985a; Eisenberg 1990), running (Hildebrand 1985b; Biewener 1989), and hopping (Dawson and Taylor 1973), among others. Thus, the magnitude of postcranial modifications necessary to exploit novel locomotor niches is greater for larger-bodied mammals, which in turn drives increased disparity among locomotor specialists within broader tree-dwelling and ground-dwelling guilds.

These observations are borne out by our analyses. Medium-sized tree-dwellers and ground-dwellers exhibit greater postcranial morphological disparity and stationary variance within their respective adaptive zones (Figure 3A and C; Tables 3; Supplementary Tables S3, S5, and S7). This suggests that adaptive landscapes may be more complex for larger mammals than smaller mammals. Whereas smaller mammals may experience stronger attraction towards a single tree-dwelling or ground-dwelling adaptive peak, the adaptive



landscape for larger mammals may consist of many local peaks for locomotor specialists. Taken together, these results indicate that body size plays a major role in modulating the tempo and mode of locomotor ecomorphological evolution in mammals.

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## Authors' Contributions

L.N.W. and D.M.G. contributed equally to designing the study, collecting data, and writing the manuscript.

## Conflict of Interest

The authors declare that they have no competing interests.

## Supplementary Material

[Supplementary material](https://academic.oup.com/cz) can be found at <https://academic.oup.com/cz>.

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